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Final Report

Effects of Fertility Gradients on *Typha sp* Net Primary Productivity in newly formed Wetlands

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Abstract

The Wax Lake Delta, located in coastal Louisiana, is an area where wetlands are forming as result of the construction of the Wax Lake Outlet in 1943. This Outlet extends south from Six Mile Lake, across the Teche Ridge, into Atchafalaya Bay and has catalyzed the growth of delta lobes, i.e., areas of sandy sediment that have risen above the sea level. A native plant inhabiting the lobe's back levees in the Wax Lake Delta is *Typha sp,* which is widely distributed across the Southern United States, especially in freshwater regions along the Louisiana coastline. The main objective of this project was to evaluate the net primary productivity of the dominant wetland species *Typha sp* and how fertility gradients (concentrations of both nitrogen and phosphorus in soil) determine their spatial distribution and contribution to soil formation. Three sites were selected based on different stages in delta formation based on distance from the mouth of the Wax Delta Outlet and thus representing different ages (old, intermediate, young) as indicated by sedimentation rates. I hypothesize that depending on the limiting nutrient in this environment; net primary production will be significantly different between sites. If the soil total N concentration is high, then (1) the above and below net primary production (ANPP and BNPP) of *Typha sp* will be greater than in sites where soil N concentration is low. However, under the same conditions with respect to N concentration, and if soil total P is a limiting factor, then (2) net primary production would be lower in older delta lobes than in younger lobes, where soil total P concentration is expected to be higher as result of greater P availability. The sediment at the old site showed the highest organic matter content (8%) and lowest bulk density (0.87 mg cm^3), while the young site experiences more sedimentation (OM= 3.07%) as indicated by more mineral content in the soils (bulk density= 1.21 mg cm^3). The highest ANNP was in the old site (5.2 gdw m^{-2} day^{-1}) followed by the intermediate and young sites (3.5 gdw m^{-2} day^{-1}); these values were associated with the highest TN in soil (1.26 mg cm^{-3}) (integrated by depth). Depth integrated TP also show differences, with the highest concentration in the old site (0.51 mg cm-3). Root biomass (600-800 gdw m^{-2}) and belowground productivity (2.5 gdw m^{-2} day^{-1}) at the young site were the highest, indicating that more energy is allocated

belowground for the acquisition of nutrients from the soil than at the other sites. My results show that *Typha sp* retranslocate nitrogen and phosphorus to conserve nutrient loss and maximize growth rates in each annual production cycle in the Wax Lake delta. The significant differences in belowground productivity among lobe sites of different age also indicates that *Typha sp* could promote the rapid formation of soil, by developing roots and rhizomes on seasonal basis, especially in newly formed land (young site), and thus significantly influencing changes in soil elevation as newly mineral sediment is deposited by river discharge and sediment resuspension.

I. Introduction

One of the most pressing issues in environmental science today concerns the continued land loss in coastal Louisiana, and the deterioration of fragile wetland environments from the impacts of anthropogenic activities. Although these wetland ecosystems are adapted to a constant shifting of environmental factors controlling wetland dispersion and productivity, a combined influence of human engineering and natural disturbances could negatively affect wetland development and survival. The Atchafalaya River, a tributary of the Mississippi River, is actively forming deltaic wetlands from sediment discharge, buffering the constant loss of wetlands. Wax Lake Delta, the site of this project, is an area where wetlands are also forming as result of construction of the Wax Lake Outlet in 1943 (Brix 2010) . This Outlet extends south from Six Mile Lake, across the Teche Ridge, into Atchafalaya Bay and has catalyzed the growth of delta lobes, areas of sandy sediment that have risen above the sea level.

Most of these deltaic lobes are being formed and expanded with the continued deposition of sediment from Wax Lake Outlet. The oldest islands are located closest to the outlet discharge point, while the younger islands are near to the Gulf of Mexico. Dissolved inorganic nutrients and sediment in the water are widely distributed through the delta system by distributary channels. Inorganic nutrients transported by tides and flooding are uptake by plants and soil microbial communities (e.g. denitrification). This nutrient and sediment transport results in greater accumulations of nitrogen (N) in older landforms, and greater accumulations of phosphorus (P) in younger islands (Henry 2012).

A native plant inhabiting the lobe's back levees in the Wax Lake Delta is *Typha sp,* which is more commonly known as the Southern Cattail, and widely distributed across the Southern United States, especially in freshwater regions of the Louisiana coastline. *Typha sp* is an opportunistic species, colonizing all available land within its preferred range of tolerance to flooding regime (elevation), salinity, nutrient availability, and other factors (Brix 2010). As a macrophyte that produces both sexually and asexually, *Typha* is a persistent, rapidly developing grass that colonizes any area of exposed sediment with optimal levels of tolerance to elevation, salinity, and other factors. As result of its rapid growth and dispersion, *Typha sp* is a key dominant plant species in regulating nutrient cycling, particularly in areas with high nitrate concentrations. In addition, *Typha sp* provides a habitat for many animals (e.g. mammals, birds) that use wetlands at different times of the year.

The main objective of this project was to evaluate the net primary productivity of the dominant wetland species *Typha sp* and how fertility gradients (concentrations of both nitrogen and phosphorus in soil and sediments) determine their spatial distribution and contribution to soil formation. *Typha sp* rapidly colonized recently emerged land in the Wax Lake Delta (Atchafalaya deltaic region) and apparently has a major role in the contribution of significant amounts of organic matter, which affect land stabilization and soil formation. Due the vegetative reproduction of *Typha sp*, this wetland plant has a rapid expansion in areas where high inorganic nutrient concentrations are available both in the soil and the water column. As a "pioneer" species in the succession trajectory, as new landforms, *Typha sp* is an excellent indicator of wetland development and expansion in the context of coastal restoration programs, and can be used as indicator of habitat development.

Since total nitrogen (N) concentrations in older landforms in Wax Lake Delta are higher than the concentrations of the same element in younger landforms, while the trend for phosphorus (P) is apparently reversed (Henry 2011), I hypothesize that depending on the limiting nutrient in this environment, net primary production will be significantly different between sites. If the soil total N concentration is high, then (1) the net primary production of *Typha sp* will be greater than in sites where soil N concentration is low. However, under the same conditions with respect to N concentration, and if soil total P is a limiting factor, then (2) net primary production would be lower in older delta lobes than in younger lobes, where soil total P concentration is expected to be higher as result of greater P availability.

II. Materials and Methods

Site description. Three sites were selected that represented different stages in delta formation (Figure 1). The criteria for the selection was based on distance from the mouth of the Wax Delta Outlet and representing different ages indicated by sedimentation rates.

Vegetation . *Aboveground.* At each of these sites, duplicate measurements of aboveground biomass, as well as nutrient content, were determined on a per area basis. Aboveground plant biomass was measured using duplicate clip-plots (0.5 m^2) at each site and in two occasions. The first sampling occurred in July 2012 (harvest 1) and the second in September at the end of the growing season (harvest 2). This plant material was stored in paper bags and transported to the laboratory. Plant matter was separated into alive and dead components, dried at 60°C, and weighed (Castaneda-Moya et al. 2011). A split-plot repeated analyses of variance was be used to estimate differences in aboveground productivity across sites while soil variables were analyzed using a two way ANOVA (Zar 1984).

Belowground. Using a PVC suction-coring device (10 cm diameter x 20 cm length; Meriwether et al. 1996), six cores were collected at each site to determine belowground biomass. To estimate root productivity, the area exposed by the coring device was filled with an ingrowth bag of same dimension containing sphagnum peat moss. The subsequent root growth within the ingrowth bag was used to estimate root production. Ingrowth bags were removed five months after deployment over the course of the study period. Samples were stored in plastic bags at a constant temperature and transported back to the laboratory. Root samples were rinsed with water through a 1mm synthetic mesh screen to remove soil particles and then the roots will be sorted by hand into categories of live and dead roots. Finally, samples were dried in paper bags at 60°C and weighed (Castaneda-Moya et al. 2011);(Saldana and Castaneda-Moya). A split-plot repeated analyses of variance was also used to estimate differences in belowground productivity across sites.

Nutrients. Total nitrogen and carbon concentration in plant root, leaves, stem material, and sediment was quantified on two analytical replicates of each sample with an ECS 4010 elemental analyzer (Costech Analytical Technologies, Inc., Valencia, California). Total P will be extracted on duplicate analytical replicates with 1 N HCl after combustion in a furnace at 550°C (Aspila et al. 1976) and determined by colorimetric analysis using a segmented flow analysis Flow Solution IV autoanalyzer (OI Analytical, College Station, Texas).

Sediment. *Cores.* Sediment cores were obtained using a PVC suction-coring device (10 cm diameter, 20 cm length). At each plot, two cores were sampled and transported back to the laboratory, where they were extruded into four depths of 5 cm. The samples were analyzed for bulk density, organic matter content, total phosphorus, carbon, and nitrogen. Soil and plant nutrient data was analyzed using a two-way analysis of variance to determine differences between sites (lobes of different age).

Pore water. At each site, duplicate 60 ml samples of porewater were collected from a depth of 30 cm using rigid aquarium tubing fixed to a 60 ml syringe. Porewater salinity, pH, and temperature were analyzed in the field. The porewater samples were transported back to the laboratory, filtered with a Whatman GF/F glass fiber filter, determined by colorimetric analysis using a segmented flow analysis Flow Solution IV autoanalyzer (OI Analytical, College Station, Texas).

