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The effects of nutrient enrichment on the decomposition of belowground organic matter in a *Sagittaria lancifolia* - dominated oligohaline marsh

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THE EFFECTS OF NUTRIENT ENRICHMENT ON THE DECOMPOSITION OF
BELOWGROUND ORGANIC MATTER IN A *SAGITTARIA LANCIFOLIA* -
DOMINATED OLIGOHALINE MARSH

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Master of Science

In

The Department of Oceanography and Coastal Sciences

by
Kristen Raye Laursen
B.S., The College of William and Mary, 2001
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ABSTRACT

Wetlands improve water quality through sedimentation and the uptake of excess nutrients. As human population increases in the coastal zone, wetlands receive greater nutrient inputs. These additional nutrients may accelerate microbial activity, leading to faster decomposition rates. This decomposition could exceed belowground organic matter production, resulting in a net reduction in soil organic matter accumulation and vertical marsh accretion. The effects of nutrient enrichment on belowground organic matter decomposition in subtropical marshes have received little attention. As such, this research examined the effects of four levels of nitrogen combined with two levels of phosphorus enrichment on belowground decomposition through the use of cotton strip and litter bag assays in a *Sagittaria lancifolia* dominated marsh in Madisonville, Louisiana. Litter bags contained *S. lancifolia* root or shoot tissues; roots were of uniform tissue quality while shoots were from unenriched or enriched soils. Soil nitrogen and phosphorus applications both significantly increased belowground decomposition rates of cotton strips. The effect of tissue quality on shoot decomposition was dependent on nitrogen soil enrichment level. At low nitrogen enrichment levels, low quality shoot tissues decomposed more slowly than high quality tissues; this relationship was reversed at high nitrogen soil enrichments. Also, the effect of phosphorus enrichment on shoot decomposition was dependent on the level of nitrogen enrichment. Phosphorus soil enrichment only increased decomposition at the high nitrogen levels. Similarly, phosphorus enrichment combined with moderate nitrogen enrichments raised the decomposition rate of labile root tissue components. However, neither nitrogen nor phosphorus enrichments affected the decomposition rate of recalcitrant root components.

Cellulose decomposition was positively correlated with interstitial pH. Shoot decomposition and the recalcitrant root decomposition rate also positively correlated with interstitial pH. This research demonstrated that nitrogen and phosphorus soil enrichments affect the decomposition of roots, shoots, and cotton strips, though in different ways. Variations in the nutrient and carbon quality of the individual tissues, as well as abiotic factors such as pH, modify the effects of soil nutrient enrichments on the decomposition of different tissues in the study marsh.

INTRODUCTION

Wetland ecosystems are highly valued for the variety of functions and services they perform, with one estimate of their global value being $\$4,879 \times 10^9 \text{ yr}^{-1}$ (Costanza et al. 1997). They are economic assets partly because they provide key habitat and sustenance for fisheries and game animals and are a source of timber (Mitsch and Gosselink 2000). In addition, wetlands are buffers for human settlements against floods and storm events and improve water quality through the process of sedimentation and the uptake of excess nutrients in water (Patrick 1994). This capacity to retain and process nutrients contained in water prior to its entry into adjacent estuaries and coastal waters is an especially important function of coastal wetlands.

However, nutrient enrichment resulting from the assimilatory capacity of wetlands may have complex effects on the structure and function of these systems. For example, nutrient enrichment may stimulate plant biomass production, leading to increased accumulation of organic matter in the soil. Increased soil fertility may also accelerate microbial activity, leading to a more rapid decomposition rate (Rybczyk et al. 1996). This decomposition via bacterial and fungal activities could exceed belowground organic matter production, resulting in a net reduction in soil organic matter accumulation and vertical marsh accretion due to nutrient addition. Wetland soils can be very high in organic matter content (Mitsch and Gosselink 2000). Even in mineral wetland soils, organic matter accumulation is important. For example, wetland soils in the Mississippi River Deltaic Plain can range from 43% organic matter (by volume) in more mineral saline marsh soils to 75% organic matter in more organic intermediate marsh soils, excluding water and gas from the calculations (Nyman et al. 1990). As such,

the accumulation of organic matter is an important process influencing vertical marsh accretion.

Vertical marsh accretion and resulting elevation change are important processes in maintaining marsh elevation as sea level increases. This is especially important in Louisiana where land subsidence in conjunction with eustatic sea level rise has resulted in a relative sea level rise roughly ten times the world average (Penland and Ramsey 1990). Louisiana contains a vast area of coastal wetlands, accounting for approximately 40% of the United States total. Louisiana also experiences a high rate of wetland loss, approximately 80% of that for the United States (Penland et al. 1990). Both natural and human-induced factors contribute to this rapid land loss. Natural causes include compaction, subsidence, sea level rise, storms, and land degradation due to the delta cycle. Human actions leading to wetland loss include sub-surface fluid withdrawal, dredging canals, and building dams and levees (Penland et al. 1990). River diversion projects may partially alleviate the impacts of dams and levees by allowing nutrients and sediments to flow into wetland systems (Lane et al. 1999, DeLaune et al. 2003). Waters entering marshes and surface water bodies, both naturally and through diversions, are becoming increasingly eutrophic due to human activities, and marshes will likely be more commonly used as filters to improve water quality in the future. Due to this increase in nutrients in the waters entering marsh systems, information regarding nutrient enrichment of wetlands and its effects on decomposition will become increasingly critical. As this water transports both nitrogen and phosphorus, which are primary limiting nutrients, this study concentrates on how these nutrients, both individually and in concert, affect decomposition in marsh systems. In addition to the availability of nutrients, tissue

nutrient quality, tissue carbon quality, and the interactions of all these factors can affect decomposition processes. As such, this study also addresses the relationship between nutrients, tissue characteristics, and decomposition.

One of the primary factors influencing decomposition is the availability of nutrients. Nitrogen is commonly the limiting nutrient for decomposition. However, phosphorus can further accelerate decomposition rates when combined with nitrogen, and can sometimes limit decomposition by itself. Higher natural soil concentrations of inorganic nitrogen and phosphorus raised the decomposition rate of cotton strips in a *Phragmites* marsh along a salinity gradient (Mendelssohn et al. 1999). Nitrogen addition significantly increased biomass loss from *Lotus corniculatus* litter, though acid conditions in a section of the study area limited its effect (Kalburtji et al., 1997). In contrast, phosphorus most strongly affected cellulose decomposition in a study involving both the water column and peat layer in the Florida Everglades (Maltby 1988). However, the study did find that the fastest decay rates occurred in plots treated with both nitrogen and phosphorus (Maltby 1988). Microbial activity in the Everglades may be phosphorus limited (Koch-Rose et al. 1994), and in various other systems phosphorus may limit microbial activity even when plant productivity is nitrogen limited. Sundareshwar et al. (2003) found that though nitrogen limited plant production in a salt marsh, microbial decomposer activities increased with the additions of N and P together. This indicated that microbes were more limited by phosphorus than nitrogen. Similarly, Feller et al. (2002) found that phosphorus increased decomposition across the zones of a mangrove forest, even in areas where nitrogen limited mangrove production. These studies highlight contrasting effects of nitrogen and phosphorus enrichment on decomposition.

The current research is designed in a factorial arrangement of nitrogen and phosphorus enrichments with the aim to further resolve the effects of different levels of nitrogen and phosphorus enrichment, both separately and in combination.

Nutrient content in tissues may also affect decomposition rates. Additional nutrients in the tissue can increase the concentration of nutrients available to decomposers and potentially reduce the proportion of refractory structures within the litter (Rybczyk et al. 1996). Decomposition tended to increase with tissue nitrogen and phosphorus concentrations in a review by Enríquez et al. (1993). In addition, Neely and Davis (1985) found that enriched litters of *Sparganium eurycarpum* and *Typha glauca* decomposed faster than unenriched litters. The current study examines tissues of several differing nutrient qualities. This allows the comparison of decomposition between these differing tissues under similar circumstances. Further, all of these tissues are exposed to varying levels of soil enrichment, allowing examination of the cumulative effect of tissue and soil nutrients on decomposition.

The effects of nutrient loading on belowground organic matter decomposition have received little attention. Thus, this thesis examines the effects of nutrient enrichment on belowground decomposition rates in a *Sagittaria lancifolia* L. (Alismataceae) dominated oligohaline marsh. The study attempts to quantify the effects of nitrogen and phosphorus enrichment on belowground decomposition of *S. lancifolia* shoot and root material and a standard cellulose source via the litter bag and cotton strip assays, respectively. As part of this goal, the study helps to determine whether nitrogen or phosphorus limits belowground decomposition in the subject marsh. This study also compares two primary methods of evaluating belowground decomposition, the cotton

strip and litter bag assays, as tools to examine decomposition rates and soil biogeochemical response to nutrient enrichment. I hypothesized that nitrogen availability limits the decomposition rate of cotton strips and litter tissues. Once the demand for inorganic nitrogen is satisfied, phosphorus will become a limiting factor and its addition will augment decomposition. I further hypothesized that shoot tissues will decompose faster than belowground tissues due to structural differences between roots and shoots.

Few studies have utilized the cotton strip assay in subtropical marshes, and to my knowledge a comparison of litter bags and cotton strips has not been conducted in subtropical wetlands. In addition, few studies of belowground organic matter decomposition as determined by the litter bag method have been conducted in *Sagittaria* marshes, which form a dominant fresh marsh habitat in the southeast United States. This research will augment the information available on *Sagittaria* and cellulose belowground decomposition, allowing a more complete picture of the factors controlling decomposition processes in this system.