III. Results

III.A. Soil properties and nutrients

III.A . 1. Bulk density..

Average bulk density (Figure 2) was significantly higher in the Young site compared to the Intermediate and Old sites, and ranged from 0.87 ± 0.03 g cm^{-3} (Old) to 1.21 ± 0.14 g cm^{-3} (Young) across all sites (Tables 1 and 2). Bulk density significantly increased with depth ranging from 0.73 ± 0.08 to 1.12 ± 0.11 g cm^{-3}. There was no significant interaction between sites and depths (Table 1).

III.A . 2. Organic matter.

Figure 3 shows the percentage of organic matter found in the cores taken at each site, in four different depths. Both the Young and Old sites follow a trend of decreasing percentages of organic matter with increasing depth. The Intermediate site follows the same trend after the first 5 cm of soil. Organic matter had an opposite trend compared to that of bulk density, with the highest percentage at the Intermediate (6.76 ± 1.01 %) and Old (8.04 ± 0.28 %) sites and the lowest at the Young site (3.07 ± 0.52 %). Across depths, organic matter was higher in the top 0-5 cm soil interval and consistently decreased with depth (Tables 1 and 2). There was no significant site and depth interaction (Table 1).

III.A . 3. Soil total carbon and nutrients

The highest carbon concentration was observed in intermediate and young sites (>12 mg cm-^{3}) while the older site showed the lowest concentrations ranging from 6-8 mg cm^{-3} (Figure 4a). Soil total C density did vary significantly among sites, with the highest C density at the Intermediate (13.20 ± 0.41 mg cm^{-3}) and Old (14.13 ± 0.74 mg cm^{-3}) sites.

Carbon density did not change with soil depth and there was no significant interaction between sites and depths (Tables 1 and 2).

There was a distinct difference in TN concentration with the low lowest values in the young site (specially at 5-15 cm depth) and similar mean values with depth (>1 mg cm-^{3}) in the old and intermediate site (Figure 4b). Soil total N density differed significantly among sites, with higher values at the Intermediate (1.13 ± 0.04 mg cm^{-3}) and Old (1.26 ± 0.06 mg cm^{-3}) sites and lower values at the Young site (0.29 ± 0.18 mg cm^{-3}; Tables 1 and 2). Soil N density did not vary with soil depth. There was a significant site and depth interaction, with the lowest values in the Young site for all sampling depths compared to the other sites (Table 1). Soil P density in the top 20 cm of soils showed a similar trend to that of N density across sites, with higher values in the Old site (0.51 ± 0.01 mg cm^{-3}) relative to the Intermediate and Young sites (0.41 ± 0.04 and 0.44 ± 0.03 mg cm^{-3}, respectively). Across depths, soil P density was higher at intermediate depths (5-10 cm) and lower in the top 0-5 cm soil interval (Tables 1 and 2). Soil atomic C:N ratios did not vary across sites and depths ranging from 13.08 ± 0.38 to 13.91 ± 0.35 (Tables 1 and 2). In contrast to soil C:N ratios, N:P ratios were higher at the intermediate site (6.20 ± 0.55) and lower at the Young site (4.22 ± 0.44). Soil N:P did not change significantly with soil depth (Tables 1 and 2).

III.A .4.Pore water Dissolved Inorganic N and P

Figure 5 shows that the Intermediate site has overall the highest N+N concentrations (1.2 uM), followed by the Old site. The levels of N+N exhibited in the Young site are not statistically different throughout the year of sampling, while the Old site shows wide variability with a trend in reduction at the end of the growing season. Overall N+N concentrations were significantly lower that values reported in the overlying water in other studies (>10 uM) (Branoff 2012) or adjacent channels indicating a rapid reduction or uptake by plants. In contrast to N+N concentrations NH_4 values were higher overall throughout the study period (20-60 uM) (Figure 6). The intermediate site showed the highest value (60uM) in the middle of he summer season. SRP values in pore waters for all sites were low (<0.8 uM), although as in the case of NH4 concentrations, a peak (4 uM) was observed in summer 2012 (Figure 7). The old site also showed a high value at the beginning of spring (2 uM).

III.A . 5. Iron.

Iron mean concentrations were highest in the intermediate site (550 uM) followed by the old site ((90 uM) (Figure 8). In both case the iron concentration declined towards the end of the study period coinciding with the end of summer. The lowest iron concentrations were systematically registered in the young site where the maximum mean value was 80 uM in may 2012.

III. B. Biomass

III. B. 1.Aboveground Biomass (Live and Dead).

Figure 9 shows the variation in live aboveground biomass between plots at each site. All of sites followed the same general trend of seasonal growth with increasing values from at the beginning of the growing season (March 2012) to the first harvest, in July, and then a decrease in biomass by September 2012. Maximum biomass values were 700, 500, and 600 gdw m^{-2} in the old, intermediate and young site, respectively. Dead aboveground biomass (Figure 10) followed the same seasonal pattern as the live biomass, although the Intermediate site had the lowest total amount of dead biomass (~250 gdw m^{-2}), while the Old and Young sites were relatively similar in value throughout the study period (380 gdw m^{-2}).

III. B. 2. Aboveground Biomass Carbon and nutrient content

There was no significant difference in the total carbon concentrations in aboveground biomass (AGB) at each site per harvest (range: 400-420 mg/g). Neither harvest shows significant variability per site, although the second harvest has higher carbon concentrations (Figure 11). In contrast, TN concentrations in the AGB showed a distinct spatial difference with a higher value in the Old site (16 mg g^{-1}) followed by the intermediate (13 mg g^{-1}) and young site (12 mg g^{-1}). Similar TN value in the second harvest (September 2012) for all sites indicates a significant re-translocation of nitrogen into the plant (~50%). The TP value in the AGB also follows a similar retranslocation spatial and temporal pattern as for TN, with the highest value registered in the first harvest in the old site (1.0 mg g^{-1}), and followed by almost half of the initial values in the intermediate and (0.8 mg g^{-1}) and young site (0.7 mg g^{-1}).

III. B. 3. Belowground Biomass (Live and Dead).

Figure 14 shows live belowground biomass (BGB) values for each site. There were not significant differences between the top and bottom layers, however there was a significantly difference across the sites. The highest BGB was registered in the young site (mean range: 600-800 gdw m^{-2}) with significantly lower values in the old (200-300 gdw m-2) and intermediate (80-100 gdw m^{-2}) sites. Dead BGB did not follow the same pattern that the live BGB since the highest values (500-900 gdw m^{-2}) were recorded in the intermediate site (Figure 15). This differential pattern per site and location with depth suggest a dynamic accumulation and storage of recalcitrant material in the soil regardless of site age.

III. B. 4. Belowground Biomass Carbon and nutrient content.

Mean total Carbon in belowground biomass ranged from 160-290 mg g^{-1} across all sites and depths. There was not significant difference between the top and bottom of the sampling cores. The highest TC concentration was observed in the intermediate site (290 mg g^{-1}) and the lowest in the young site (160 mg g^{-1}) (Figure 16). Total N was also highest in the intermediate site (mean: 8 mg g^{-1}), although there was more variation with depth, particularly in the old and intermediate site (Figure 17). The lowest value was recorded in the young site with similar values in the top (3.8 mg g^{-1}) and bottom (4.1 mg g^{-1}) depths. Overall, TP in the belowground biomass was higher in the soil top section (2.9 mg g^{-1}) of the old site in comparison to the intermediate (2 mg g^{-1}) and young (1.5) sites. TP concentration in belowground biomass at the bottom depth was no significantly different among the sites (Figure 18).

III. C. Productivity.

III. C. 1.Aboveground and Belowground Productivity.

There was a clear gradient in above net primary productivity (ANPP) from the old (5.2 gdw m^{-2} day^{-1}) to the young site (3.5 gdw m^{-2} day^{-1}) in the first study period (harvest) (Figure 19). This difference is associated to the end of the growing season represented by the second harvest (July 2012). NPP values registered at the end of the second harvest (September 2012) were significantly lower than the NPP value registered in first harvest (July 2012) and ranged from 1-1.4 gdw m^{-2} day^{-1}. Lower values coincided with decreasing ambient temperatures.

Overall belowground productivity values were lower than aboveground (Figure 20). Belowground productivity was higher in the young site (2.5 gdw m^{-2} day^{-1}) in contrast to the old (0.7 gdw m^{-2} day^{-1}) and intermediate (0.6 gdw m^{-2} day^{-1}) age site (Figure 20); although most of the productivity was allocated in the top section of the soil, particularly in the young and old sites. The intermediate site sow the lowest productivity, particularly in the top soil section (0.2 gdw m^{-2} $day^{-1)}$.

Mean total carbon values in belowground tissue at the top and bottom soils depths across sites ranged from 390 -433 mg g^{-1} and no statistical difference was observed among mean values (Figure 21). In contrast, nitrogen content was higher in the intermediate site (7-8 mg g^{-1}), particularly in the top section (Figure 22). Mean TP values also showed difference among sites with the highest value recorded in the intermediate site (2.2 mg g^{-1}) at the bottom section. There was a significant difference among the old and young sites with the lowest values in the old (1 mg g^{-1}) in comparison to the young site (1.7 mg g^{-1}) (Figure 23).

IV. Discussion

My study focused on assessing how net primary productivity of one of the dominant wetland species, *Typha sp,* changed along fertility gradients in the different delta lobes formed in Wax Lake Delta. In this experimental set up, the delta lobes represented different soil "age" where the Old site, the delta lobe closest to the mouth of the delta, was the oldest soil. Because of the different age, this site would be characterized by the highest nitrogen availability. I found that the highest ANNP was in the old site followed by the intermediate and young sites; these values were associated with the highest TN in soil (1.26 mg cm^{-3}) (integrated by depth) (Figure 4) as expected in my original hypothesis. Depth integrated TP also show differences, with the highest concentration in the old site (0.51 mg cm-3); although the TP concentration in the intermediate (0.41 mg cm^{-3}) and young (0.44 mg cm^{-3}) site were inversed, but not significantly different. This soil TP spatial pattern indicates that TP is higher in the old than in the young delta lobe, contrary to my original hypothesis. I assumed that because of higher deposition of mineral sediment, TP would be higher in the younger site. I suggest this difference in TP concentrations is due to sediment depositional differences and potential site-specific accretion rates.

Due to the characterization of *Typha* sp as a species that is the first to colonize newly formed land, I expected a greater biomass at the oldest site, which was geographically the closest to the mouth of the outlet, and in contrast, a more patchy, loose distribution of *Typha sp* at the Young site, where the land was comparatively newer. The age of the sediment could be determined from bulk density and the percentage of organic matter present. The old site exhibited a trend of less dense soils (Figure 2), which is composed of more organic matter than minerals. As higher mineral composition is indicative of sedimentation, organic material at the Old site suggests that this lobe has been present longer, continually depositing organic matter with the detritus produced by the plan community and potential imports from tides and storm flooding (Figure 3). However, the Young site is composed of mainly minerals, showing a higher bulk density, indicating the lack of organic material accumulation, and high deposition of more mineral-laden sediment.

I expected that aboveground biomass would vary throughout the year, since it is controlled by nutrient content in the soil and ambient temperature. Total biomass was low during the first harvest, which took place in March (Figure 9). As the year progressed, biomass levels peaked in July, and live biomass decreased at the third harvest in September, when dead biomass began to increase (Figure 10). This data follows the production cycle of *Typha*, which begins in the spring, reaches a peak in the summer, and dies off, with the cold temperatures of winter.

Live belowground biomass was greatest in the Young site throughout the year, suggesting that due to recent colonization by *Typha* and lack of nutrients in the mineral-dominated soils, the roots of *Typha* must reach farther into the soils to find adequate nutrients to support growth. The plants are allocating more biomass and energy to the search for nutrients in the sediments than at the other sites, though the difference cannot be seen in the dense, high vegetation visible aboveground. The roots show nutrient levels that are comparatively less than the Old and Intermediate sites, once again signaling the lack of readily available nitrogen and phosphorus in the Young site.

The nutrients contained in the aboveground and belowground biomass fluctuate with each harvest. Both the phosphorus and nitrogen concentrations in the aboveground biomass are much greater during the first harvest than in the second harvest. I suggest that, in this nutrient limited environment, the individual plants, faced with the loss of the nutrients with detrital material and limiting nitrogen sources, retranslocate these nutrients as it has been reported for other type of wetlands and terrestrial plants (Tateno and Chapin 1997; Geeske et al. 2001). Thus nitrogen and phosphorus are conserved within the plant for continued growth. Due to the asexual reproduction of *Typha sp*, (vegetative growth) the plant's roots and rhizomes can survive until the next grow season until soil conditions, such as the low ambient temperature in the Wax Lake delta region during the winter season (<12 ^{o}C), are conducive to plant growth. I believe that because these plants have conserved nitrogen and phosphorus, via retranslocation, they can grow faster, denser, and higher than other species would be able to in a limiting environment where nutrient conservation mechanisms are need to maintain and conserve a minimum biomass to dominate and expand during the growing season. My results show that *Typha sp*.is well adapted to grow and expand in newly formed deltaic regions due to nutrient retranslocation strategies to maximize nutrient conservation and promote belowground growth. The significant differences in belowground productivity among lobe sites of different age indicates that *Typha sp* could promote the rapid formation of soil, by developing roots and rhizomes on seasonal basis, thus significantly influencing changes in soil elevation as newly mineral sediment is deposited by river discharge and sediment resuspension. I propose that mix and pure *Typha sp*. vegetation patches in coastal Louisiana, especially in the regions of active delta formation as is the case of the Wax Lake and Atchafalaya deltas, represent a critical successional trajectory to stabilize newly formed land due to the rapid species-specific growth rates and biomass accumulation belowground.

V. Conclusions

SEDIMENT

1) The sediment at the Old site showed the highest organic matter content (8%) and lowest bulk density (0.87 mg cm^3), while the Young site experiences more sedimentation (OM= 3.07%) as indicated by more mineral content in the soils (bulk density= 1.21 mg cm^3);
2) C:N show no significant variability between sites, or depths; however, N:P ratios reflect a significant spatial variation in N and P availability across the Wax Lake delta lobes of different age.

PLANT

1) Aboveground biomass fluctuates throughout the year, reaching a peak in the summer months (500-700 gdw m^{-2}). Low biomass levels are observed after September when dead biomass levels increase (500-900 gdw m^{-2})

2) Root biomass (600-800 gdw m^{-2}) and belowground productivity (2.5 gdw m^{-2} day^{-1}) at the Young site were the highest, indicating that more energy is allocated to the acquisition of nutrients from the soil than at the other sites.
3) Aboveground productivity was significantly different among sites with the highest productivity rate in the old site (5.2 gdw m^{-2} day^{-1}).
4) *Typha sp* retranslocate nitrogen and phosphorus to conserve nutrient loss and maximize growth rates in each annual production cycle in the Wax Lake delta;
5) The significant differences in belowground productivity among lobe sites of different age indicates that *Typha sp* could promote the rapid formation of soil, by developing roots and rhizomes on seasonal basis, thus significantly influencing changes in soil elevation as newly mineral sediment is deposited by river discharge and sediment resuspension

Tables

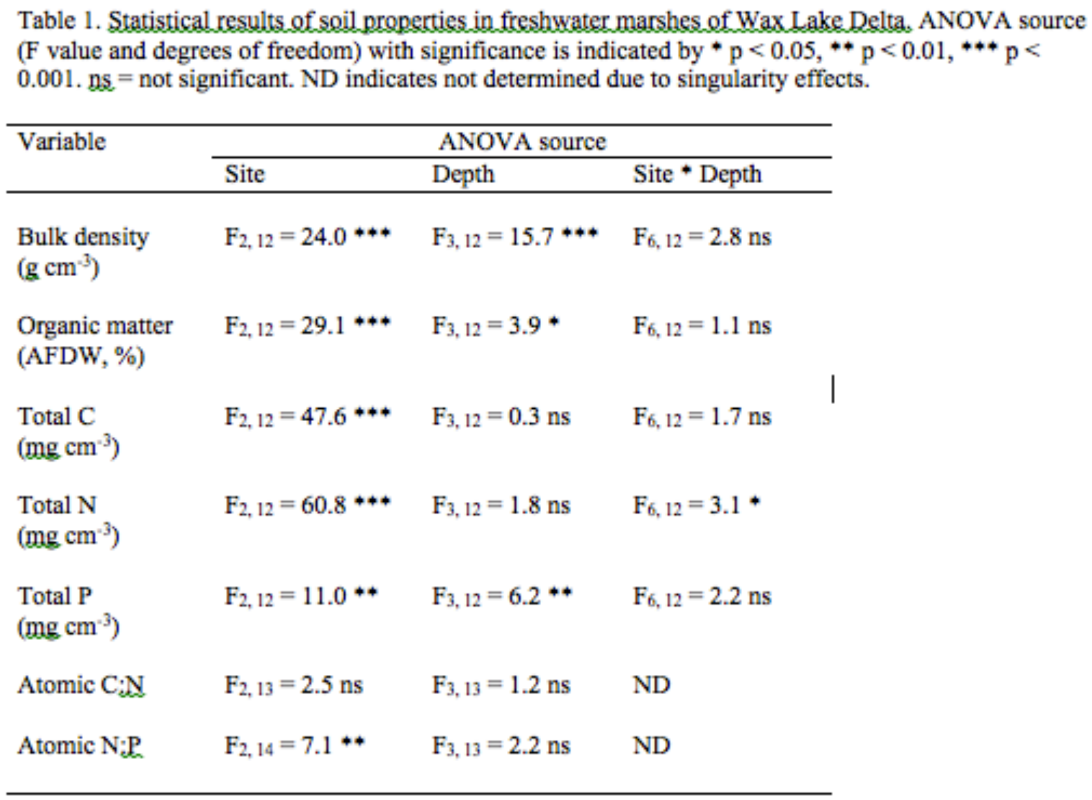

Table 1. Statistical results of soil properties in freshwater marshes of Wax Lake Delta. ANOVA source (F value and degrees of freedom) with significance is indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. ns = not significant. ND indicates not determined due to singularity effects.