MATERIALS AND METHODS

Site Description

The study site is located at approximately 30° 23.205' North latitude by 90° 09.551' West longitude in a marsh near the town of Madisonville, St. Tammany Parish, Louisiana, United States. The marsh lies adjacent to the Tchefuncte River, which drains into Lake Pontchartrain. It is an oligohaline marsh dominated by *Sagittaria lancifolia* L. (Alismataceae), and is a microtidal system with water levels dominated by frontal passages and wind direction.

Field Site Design and Fertilization

The experiment was conducted within a 4x2 factorial, randomized block design with five replicate blocks. Each block was 7m x 3m and contained eight plots measuring 1m² each. A 1m² buffer zone divided each plot from the next. For fertilization purposes only, plots were divided into sixteen subplots measuring 25cm on each side.

Within each block, I crossed and randomized four levels of nitrogen (0, 50, 200, and 1200 kg ha⁻¹ yr⁻¹) and two levels of phosphorus (0 and 100 kg ha⁻¹ yr⁻¹), yielding eight fertilizer treatment combinations. Nitrogen was applied in the form of 46-0-0 urea (Lesco) and phosphorus in the form of 0-18-0 Hi-Yield SuperPhosphate (Voluntary Purchasing Groups, Inc.). To aid the integration of fertilizer into the soil, fertilizer was enclosed in gelatin capsules (Size 10, Torpac, Inc.) and placed 15 cm belowground in the center of each subplot. This allowed the fertilizer to slowly diffuse through the soil. Fertilization occurred twice in 2002 and in 2003, for a total of four applications. One month separated the two applications during both years.

I used two primary methods to test the effect of these nitrogen and phosphorus soil enrichments on belowground decomposition. One method was the cotton strip assay and the other was the litter bag procedure.

Cotton Strip Assay

I utilized the cotton strip assay to test the decomposition of a standard material and to obtain a depth profile of belowground cellulose decomposition. I cut the strips from Shirley Soil Burial Test Fabric (Shirley Institute, Didsbury, Manchester, UK). Shirley Fabric is a 100% cotton cloth composed primarily of cellulose, and is standardized with consistent thread counts per square centimeter. Consistency within the cloth allows data comparison across sites. Cotton strips can also provide information regarding decomposition with depth in the soil profile (Latter and Howson 1977). Cotton strips were placed in the field on June 12, 2002, July 24, 2002, and June 24, 2003.

During each sampling period, one 10cm wide x 30cm long strip of Shirley Fabric was vertically inserted into each plot using a sharpshooter shovel (Latter and Howson 1977 and Harrison et al., 1988). Strips were retrieved 9-10 days after insertion, at which point control strips were inserted and removed in each block. All strips were cleaned of soil using bayou water and then rinsed with deionized water in the field. Upon returning to the laboratory, strips were rinsed again with deionized water and air-dried.

I sectioned each strip into 2cm x 10cm horizontal substrips corresponding to 1, 4, 7, 10, 13, 16, 19, 22, and 25 cm below soil surface to obtain a profile of decomposition with increasing depth in the soil. The tensile strength of each section was tested using a Dillon Quantrol™ Snapshot Tension Compression Motorized Test Stand tensometer connected to a Dillon Quantrol™ Advanced Force Gauge. The tensile strength of the

cloth provided an estimate of cellulolytic microbial activity (Sagar 1988). The percent loss of tensile strength as compared to a strip that has not undergone decomposition (e.g. a control strip) provided a measure of the degree of cellulose degradation. This measure of degradation has been used as a surrogate for natural organic matter decomposition (Maltby 1988, DeBusk 1996). Using the test and control substrip tensile strengths, Cotton Tensile Strength Loss per day (CTSL d^{-1}) was calculated by the equation:

$$CTSLd^{-1} = \frac{(1 - N/C) \times 100}{t} \quad (1)$$

where t is the time in days that a strip remains in the ground, N is the Newton value of test substrip tensile strength, and C is the average control substrip tensile strength in Newtons. CTSL d^{-1} values were analyzed to evaluate strip decomposition under the eight nutrient enrichment treatment combinations.

Litter Bag Assay

I utilized the litter bag procedure to evaluate decomposition rates of plant tissues, which are structurally more complex than the cotton strip material. I utilized both shoot and root tissues from *Sagittaria lancifolia* L. (Alismataceae).

I grew the root tissue for the litter bags from *S. lancifolia* sods collected in January 2002 near the field site and planted in Rubbermaid Roughneck tubs at Louisiana State University. The soil used was a combination of 50% commercial Sphagnum peat and 50% vermiculite. The soil also included Jiffy Mix (Jiffy Products of America, Inc.); a 50:50 mix of peat and vermiculite, which was blended in to comprise 20-22% of the soil in each tub. Species other than *Sagittaria* were weeded by hand except for *Eleocharis fallax* (Cyperaceae), which, due to its persistent roots, was removed using a 2-4% dilution of Round-Up. To maintain plant health, tubs were fertilized three times with

0.03g L⁻¹ of 15-30-15 Miracle-Gro Water Soluble All Purpose Plant Food (Scotts Miracle-Gro Products, Inc.). This dilution produced a fertilizer solution containing 5 ppm of nitrogen. Roots from the tubs were harvested in July 2002, cleaned of soil, and air-dried.

Shoot tissues used in the litter bags were taken from clip-plot material gathered during the Fall 2001 from a separate field site located in the same marsh. These *Sagittaria* leaves and petioles were grown under three soil fertility levels. These levels were control (no fertilizer), 200 kg N ha⁻¹ yr⁻¹ by 66 kg P ha⁻¹ yr⁻¹ (tissues hereafter referred to as medium or moderately enriched tissues), and 1200 kg N ha⁻¹ yr⁻¹ by 396 kg P ha⁻¹ yr⁻¹ (tissues hereafter called high or highly enriched tissues). All shoot tissues were oven-dried to dry weight and stored for use in the litter bags.

Litter bags with internal dimensions of 12 cm in height by 8 cm width were constructed of 2mm insect screening (Phifer Wire Products, Inc.). Their edges were melted closed using a soldering iron, which was also used to seal a plastic label into the corner of each bag. Five bags, each containing 1.7 ± 0.01 g of air-dried root tissue, were placed belowground in each plot on October 18, 2002. In addition, three bags of shoot tissues, e.g. one bag of combined leaf and petiole tissues from each soil fertility level (control, medium, and high), were placed belowground in each plot at the same time. Shoots were placed belowground because my goal was to evaluate belowground organic matter decomposition, and some shoot tissue is incorporated into the soil. Each shoot bag contained 1 ± 0.01 g of leaves and 2 ± 0.01 g of petioles. In total, 8 bags were placed in each plot, or 200 root bags and 120 shoot bags overall for this experiment. All bags were buried vertically in the soil by using a trowel and were centered at 15cm belowground in

the plots. To aid with locating the bags later, each was tethered by fishing line to a PVC pipe standing in the center of each plot. Starting masses of roots and shoots were later corrected to dry weight. This was accomplished by weighing several extra root and shoot samples as air-dry tissue, drying them to constant weight at 65°C, and then reweighing them to obtain average moisture correction factors for the root and shoot tissues.

One litter bag of root material was collected from each plot at 14, 28, 55, 213, and 291 days after insertion. Multiple pull dates allowed the construction of exponential loss curves for root tissues. All shoot litter bags were retrieved at 291 days to provide final percent mass remaining values. To clean the samples, I first removed all tissue from the bags and separated out invertebrates and live roots, as they were not part of the initial tissue placed in the bags. Tissues were then rinsed with tap water followed by deionized water over a #35 sieve (opening size = 500 µm) (Newark Wire Cloth Company, Newark, NJ). Samples were weighed, dried to constant weight in a 65°C oven, and reweighed. The percentage of mass remaining (MR) in each bag was calculated using the equation:

$$MR=(w_t/w_0)*100 \quad (2)$$

where dry weight at time zero and at time t are w_0 and w_t , respectively.

Root Decomposition Rate Calculations

The shoot tissues had only initial and final percent mass remaining values, so these tissues could not provide decomposition rates. As such, I analyzed their final percent mass remaining values. I calculated percent mass remaining for the root tissue as well. However, roots were collected at five times during the experiment and so I could compute decomposition rates for each plot. I used SAS statistical software (version 8, 2001; SAS Institute, Inc.) to construct double exponential decay models from the root

percent mass remaining values. These double exponential values provided decomposition rates for each plot. The exponential model is useful for evaluating decomposition because it agrees closely with biological processes. Similarly to decaying tissues, the equations are bounded by $y = 100\%$ mass remaining and 0% mass remaining. The model allows the fraction of the initial mass remaining to change with time. In addition, the absolute decay rate of the exponential equation declines with time while the relative decay rate is constant or tends to constancy (Wieder and Lang 1982). This also occurs in natural decomposition processes. The double exponential model calculates decay rates by the equation

$$y = ae^{-(b1)t} + ce^{-(b2)t} \quad (3)$$

where y is the percent of litter remaining at time t , a is a value for the labile fraction of the tissue, $b1$ is the instantaneous decay rate relating to the labile portion of the tissue, c is a value for the recalcitrant tissue fraction, and $b2$ is a decay rate relating to the recalcitrant tissue. The variables $b1$ and $b2$ are decomposition rate constants. This model is useful in cases exhibiting rapid initial decomposition (shown by the $b1$ rate) followed by much slower decomposition (shown by the $b2$ rate), as the model splits the litter into labile and recalcitrant fractions (Harmon et al 1999, Wieder and Lang 1982). This division agrees with biological explanations of decomposition, as the easily decomposed material breaks down faster and leaves the refractory portions to degrade more slowly. The equation is also useful in evaluating differences in decomposition rates for a single litter type over various sites. However, the double exponential equation does not allow transformation of labile material into recalcitrant material (Wieder and Lang 1982),

which can happen in natural decomposition. Decomposition rates provided by the model can be converted into the true percent decline per day by the equation:

$$1 - e^{-b} \quad (4)$$

where b is the $b1$ or $b2$ instantaneous decay rate from the double exponential equation.