Variable	ANOVA source		
	Site	Depth	Site * Depth
Bulk density (g cm^{-3})	$F_{2,12} = 24.0$ ***	$F_{3,12} = 15.7$ ***	$F_{6,12} = 2.8$ ns
Organic matter (AFDW, %)	$F_{2,12} = 29.1$ ***	$F_{3,12} = 3.9$ *	$F_{6,12} = 1.1$ ns
Total C (mg cm^{-3})	$F_{2,12} = 47.6$ ***	$F_{3,12} = 0.3$ ns	$F_{6,12} = 1.7$ ns
Total N (mg cm^{-3})	$F_{2,12} = 60.8$ ***	$F_{3,12} = 1.8$ ns	$F_{6,12} = 3.1$ *
Total P (mg cm^{-3})	$F_{2,12} = 11.0$ **	$F_{3,12} = 6.2$ **	$F_{6,12} = 2.2$ ns
Atomic C;N	$F_{2,13} = 2.5$ ns	$F_{3,13} = 1.2$ ns	ND
Atomic N;P	$F_{2,14} = 7.1$ **	$F_{3,13} = 2.2$ ns	ND

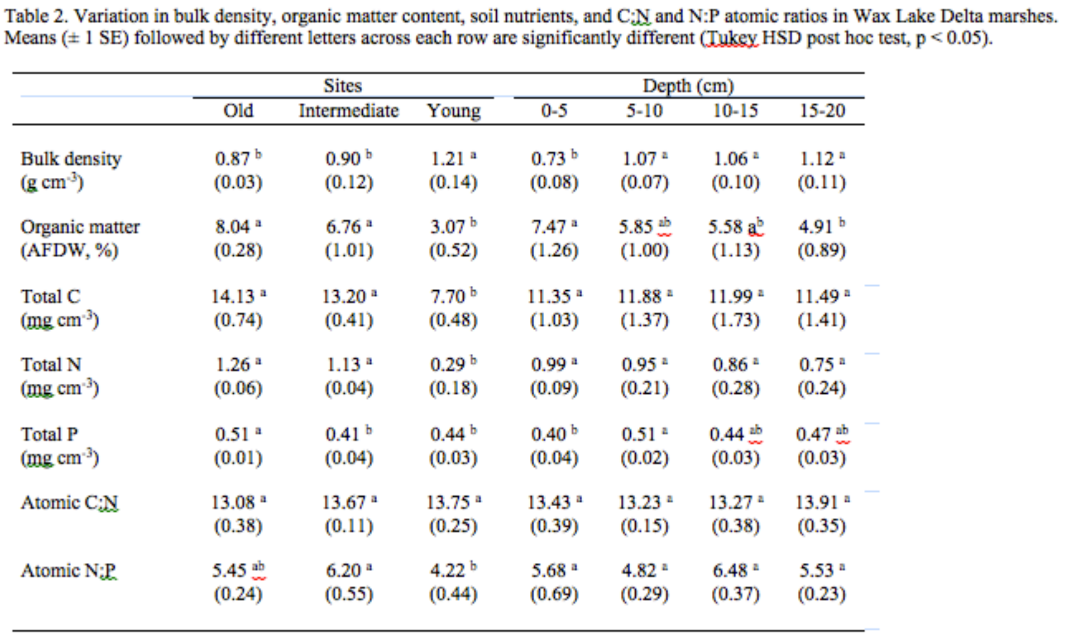

Table 2. Variation in bulk density, organic matter content, soil nutrients, and C;N and N:P atomic ratios in Wax Lake Delta marshes. Means (± 1 SE) followed by different letters across each row are significantly different (Tukey HSD post hoc test, $p < 0.05$).

	Sites			Depth (cm)			
	Old	Intermediate	Young	0-5	5-10	10-15	15-20
Bulk density (g cm^{-3})	0.87 ^{b} (0.03)	0.90 ^{b} (0.12)	1.21 ^{a} (0.14)	0.73 ^{b} (0.08)	1.07 ^{a} (0.07)	1.06 ^{a} (0.10)	1.12 ^{a} (0.11)
Organic matter (AFDW, %)	8.04 ^{a} (0.28)	6.76 ^{a} (1.01)	3.07 ^{b} (0.52)	7.47 ^{a} (1.26)	5.85 ^{ab} (1.00)	5.58 ^{ab} (1.13)	4.91 ^{b} (0.89)
Total C (mg cm^{-3})	14.13 ^{a} (0.74)	13.20 ^{a} (0.41)	7.70 ^{b} (0.48)	11.35 ^{a} (1.03)	11.88 ^{a} (1.37)	11.99 ^{a} (1.73)	11.49 ^{a} (1.41)
Total N (mg cm^{-3})	1.26 ^{a} (0.06)	1.13 ^{a} (0.04)	0.29 ^{b} (0.18)	0.99 ^{a} (0.09)	0.95 ^{a} (0.21)	0.86 ^{a} (0.28)	0.75 ^{a} (0.24)
Total P (mg cm^{-3})	0.51 ^{a} (0.01)	0.41 ^{b} (0.04)	0.44 ^{b} (0.03)	0.40 ^{b} (0.04)	0.51 ^{a} (0.02)	0.44 ^{ab} (0.03)	0.47 ^{ab} (0.03)
Atomic C;N	13.08 ^{a} (0.38)	13.67 ^{a} (0.11)	13.75 ^{a} (0.25)	13.43 ^{a} (0.39)	13.23 ^{a} (0.15)	13.27 ^{a} (0.38)	13.91 ^{a} (0.35)
Atomic N;P	5.45 ^{ab} (0.24)	6.20 ^{a} (0.55)	4.22 ^{b} (0.44)	5.68 ^{a} (0.69)	4.82 ^{a} (0.29)	6.48 ^{a} (0.37)	5.53 ^{a} (0.23)

List of Figures

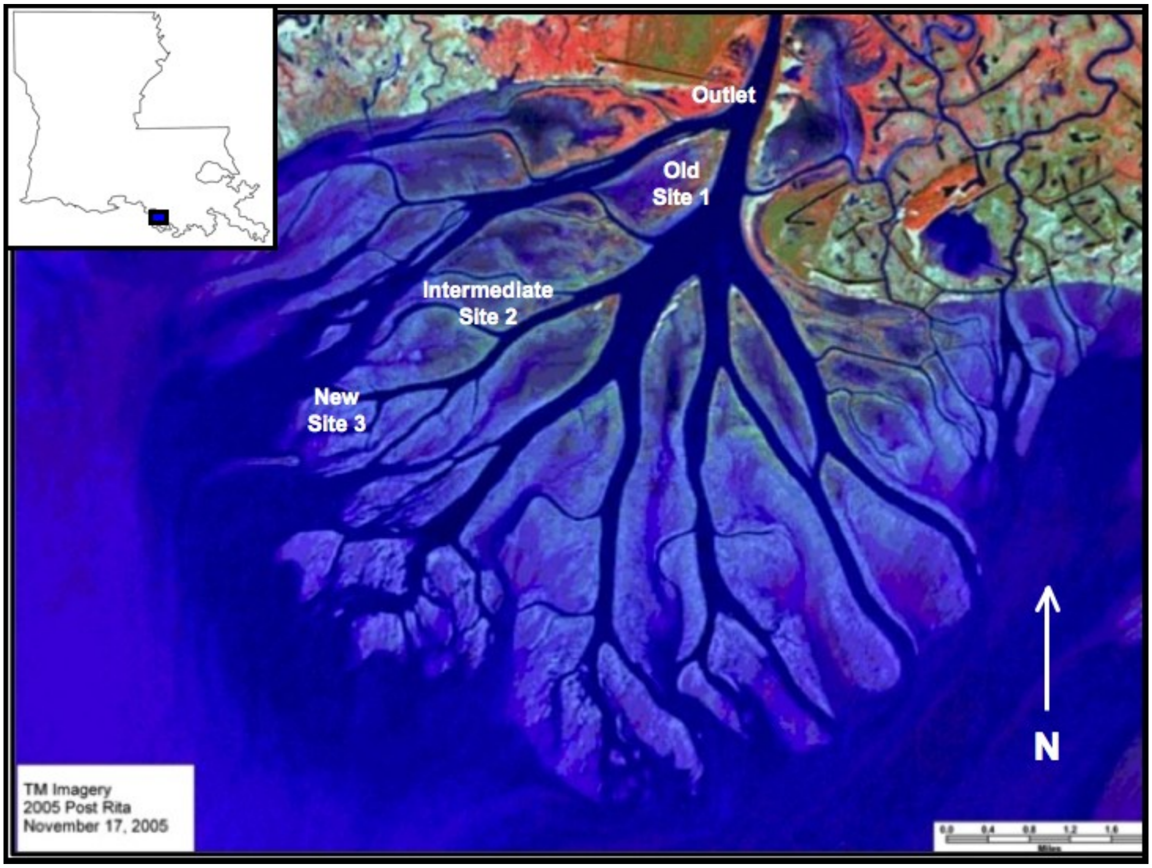

Figure 1. Location of the Wax Lake Delta, Louisiana and sampling stations (old, intermediate and young/new site).