These true decomposition rates are used to analyze root decomposition in this experiment.

Interstitial Water

Interstitial water samples from 15 cm belowground in each plot were extracted on the same dates as the cotton strip and litter bag insertions. Water samples extracted on cotton strip insertion dates (June 12, 2002, July 24, 2002, and June 24, 2003) were analyzed for electrical conductivity, pH, $\text{NH}_4\text{-N}$ concentration, and $\text{PO}_4\text{-P}$ concentration. Due to funding limitations, the October 18, 2002 water samples paired with litter bag insertion were analyzed for pH and conductivity only. Conductivity was measured using a Cole-Parmer conductivity meter (model # 19820-00) and pH was measured with an Orion pH meter (model 420A). Water samples for $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ were filtered in the field using disposable 0.45 μm nylon syringe filters (Whatman) and preserved by freezing. $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$ samples were analyzed using a LACHAT QuickChem FIA+ 8000 Series autoanalyzer. As the undiluted $\text{NH}_4\text{-N}$ samples presented values beyond the standard curve of the instrument, the samples for the 0, 50, and 200 $\text{kg N ha}^{-1} \text{ yr}^{-1}$ soil enrichment levels were diluted by 10, and samples for the 1200 $\text{kg N ha}^{-1} \text{ yr}^{-1}$ soil enrichment level were diluted by 100. $\text{PO}_4\text{-P}$ samples did not require dilution.

Tissue Analyses

I ground dried root tissue left after litter bag construction on a Wiley mill to pass a size 40 mesh. *Sagittaria lancifolia* tissue corresponding to the shoot litter tissue was processed separately from this study but using similar procedures. In addition, three healthy *S. lancifolia* shoots, each including both petiole and leaf, were taken from each experimental plot during September 2003. These shoots were cleaned with tap and deionized water and oven-dried prior to similar grinding. All tissues were analyzed for percent carbon and nitrogen using a Perkin Elmer 2400 Series II CHNS/O Analyzer. Roots, tissues corresponding to the shoot litter material, and shoot tissues from the unfertilized experimental plots were analyzed for phosphorus content on an ICP (Spectro Ciros ICAP) following nitric acid / hydrogen peroxide digestion.

Ground root tissues and unfertilized shoot tissues from the experimental plots were also analyzed for cellulose, lignin, hemicellulose, and ash content. Samples were hydrolyzed using H₂SO₄ and filtered to separate Klason lignin. These lignin samples were dried, weighed, and ashed to obtain percent lignin values. The filtered hydrolysate was brought to approximately pH 7 and analyzed by HPLC on a Dionex IC20 Ion Chromatograph with Dionex 4400 Integrator and a refractive index detector to obtain glucose, xylose, arabinose, and mannose readings. These readings were used to calculate cellulose and hemicellulose percentages in the tissues. Unusually high mannose peaks appeared in the HPLC data. As such, the hydrolysate was further analyzed via gas chromatography on an Agilent Technologies 6890 Network GC System with Hewlett Packard 7683 Series Injector to obtain mannose values excluding the unknown compound that elevated the peak in the HPLC data.

Redox and Soil Temperature

Bright platinum electrodes and a Cole-Parmer digital pH/temperature/mV/ORP meter connected to a calomel reference electrode (Corning Cat. No 476406) were used to test soil oxidation-reduction potential at the 15 cm depth in each plot. The Ec readings obtained using the calomel reference electrode were converted to Eh readings, as though the Standard Hydrogen Electrode (SHE) were used, by adding 245 mV to each value. Eh was measured weekly from July 3, 2003 to August 15, 2003. One platinum electrode was used in each plot from July 3 through July 25. To reduce error, an extra electrode was included in each plot for the two August readings. Limitations to the numbers of available electrodes prevented obtaining more than duplicate values per plot.

Soil temperature was recorded during all seasons at the 15 cm depth in each block.

Statistical Analysis

Data analysis was conducted using the SAS System (version 8, 2001, SAS Institute, Inc.) statistical software. I used PROC NLIN to obtain root decomposition rates. The effects of nitrogen and phosphorus soil enrichment levels on cellulose and litter decomposition and on interstitial water characteristics were examined through analysis of variance with PROC MIXED and PROC GLM. The Tukey-Kramer Honest Significant Difference method was used for pairwise comparisons between least squared means values in these tests. Eh data had poor homogeneity of variance and normality, so the effects of N and P soil enrichment on Eh were analyzed using a nonparametric ANOVA Kruskal-Wallis test via PROC RANK and PROC GLM. Stepwise multiple regressions with forward selection were performed using PROC REG, and correlations

were formed using PROC CORR. These multiple regressions and correlations examined relationships between interstitial water variables (pH, conductivity, $\text{NH}_4\text{-N}$, and $\text{PO}_4\text{-P}$) and decomposition. Interstitial water data corresponding to all cotton strip test periods were available for examination with the cotton strip data in the multiple regression and correlation analyses. However, only the last set of interstitial water data was compared to the root and shoot decomposition data. This final interstitial water data set was the only complete one that matched the period in which litter bags were in the field. The first two sets of water samples were retrieved prior to litter bags being placed in the soil, and the October 18, 2002 water samples were not analyzed for $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$. Eh data was not included in the multiple regressions or correlations because it was not measured concurrently with interstitial water sampling. I used square, square root, ln, or log transformations of the data in several analyses to improve normality and homogeneity of variance. However, all graphs show non-transformed data. Means for these graphs were obtained with PROC MEANS.

RESULTS

Decomposition of Cotton Strips

Nitrogen and phosphorus enrichment, as well as depth and time, had significant effects on the decomposition of the Shirley cloth strips (Table 1). Cotton tensile strength loss per day (CTSL d^{-1}) significantly increased with soil N enrichment ($p < 0.0001$) (Fig. 1). The 1200 kg $ha^{-1} yr^{-1}$ enrichment level had significantly higher CTSL d^{-1} values than the three other enrichment levels. The 200 kg N $ha^{-1} yr^{-1}$ treatments also had significantly higher CTSL d^{-1} values than the 0 kg $ha^{-1} yr^{-1}$ treatments. The plots with phosphorus soil enrichment (100 kg P $ha^{-1} yr^{-1}$) had significantly higher CTSL d^{-1} values than the plots that were not enriched with phosphorus ($p = 0.0001$). In addition to soil enrichment effects, CTSL d^{-1} changed with substrip depth below the soil surface ($p < 0.0001$) (Fig. 2). Substrips at 1 cm depth had significantly higher CTSL d^{-1} values than all other depths. The next highest CTSL d^{-1} values occurred between 13 and 19 cm depth. Sampling period also significantly affected CTSL d^{-1} ($p = 0.0001$), as August 2002 had higher values than June 2002 and July 2003. The interaction of N enrichment and depth was significant ($p = 0.0025$) (Fig. 3). At the soil surface (1 cm depth), all N enrichment levels had similar effects and relatively high CTSL d^{-1} values. In contrast, at greater depths below the soil surface the 1200 kg $ha^{-1} yr^{-1}$ enrichment had significantly greater CTSL d^{-1} values than the other enrichment levels. In addition, the interaction of P enrichment and depth was marginally significant ($p = 0.0572$) (Fig. 4). As with the interaction of N enrichment and depth, CTSL d^{-1} values for the 0 and 100 kg P $ha^{-1} yr^{-1}$ treatments were high and similar at 1 cm depth. CTSL d^{-1} values tended to be greater

Table 1. Analysis of variance indicating the effects of N and P soil enrichments, depth below soil surface, and sampling period on cellulose decomposition (CTSL d⁻¹). *: The interaction of P soil enrichment and depth is marginally significant. Significant p-values are in bold print; df signifies degrees of freedom.

| Effects | Denominator | | F-value | p |
|-------------------------------------|--------------|-----|---------|------------------|
| | Numerator df | df | | |
| Month | 2 | 182 | 9.60 | 0.0001 |
| N enrichment | 3 | 171 | 35.42 | <.0001 |
| P enrichment | 1 | 171 | 15.26 | 0.0001 |
| N enrichment * P enrichment | 3 | 171 | 1.09 | 0.3530 |
| Depth | 8 | 706 | 17.90 | <.0001 |
| N enrichment * Depth | 24 | 706 | 2.04 | 0.0025 |
| P enrichment * Depth | 8 | 706 | 1.90 | 0.0572* |
| N enrichment * P enrichment * Depth | 24 | 706 | 0.73 | 0.8284 |

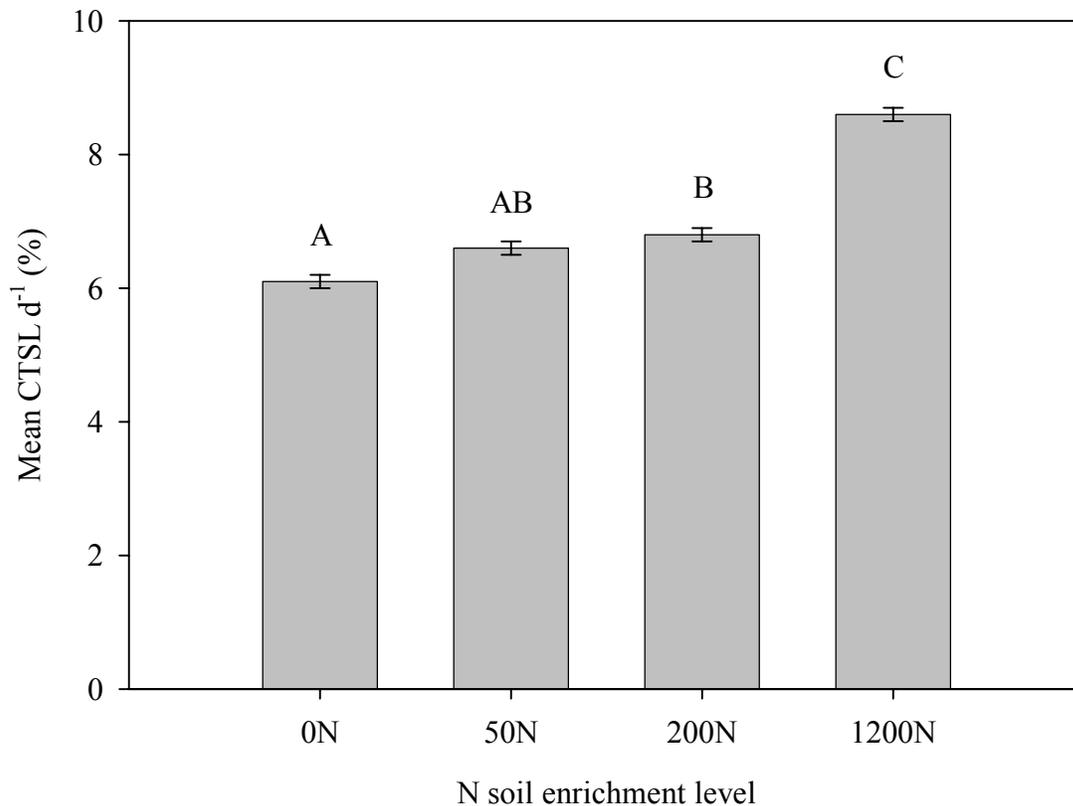


Fig. 1. The effects of nitrogen soil enrichment on the mean rates of cellulose decomposition (CTSL d⁻¹). Error bars are standard errors; different letters indicate significant differences among means ($p \leq 0.05$).

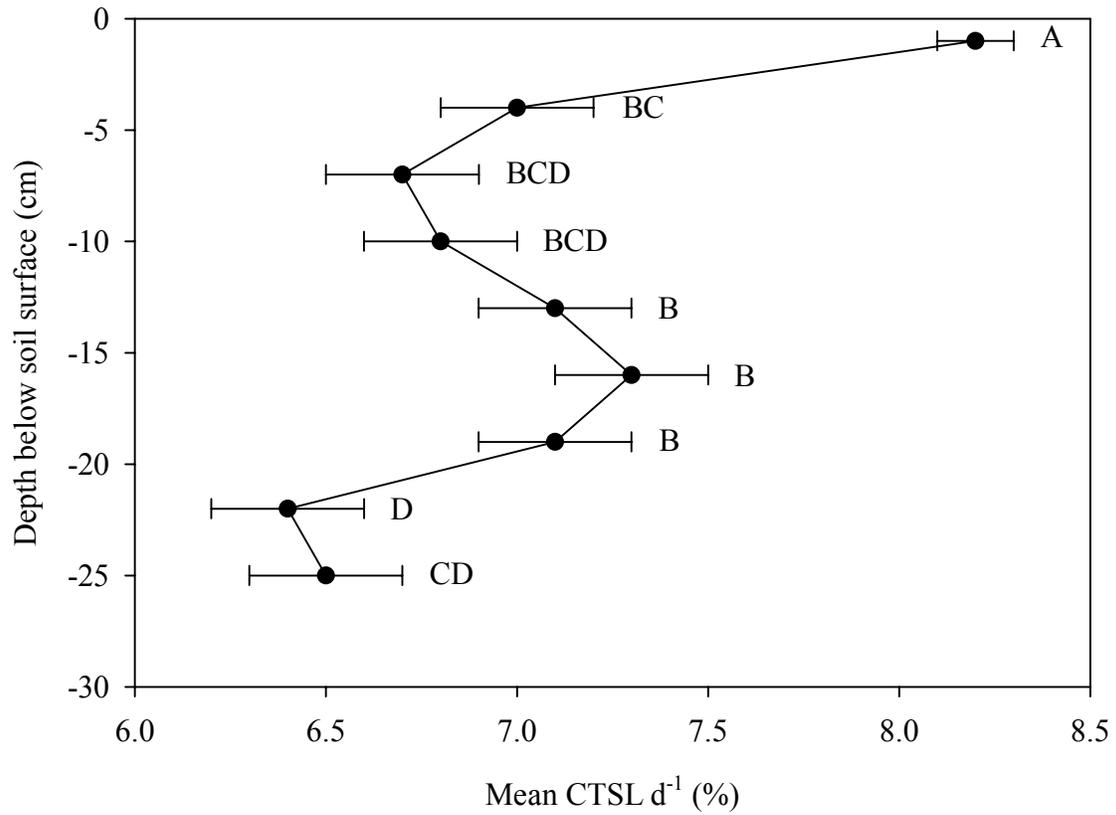


Fig. 2. The effects of depth below soil surface (cm) on the mean rate of cellulose decomposition (CTSL d⁻¹). Error bars are standard errors; different letters indicate significant differences among means ($p \leq 0.05$).

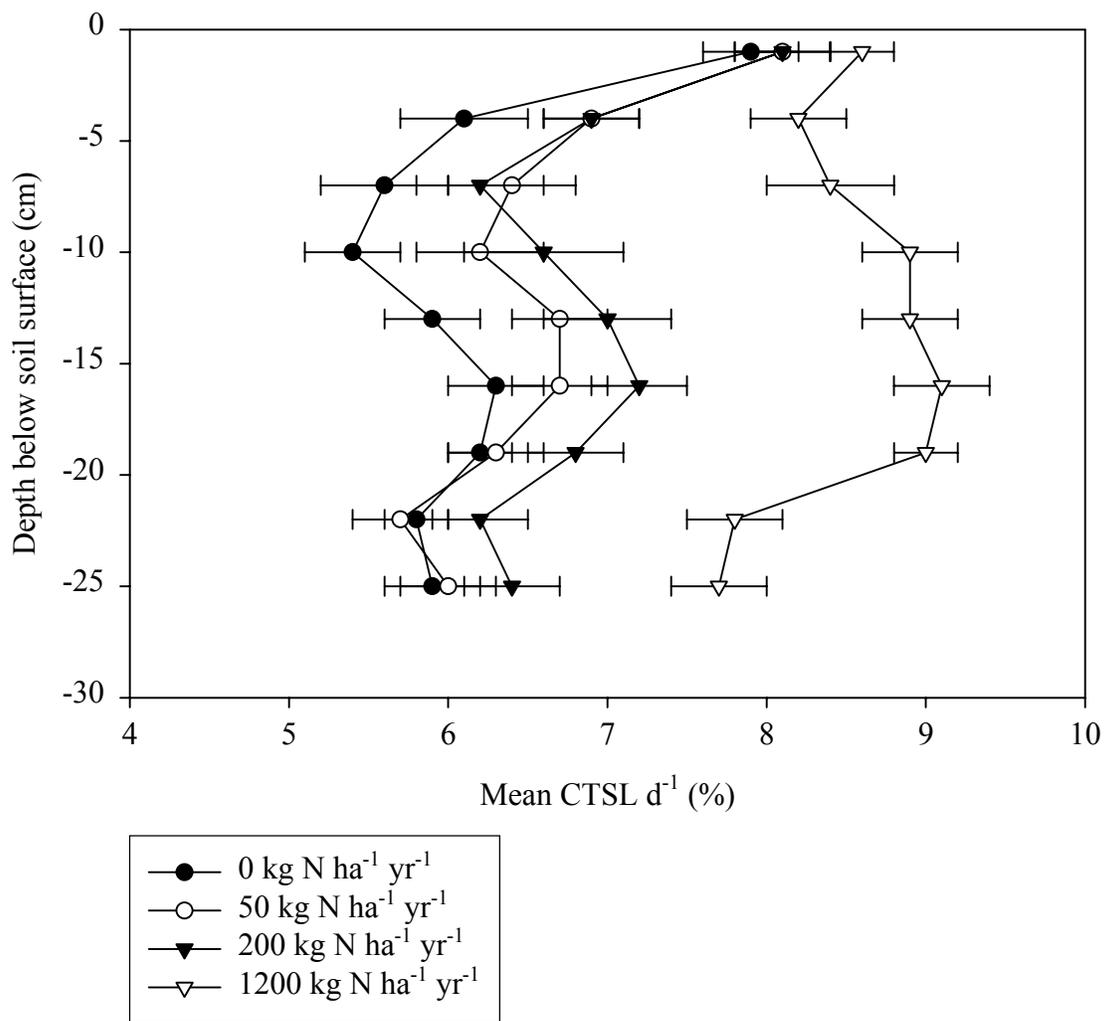


Fig. 3. The effects of depth below soil surface (cm) and nitrogen soil enrichment level on mean cellulose decomposition (CTSL d⁻¹). Values are means ± standard errors.