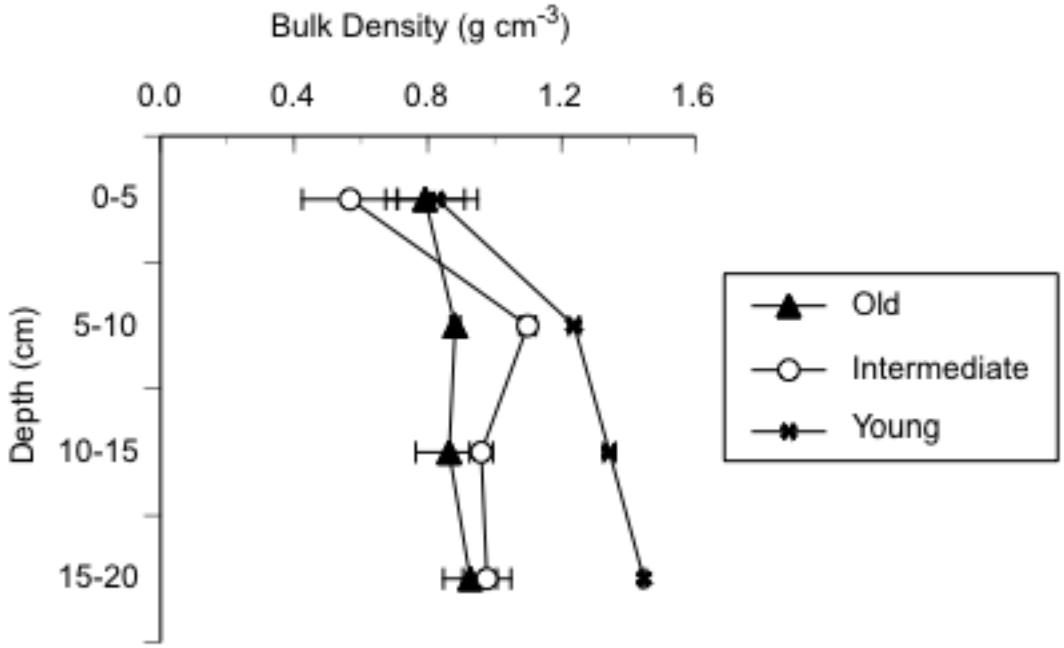

Figure 2. Soil bulk density at different depths in sampling sites.

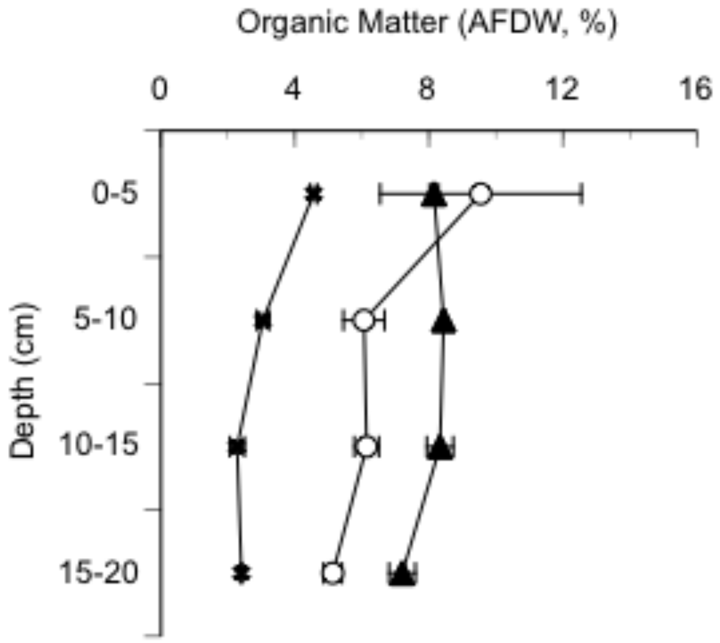

Figure 3. Percentage of organic matter at each sampling site with respect to depth.

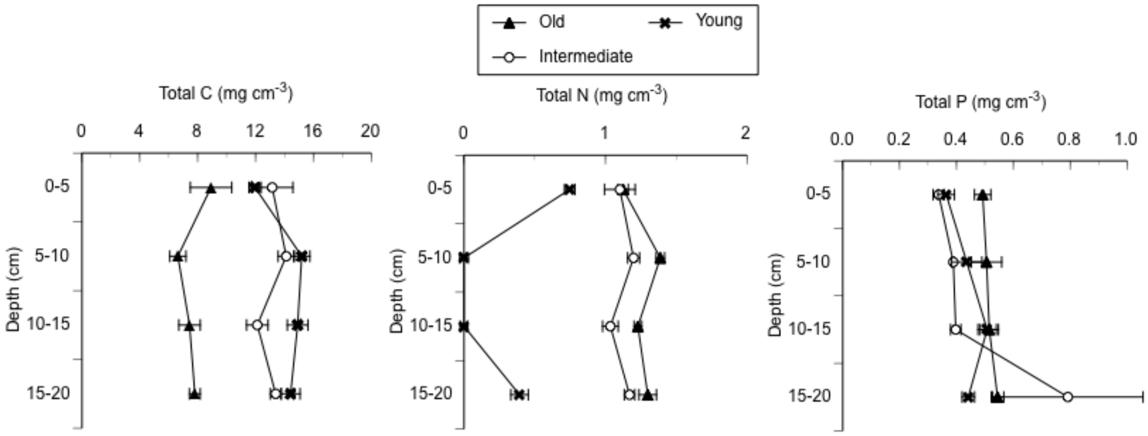

Figure 4. Total carbon (a), nitrogen (b), and phosphorus (c) concentrations in soil at each sampling site with respect to depth.

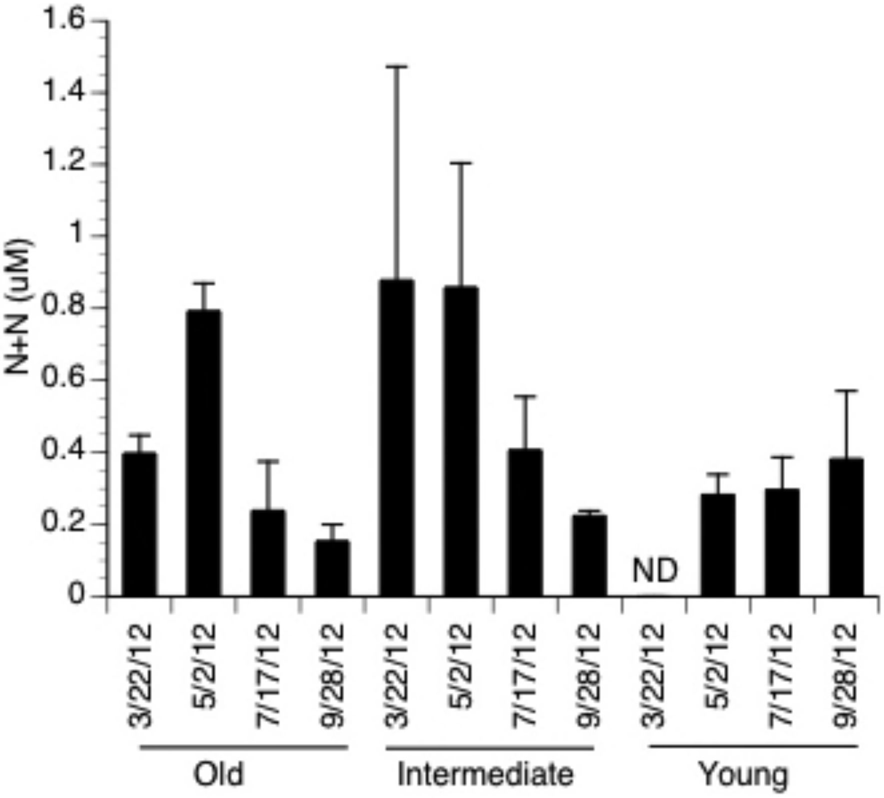

Figure 5: N+N concentrations in porewaters at each site.

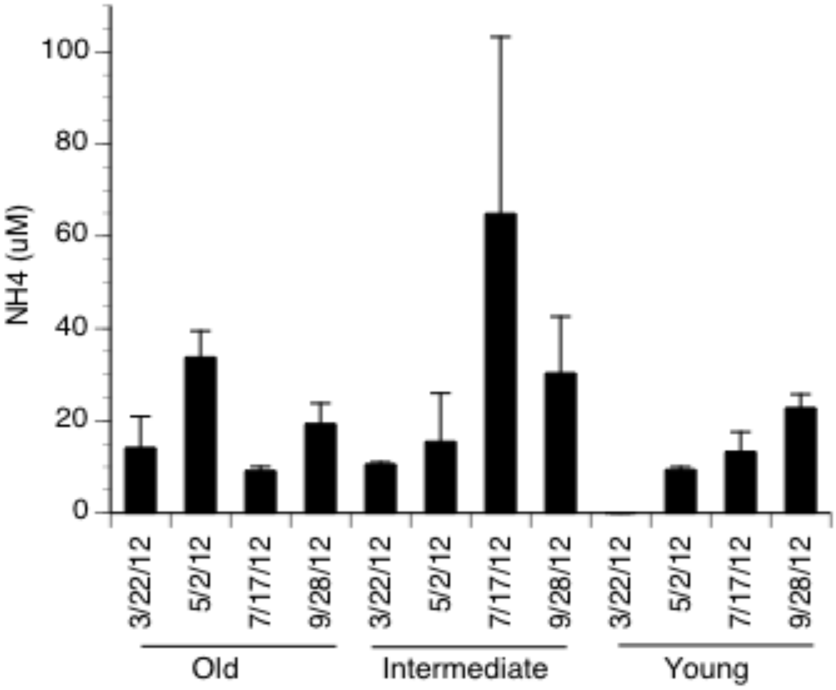

Figure 6: NH4 concentrations in porewaters at each site.