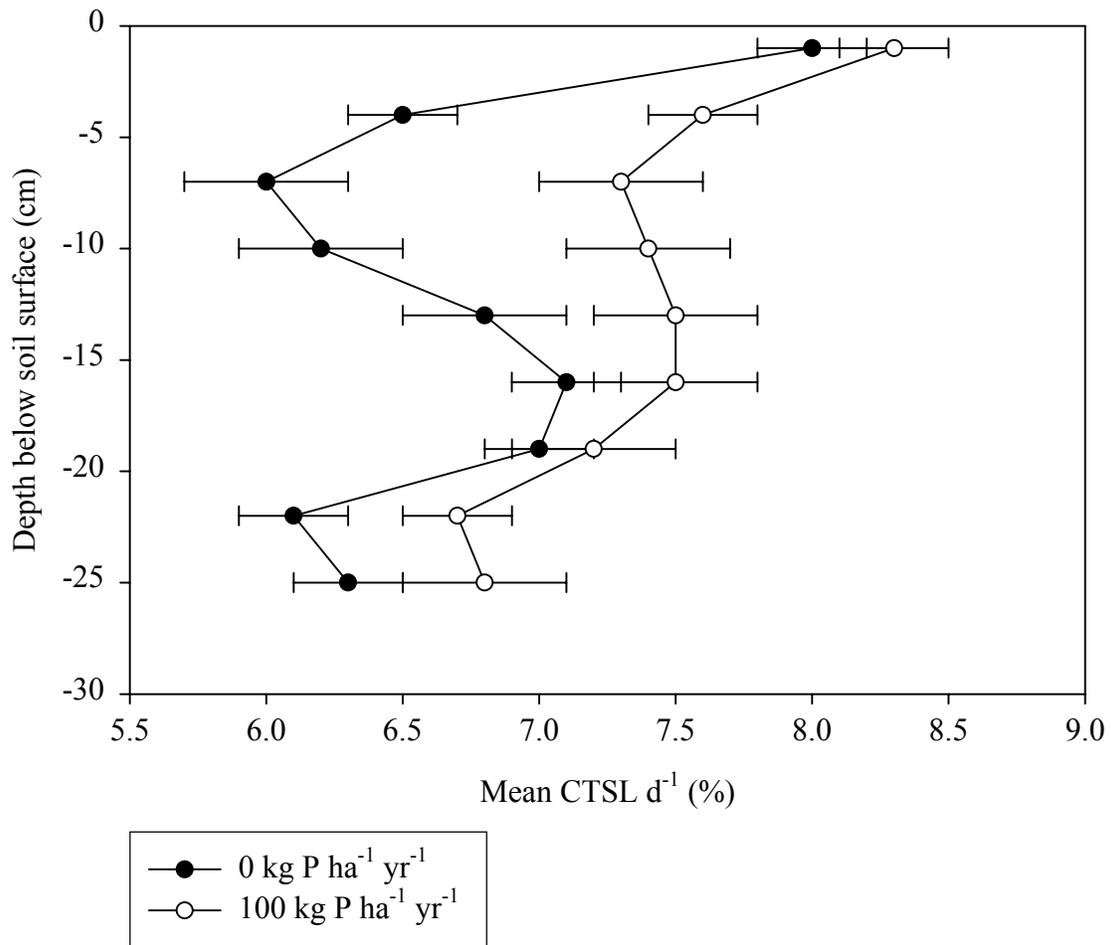


Fig. 4. The effects of depth below soil surface (cm) and phosphorus soil enrichment on mean cellulose decomposition (CTSL d⁻¹). Values are means ± standard errors.

with the addition of phosphorus at all depths; this effect was most apparent between 4 and 10 cm below the surface.

Decomposition of Plant Matter

Shoot Decomposition, Measured as Percent Mass Remaining

Nitrogen soil enrichments significantly affected the degradation of shoot tissue regardless of its tissue nutrient level (Table 2). Nitrogen soil enrichment significantly decreased aboveground percent mass remaining in some treatments ($p = 0.0179$) (Fig. 5).

Significantly more tissue remained in the litter bags at 50 kg N ha⁻¹ yr⁻¹ than at 1200 kg N ha⁻¹ yr⁻¹, while the mass remaining at the 0 kg N ha⁻¹ yr⁻¹ and 200 kg N ha⁻¹ yr⁻¹ treatment levels were not significantly different from those at the other N levels. Though phosphorus soil enrichment was not significant ($p = 0.4567$), the interaction of N and P soil enrichment was significant ($p = 0.0409$) (Fig. 6). At low nitrogen enrichment levels (0 and 50 kg N ha⁻¹ yr⁻¹), phosphorus enrichment had little, if any, effect on leaf decomposition, whereas at higher nitrogen loadings, P enrichment tended to increase decomposition. However, this interaction was not sufficiently strong to generate many significant differences among the N and P treatment-level combinations (Table 3).

In addition to the effects of soil enrichments, the nutrient quality of the litter tissue itself affected shoot tissue decomposition. The soil fertility level at which the shoot tissue grew had a highly significant ($p < 0.0001$) effect on shoot tissue % mass remaining. Shoot tissue that grew at medium soil fertility (200 kg N ha⁻¹ yr⁻¹ with 66 kg P ha⁻¹ yr⁻¹) had significantly lower percent mass remaining than either the control or highly enriched tissues (1200 kg N ha⁻¹ yr⁻¹ with 396 kg P ha⁻¹ yr⁻¹), which were similar to each other. Mean percent mass remaining for the medium shoot tissues was 19.69% (SE = 0.54%), while the mean for control tissue was 23.25% (SE = 0.74%) and that for highly enriched tissues was 22.43% (SE = 0.54%). The interaction between soil N enrichment level in the study plots and tissue nutrient level was also significant ($p = 0.0097$) (Fig. 7). At low nitrogen soil enrichment, the control tissue decomposed slower than the highly enriched tissue. However, at high nitrogen soil enrichment, this trend was reversed. Decomposition of shoot tissues grown in medium soil fertility did not significantly vary with nitrogen enrichment. These medium tissues also consistently had

Table 2: Analysis of variance illustrating the effects of nitrogen and phosphorus soil enrichment levels and the fertilization levels in which the shoots grew (tissue nutrient levels) on *Sagittaria lancifolia* shoot tissue decomposition (% mass remaining). Significant p-values are in bold print; df = degrees of freedom.

| Effects | Denominator | | F-value | p |
|--|--------------|------|---------|------------------|
| | Numerator df | df | | |
| N enrichment | 3 | 89 | 3.54 | 0.0179 |
| P enrichment | 1 | 88.9 | 0.56 | 0.4567 |
| N enrichment * P enrichment | 3 | 89 | 2.87 | 0.0409 |
| Tissue nutrient level | 2 | 88.9 | 13.19 | <.0001 |
| N enrichment * Tissue nutrient level | 6 | 88.9 | 3.03 | 0.0097 |
| P enrichment * Tissue nutrient level | 2 | 88.9 | 0.95 | 0.3889 |
| N enrich. * P enrich. * Tissue nutrients | 6 | 89 | 1.49 | 0.1919 |

Table 3. Tukey HSD analysis comparing shoot decomposition (% mass remaining) between the different N and P soil enrichment treatment combinations. Similar letters between treatment combinations indicate no significant difference between the combinations ($p \geq 0.05$).

| N enrichment | P enrichment | Letter Group |
|--------------|--------------|--------------|
| 0 | 0 | AB |
| 0 | 100 | AB |
| 50 | 0 | AB |
| 50 | 100 | A |
| 200 | 0 | A |
| 200 | 100 | AB |
| 1200 | 0 | AB |
| 1200 | 100 | B |

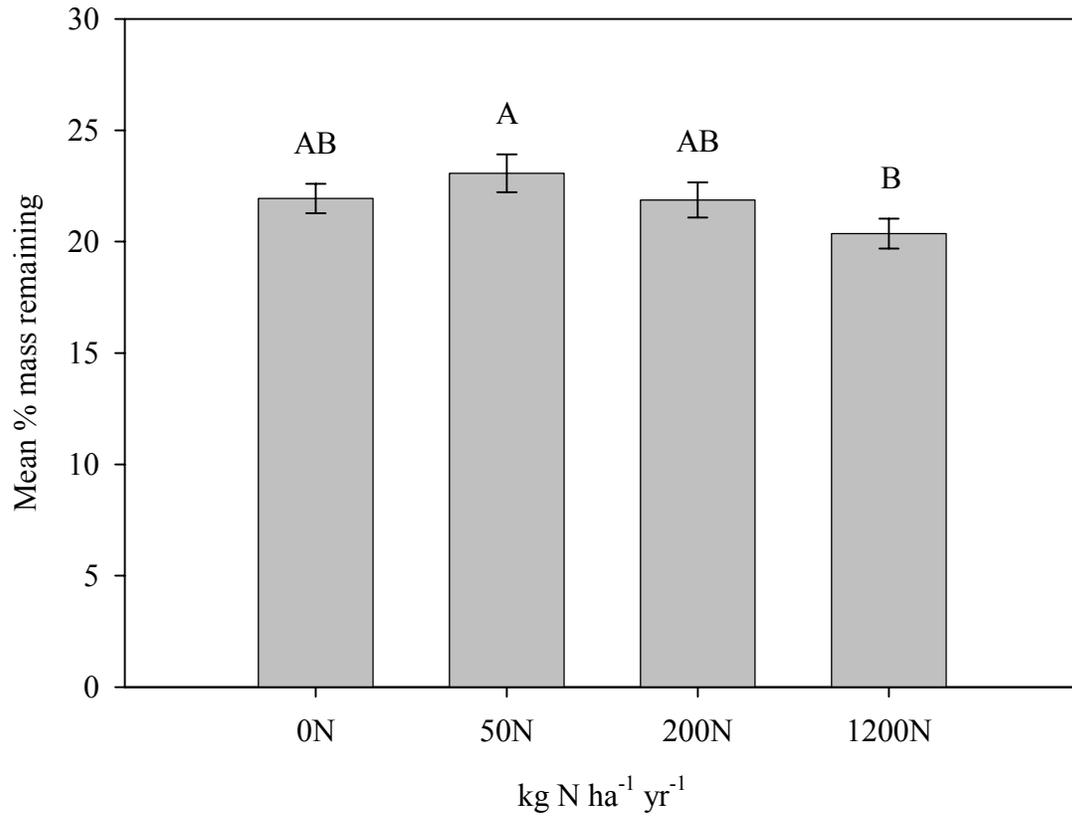


Fig. 5. The effects of soil N enrichment on the mean percent mass remaining of shoot tissue. Error bars are standard errors; different letters indicate significant differences among means ($p \leq 0.05$).

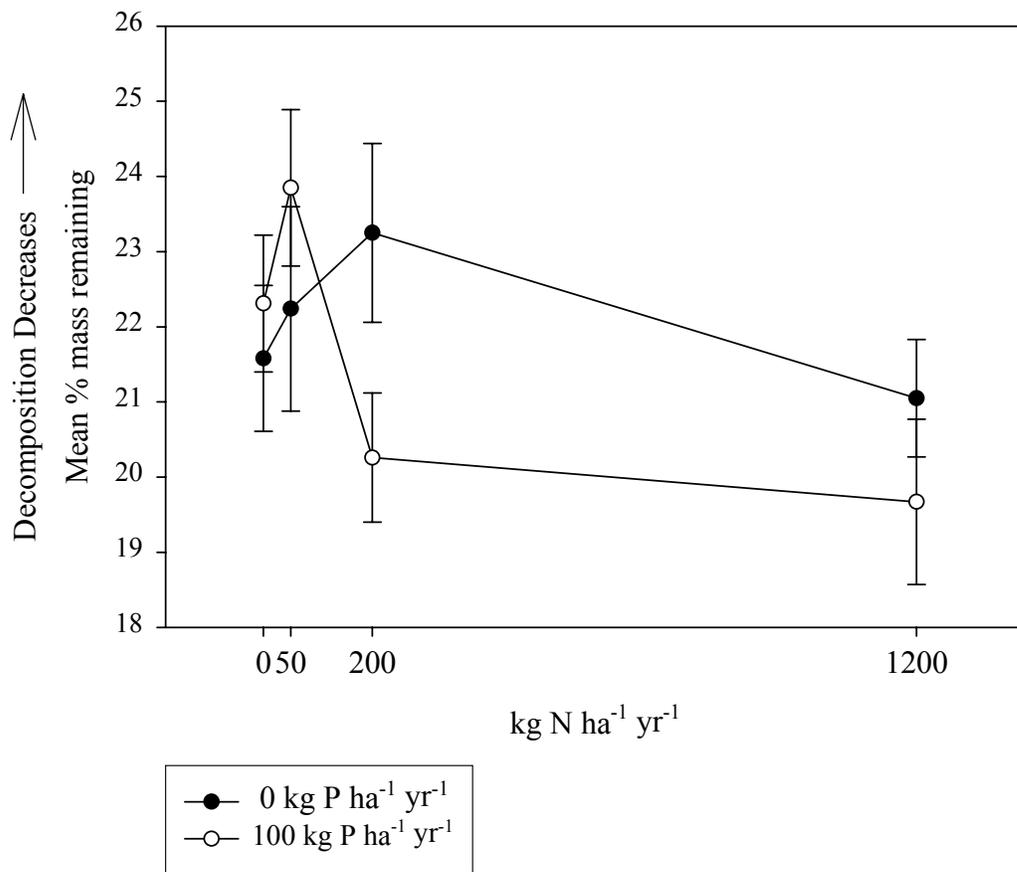


Fig. 6. The effects of nitrogen and phosphorus soil enrichments on the mean decomposition (% mass remaining) of shoot tissue. Decomposition is lower at higher values of percent mass remaining. Error bars are standard errors.

the lowest percent mass remaining, and therefore greatest decomposition, in all soil N enrichments.

Decomposition of Root Tissue

Nitrogen and phosphorus soil enrichments had different effects on root decomposition (Table 4), depending on the stage of decomposition. The rate for the initial, rapid phase of decomposition (b1) had a mean decomposition value of 0.1373 % per day (SE = 0.0225). Though the b1 rate was not significantly affected by soil N or P enrichments, it was affected by the interaction of the two ($p = 0.0069$) (Fig. 8). However,

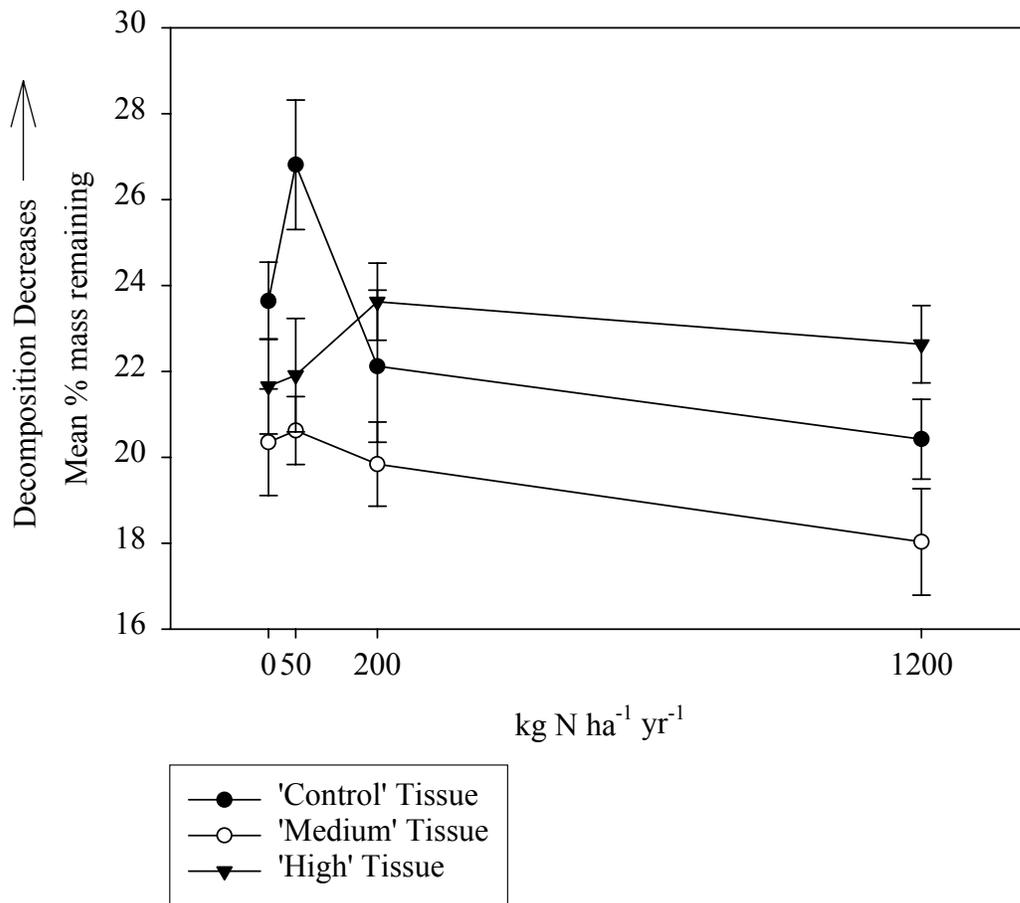


Fig. 7. The effects of soil N enrichment and the fertility levels in which the shoot tissues grew on the decomposition (% mass remaining) of shoot tissue. Control tissues were raised in non-fertilized plots, medium tissues were raised with 200 kg N ha⁻¹ yr⁻¹ and 66 kg P ha⁻¹ yr⁻¹ soil enrichment, and high tissues were raised with 1200 kg N ha⁻¹ yr⁻¹ and 396 kg P ha⁻¹ yr⁻¹ soil enrichment. Error bars are standard errors.

Tukey's Honest Significant Difference comparisons of lsmeans indicated no differences among treatment-level combinations. Unadjusted LSD comparisons indicated that the b1 rate was significantly higher with phosphorus enrichment at 50 and 200 kg N ha⁻¹ yr⁻¹. At 1200 kg N ha⁻¹ yr⁻¹, there was no significant difference with P addition. Interestingly, unadjusted LSD comparisons also indicated that under ambient nitrogen conditions (no N enrichment), the b1 rate of the rapid phase of decomposition was significantly greater in the absence of P enrichment. Overall, the addition of N without P tended to reduce decomposition rate from the control level and produced fairly uniform decomposition rates between the N enrichment levels. The addition of P at 0 kg N ha⁻¹ yr⁻¹ decreased the b1 decomposition rate, but at 50 and 200 kg N ha⁻¹ yr⁻¹ the addition of P increased the decomposition rate. In contrast, 0 and 100 kg P ha⁻¹ yr⁻¹ had similar, relatively low decomposition rates at 1200 kg N ha⁻¹ yr⁻¹.