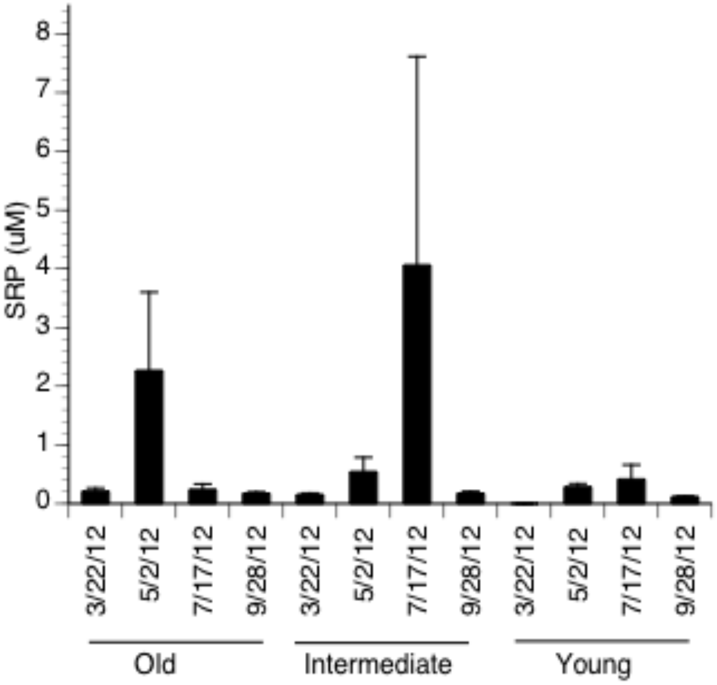

Figure 7: Soluble reactive phosphorus (SRP) concentrations in porewaters at each site.

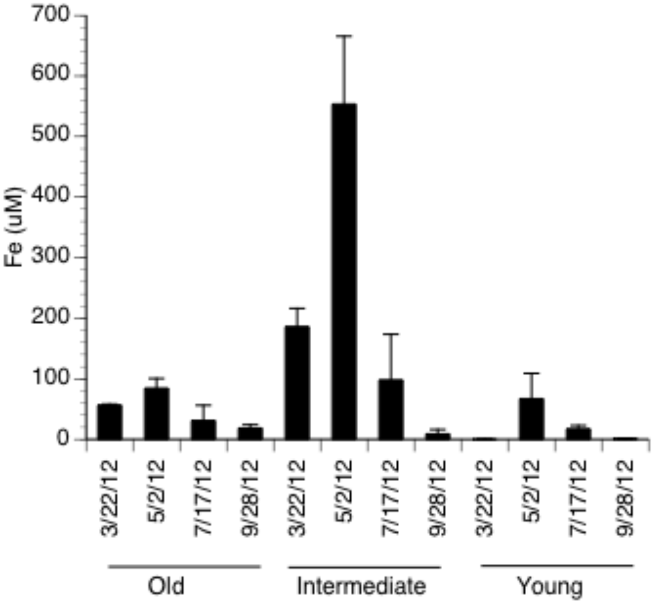

Figure 8: Iron concentrations in porewaters at each site.

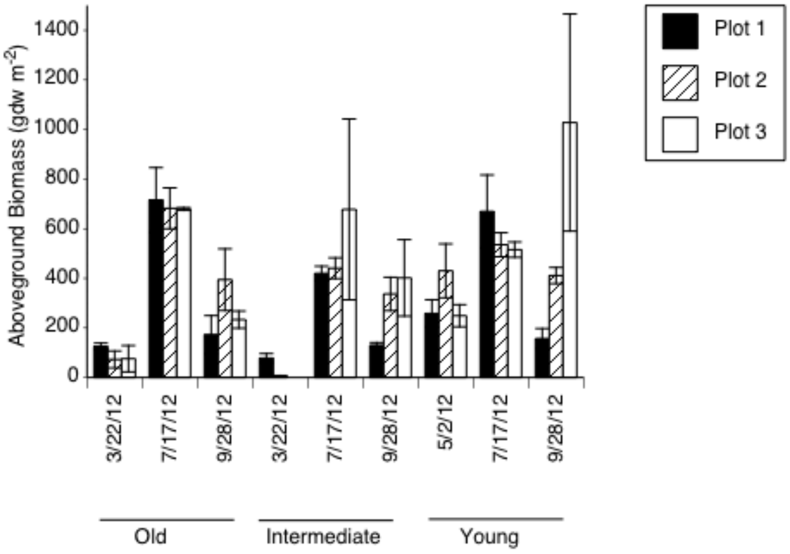

Figure 9: Live aboveground biomass per plot at each site.

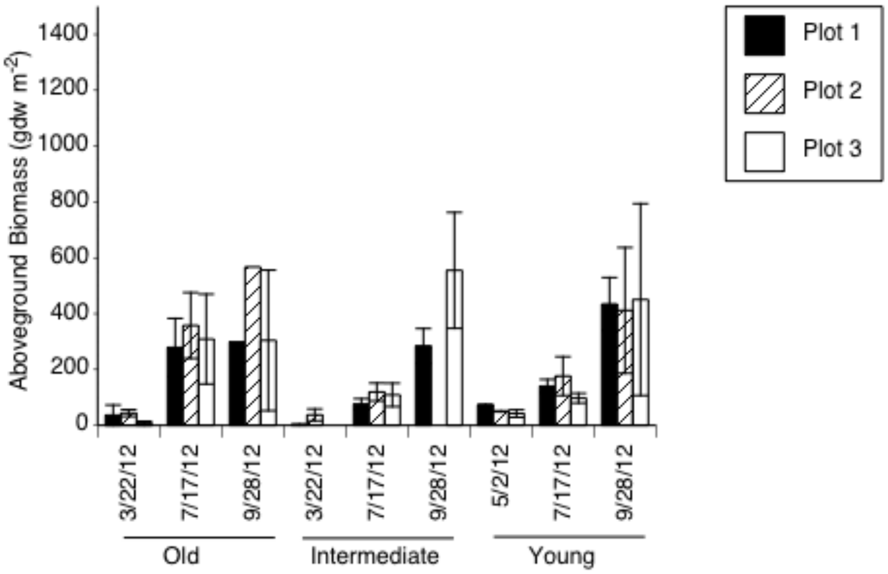

Figure 10: Dead aboveground biomass per plot at each site.

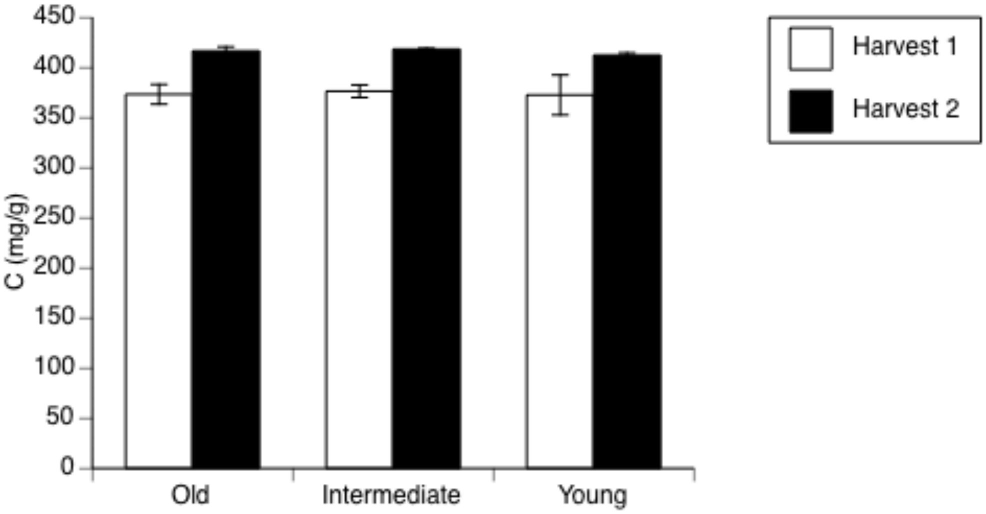

Figure 11: Total carbon concentration in aboveground biomass at each sampling site.

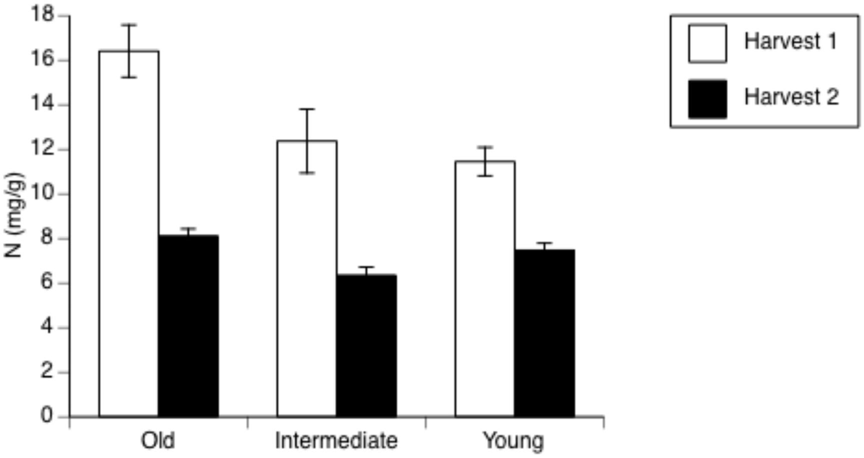

Figure 12: Total nitrogen concentration in aboveground biomass at each sampling site.

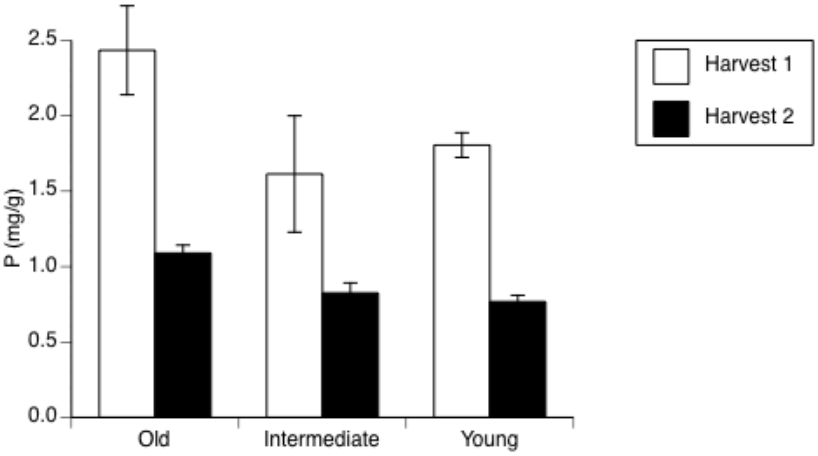

Figure 13: Total phosphorus concentration in aboveground biomass at each sampling site.

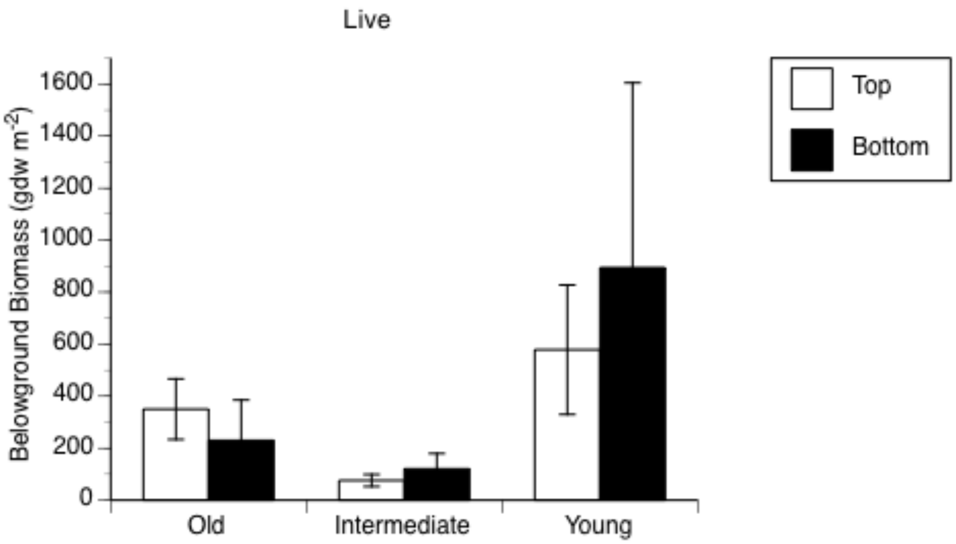

Figure 14: Live belowground biomass at each sampling site.

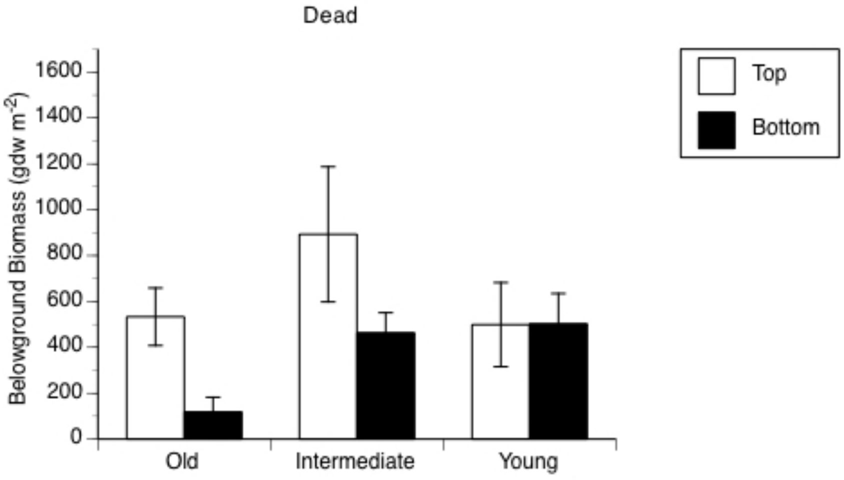

Figure 15: Dead belowground biomass at each sampling site.

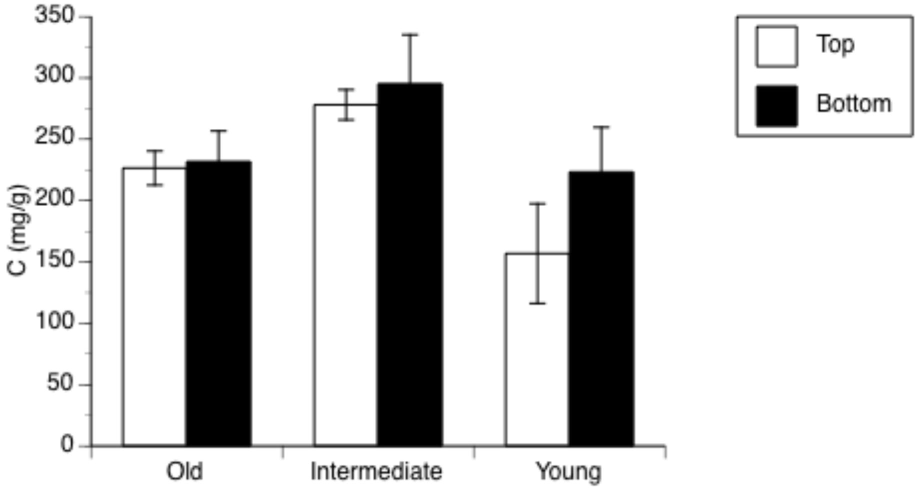

Figure 16: Total carbon concentration in belowground biomass at each sampling site.

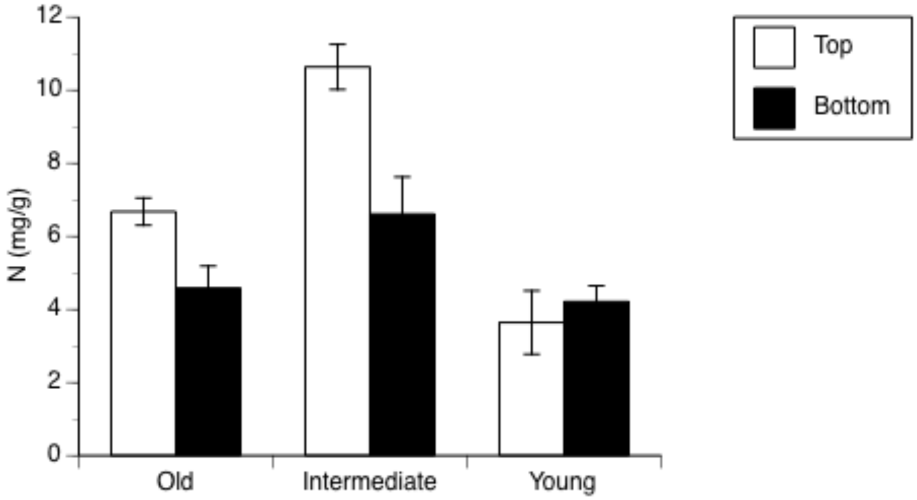

Figure 17: Total nitrogen concentration in belowground biomass at each sampling site.

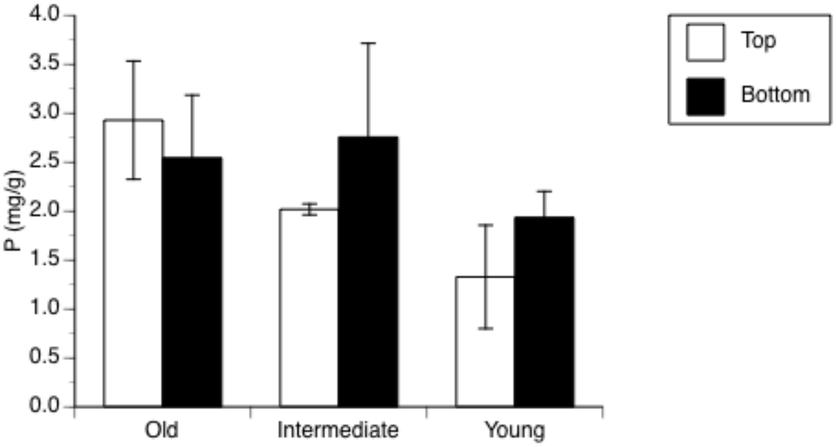

Figure 18: Total phosphorus concentration in belowground biomass at each sampling site.