The rate for the slower phase of decomposition (b2), which involved the more recalcitrant tissues, had a mean value of 0.0013 % per day (SE = 0.000053412). Unlike the faster b1 rate, b2 was not affected by N enrichment, P enrichment, or the interaction of N and P (all p > 0.05).

Summary of the Decomposition of Cotton Strips and Plant Tissues

Nitrogen and phosphorus soil enrichments affected the decomposition of the different tissues in several ways. Both N and P enrichments increased the decomposition of cotton strips, which were composed primarily of cellulose. Depth also significantly affected cellulose decomposition, as decomposition peaked at 1 cm depth and between 13 and 19 cm depth. Several factors affected shoot tissue decomposition; these were N

Table 4. Analysis of variance illustrating the effects of N and P soil enrichments and their interaction on the decomposition rates of *Sagittaria lancifolia* root tissue for the initial, rapid phase of decomposition and the later, slower phase of decomposition. Significant p-values are in bold print; df indicates degrees of freedom.

| Rate | Effects | Denominator | | F-value | p |
|---------------------|-----------------------------|--------------|----|---------|---------------|
| | | Numerator df | df | | |
| b1 (rapid phase) | N enrichment | 3 | 31 | 2.35 | 0.0918 |
| | P enrichment | 1 | 31 | 2.40 | 0.1318 |
| | N enrichment * P enrichment | 3 | 31 | 4.86 | 0.0069 |
| b2 (slow phase) | N enrichment | 3 | 28 | 0.47 | 0.7045 |
| | P enrichment | 1 | 28 | 0.07 | 0.7999 |
| | N enrichment * P enrichment | 3 | 28 | 1.88 | 0.1567 |

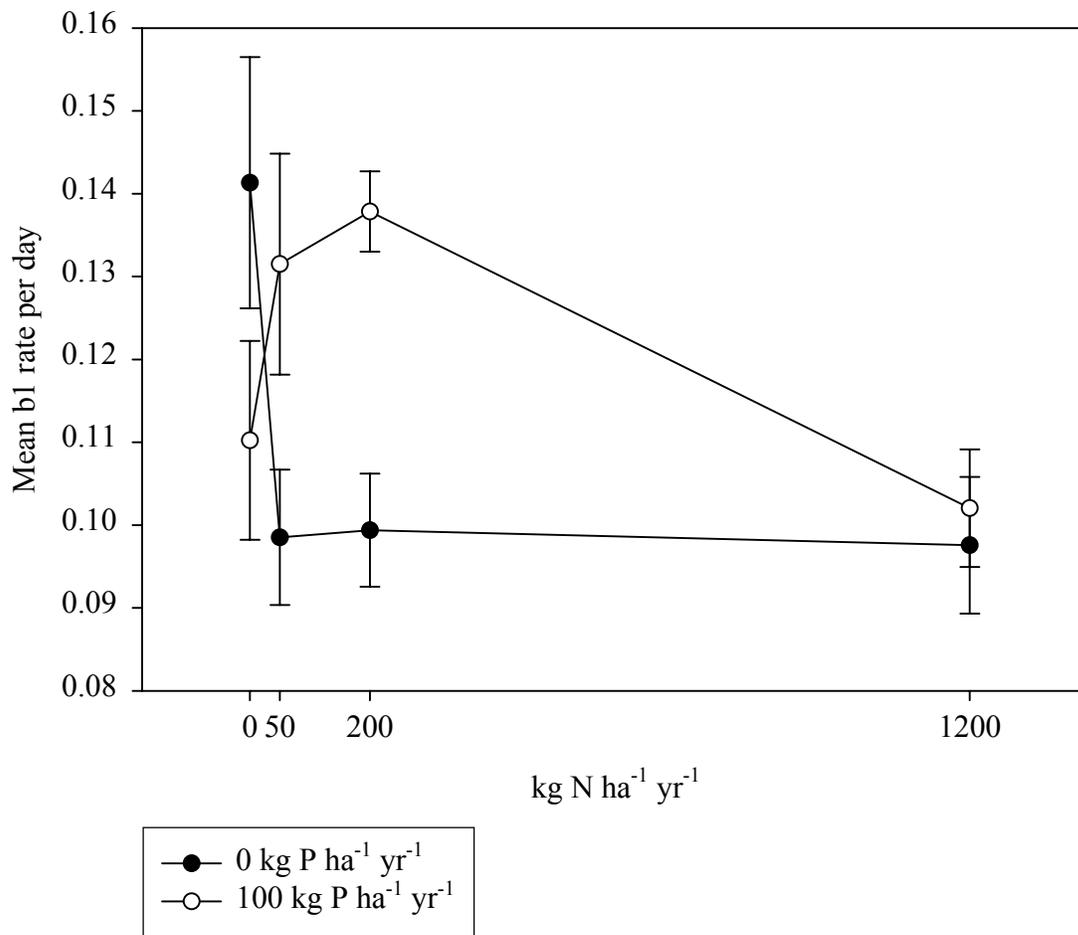


Fig. 8. The effect of N and P soil enrichments on the mean rates of decomposition (b1) for the initial, rapid decay phase. Values are means \pm standard errors.

enrichment, the interaction of the N and P enrichments, the soil fertility level under which the shoot tissues grew (tissue enrichment), and the interaction of the N soil enrichment and the tissue enrichment. N enrichment tended to increase shoot decomposition. For the N and P enrichments, tissues at 0 and 50 kg N ha⁻¹ yr⁻¹ decomposed slightly faster without additional P, while at 200 and 1200 kg N ha⁻¹ yr⁻¹ shoots decomposed faster with the addition of P. Among the tissue enrichments, the medium enrichment level tissues experienced the greatest amount of decomposition. This also held for the interaction of N soil enrichment and tissue enrichment; the medium enrichment tissues consistently decomposed to a greater extent than the control or highly enriched tissues. The interaction of the N and P soil enrichments affected the rapid phase of root decomposition, leading to differences in decomposition rates depending on the amount of each nutrient present in the system. Unlike the rapid phase of decomposition, the slow phase was not affected by N enrichment, P enrichment, or the interaction of the enrichments.

Interstitial Ammonium, Phosphate, pH, and Conductivity

In addition to influencing tissue decomposition, the soil nitrogen enrichment levels strongly affected interstitial NH₄-N content of water samples. Interstitial NH₄-N concentrations were significantly affected by N soil enrichment level ($p < 0.0001$) (Table 5 and Fig.9). Interstitial NH₄-N amounts were significantly higher at 1200 kg N ha⁻¹ yr⁻¹ than at all other nitrogen treatment levels. In addition, the 200 kg N ha⁻¹ yr⁻¹ application yielded significantly higher interstitial NH₄-N levels than the 0 kg N ha⁻¹ yr⁻¹ level. Sampling time also affected interstitial N ($p = 0.0002$), as NH₄-N levels were significantly lower in June 2003 (mean NH₄-N concentration = 17.48 ppm, SE = 4.33

Table 5: The effects of soil N enrichment, soil P enrichment, sampling date, and their interactions on interstitial $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$, pH, and conductivity. Values provided are p-values; NS indicates a non-significant effect ($p > 0.05$).

| Effects | $\text{NH}_4\text{-N}$ | $\text{PO}_4\text{-P}$ | pH | Conductivity |
|------------------------------|------------------------|------------------------|---------|--------------|
| N enrichment | <0.0001 | 0.0168 | <0.0001 | 0.0028 |
| P enrichment | NS | <0.0001 | NS | NS |
| N enrichment * P enrichment | NS | NS | NS | 0.0143 |
| Sampling date | 0.0002 | NS | <0.0001 | <0.0001 |
| N enrich. * date | NS | NS | NS | NS |
| P enrich. * date | NS | NS | NS | NS |
| N enrich. * P enrich. * date | NS | NS | NS | NS |

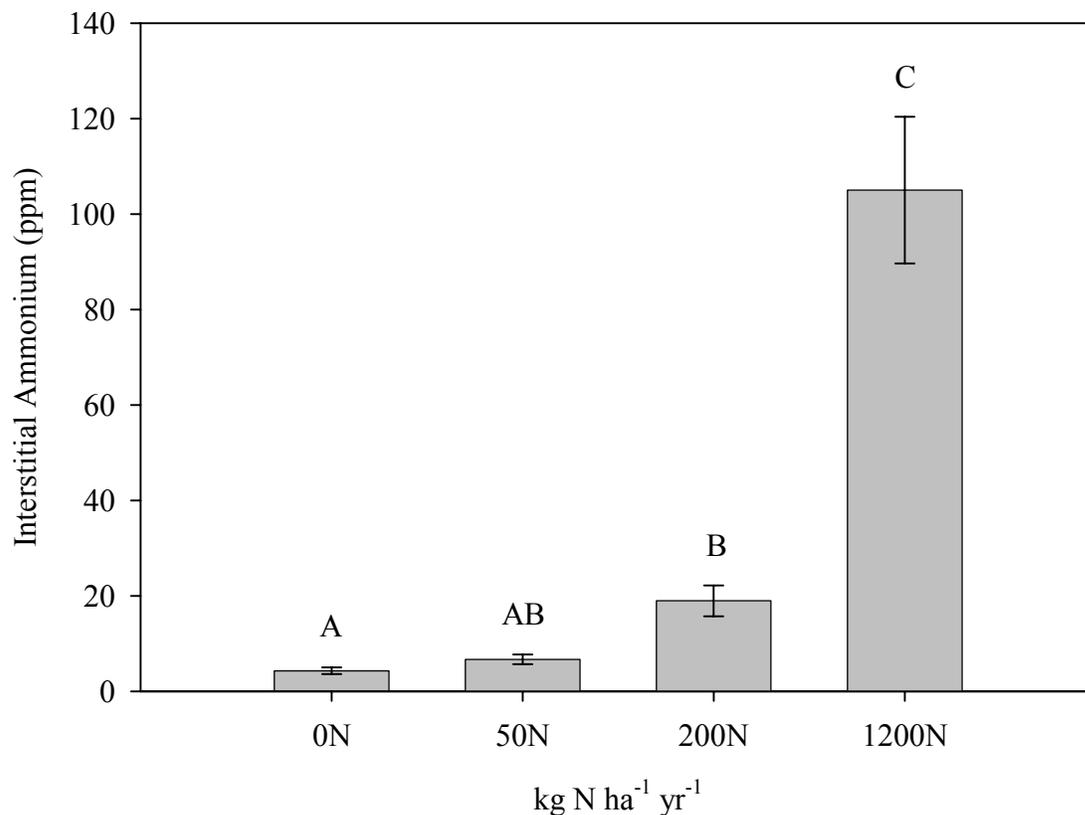


Fig. 9. The effect of soil N enrichment on the concentrations of $\text{NH}_4\text{-N}$ in interstitial water samples. Error bars are standard errors; different letters indicate significant differences among means ($p \leq 0.05$).