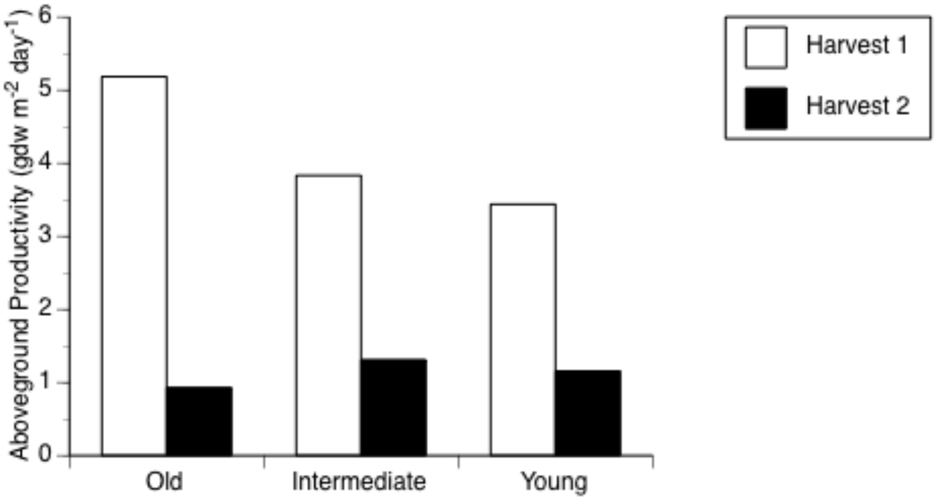

Figure 19. Vegetation aboveground net productivity per harvest in study sites.

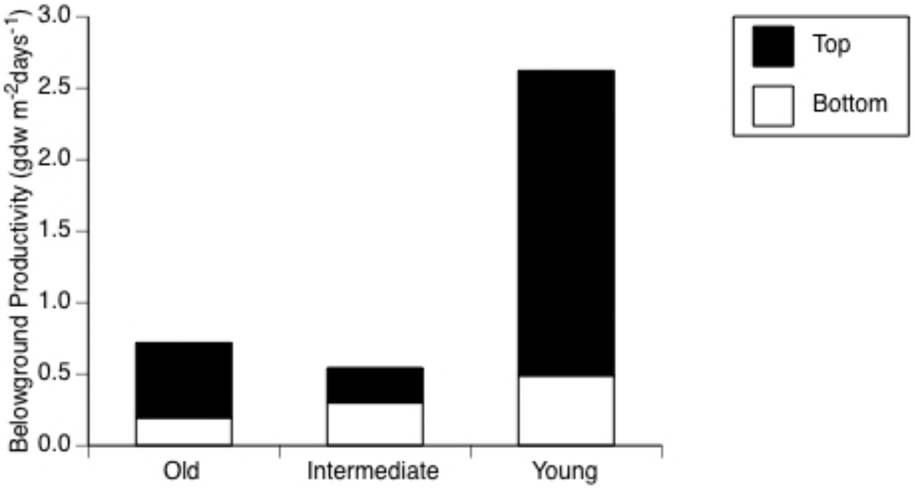

Figure 20 Vegetation belowground net productivity per harvest in study sites..

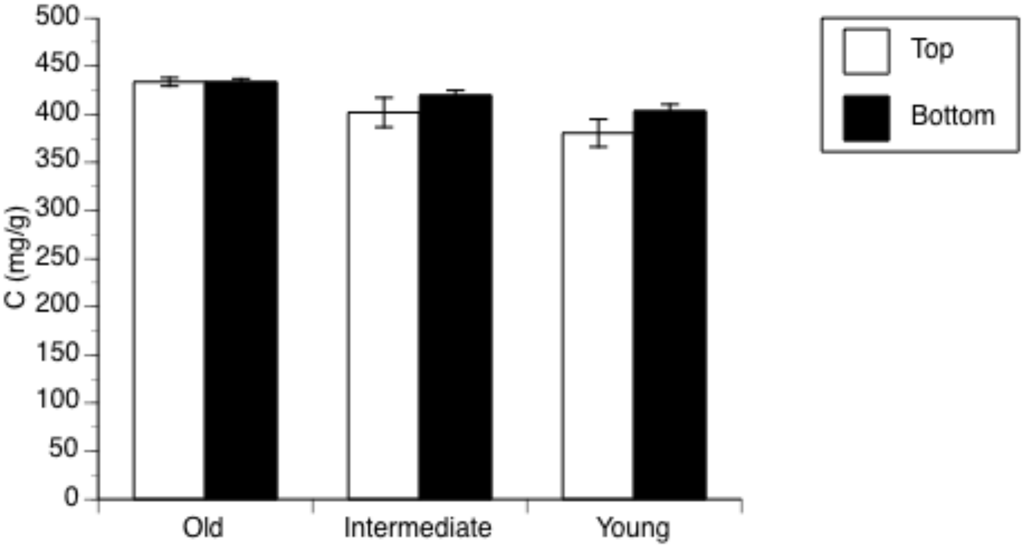

Figure 21. Total carbon content in belowground biomass per depth at each sampling site.

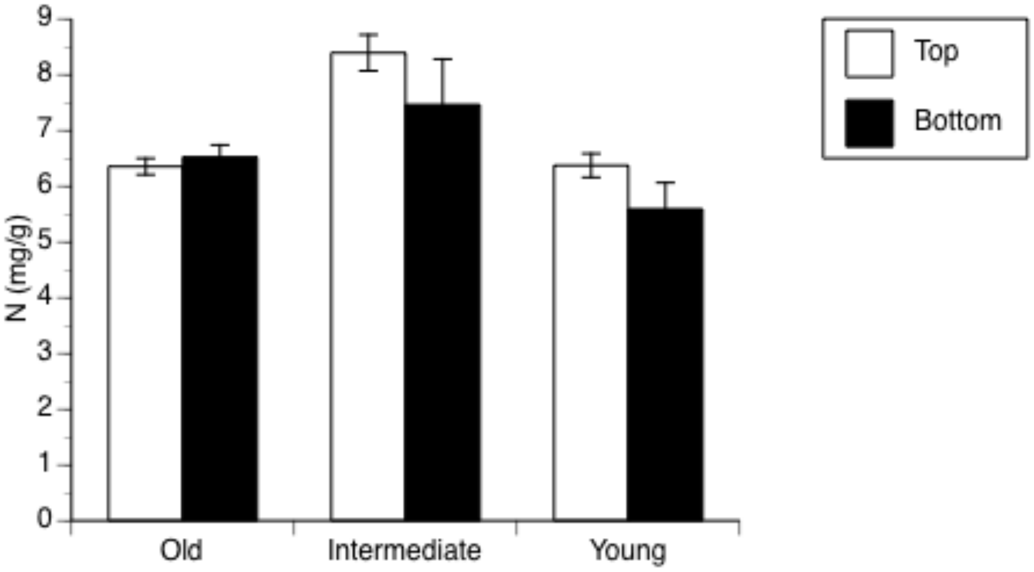

Figure 22. Total nitrogen content in belowground biomass per depth at each sampling site.

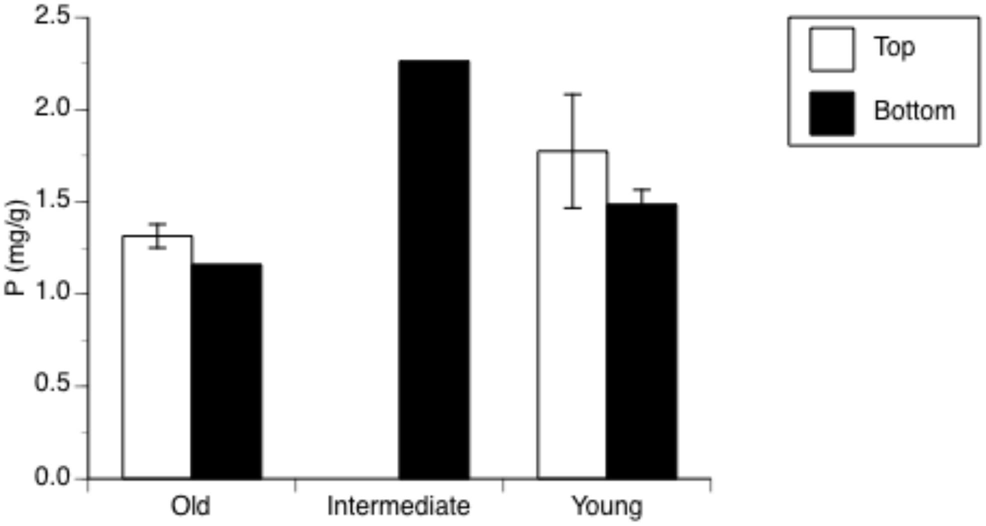

Figure 23. Total phosphorus content in belowground biomass per depth at each sampling site. No value was estimated for the top depth in the intermediate site.

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