ppm) than in either June or July of 2002 (mean $\text{NH}_4\text{-N}$ concentrations = 41.10 ppm and 42.69 ppm, SE = 11.08 and 10.90, respectively).

Interstitial P was also affected by soil nutrient enrichments (Table 5). Soil P enrichment significantly affected interstitial $\text{PO}_4\text{-P}$ concentrations ($p < 0.0001$) (Fig. 10). The addition of $100 \text{ kg P ha}^{-1} \text{ yr}^{-1}$ yielded higher interstitial P concentrations than without added P. Interestingly, $\text{PO}_4\text{-P}$ was also significantly affected by soil N enrichment ($p = 0.0168$) (Fig. 11). Plots enriched with $1200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ had significantly greater interstitial $\text{PO}_4\text{-P}$ concentrations than plots that received 50 or $200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. Plots that were not enriched with nitrogen had similar concentrations of $\text{PO}_4\text{-P}$ to plots that received 50 or $200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. However, marginal significant differences existed between $\text{PO}_4\text{-P}$ concentrations in plots that did not receive nitrogen and plots that received $1200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ($p = 0.0604$).

Interstitial pH was significantly affected by soil N enrichment ($p < 0.0001$) (Table 5 and Fig. 12). The pH value for $1200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ was significantly higher than for the other N enrichment levels, which were similar to each other. Interstitial pH was also highly significantly affected by sampling time ($p < 0.0001$); the June 2002 samples had significantly higher pH values than samples from July 2002, October 2002, or June 2003 (Fig. 12). Interstitial pH was not significantly affected by soil P enrichment or the interactions of soil N and P enrichments and sampling date.

Conductivity was affected by the soil enrichments as well (Table 5). Interstitial conductivity was significantly affected by N enrichment ($p = 0.0028$) (Fig. 13); the conductivity for the $1200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ treatment was significantly higher than those at 0 and $50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. The interaction of N enrichment and P enrichment also affected

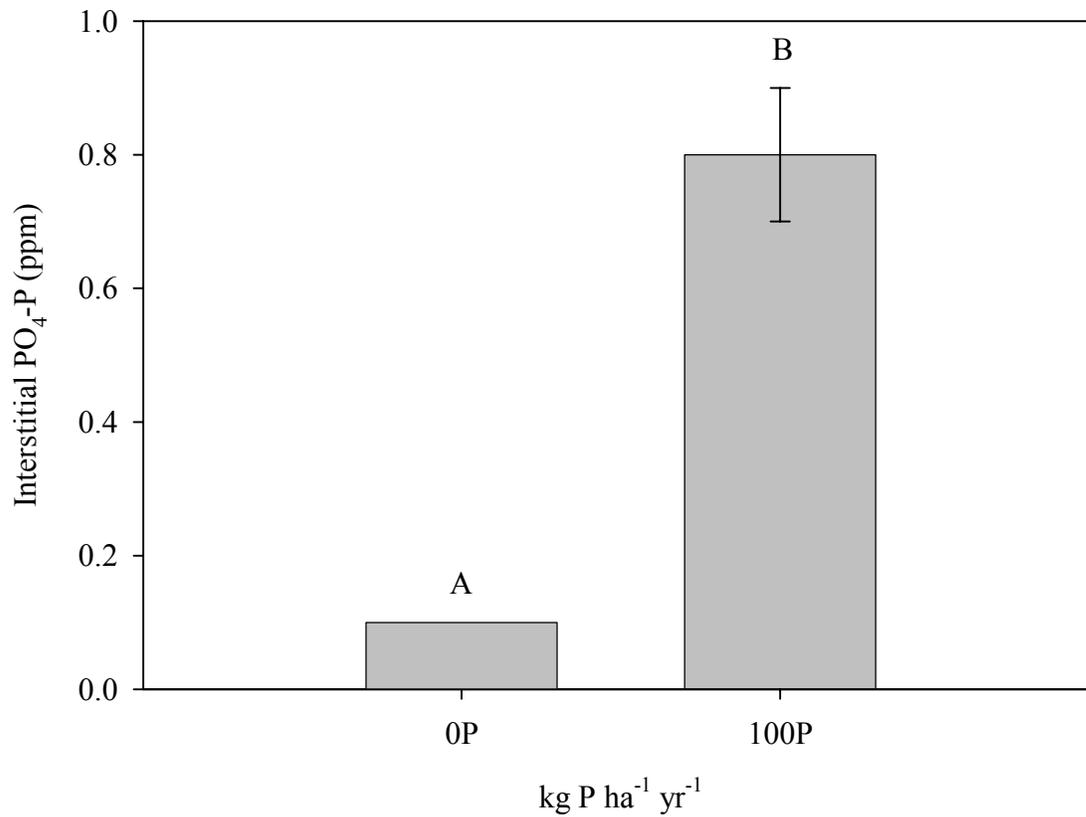


Fig. 10. The effects of soil P enrichment on the mean interstitial water PO₄-P concentrations. Error bars are standard errors; the standard error bar for the mean without P enrichment was negligible. Different letters indicate significant differences among means ($p \leq 0.05$).

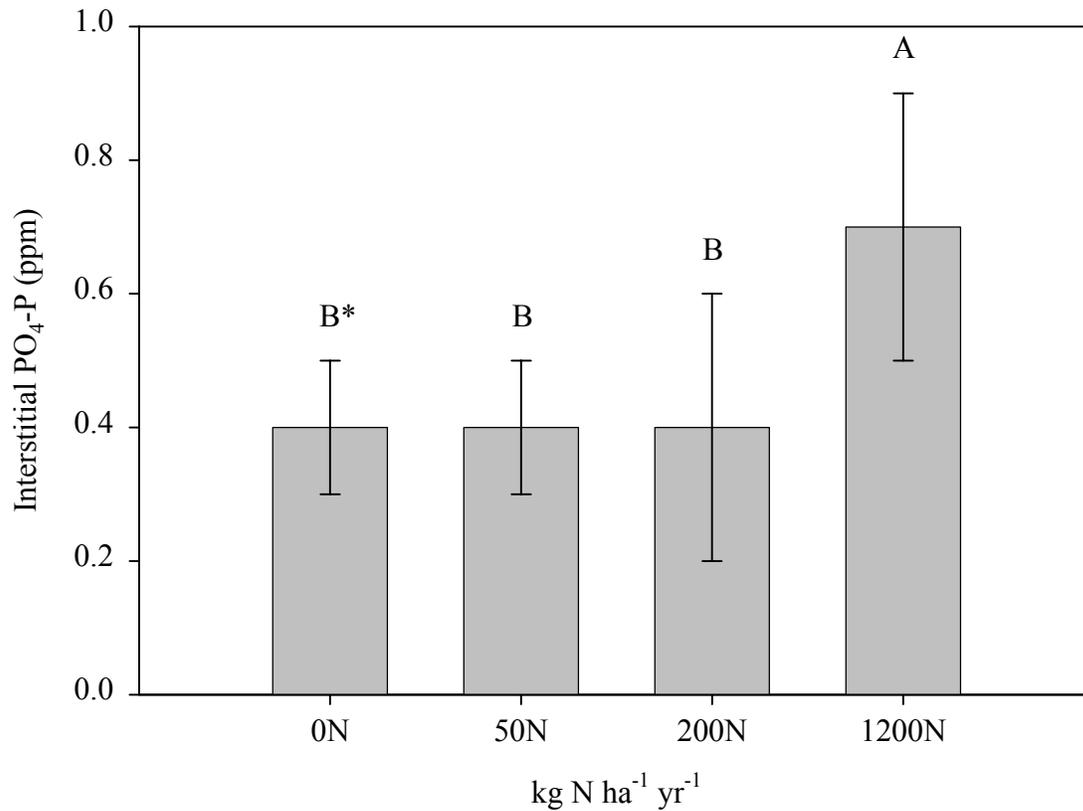


Fig. 11. The effects of soil N enrichment on mean interstitial water phosphate concentrations. B*: Phosphate concentrations in 0 kg N ha⁻¹ yr⁻¹ plots were significantly different from those in 1200 kg N ha⁻¹ yr⁻¹ plots at $p = 0.0604$. Error bars are standard errors; different letters indicate significant differences among means ($p \leq 0.05$).

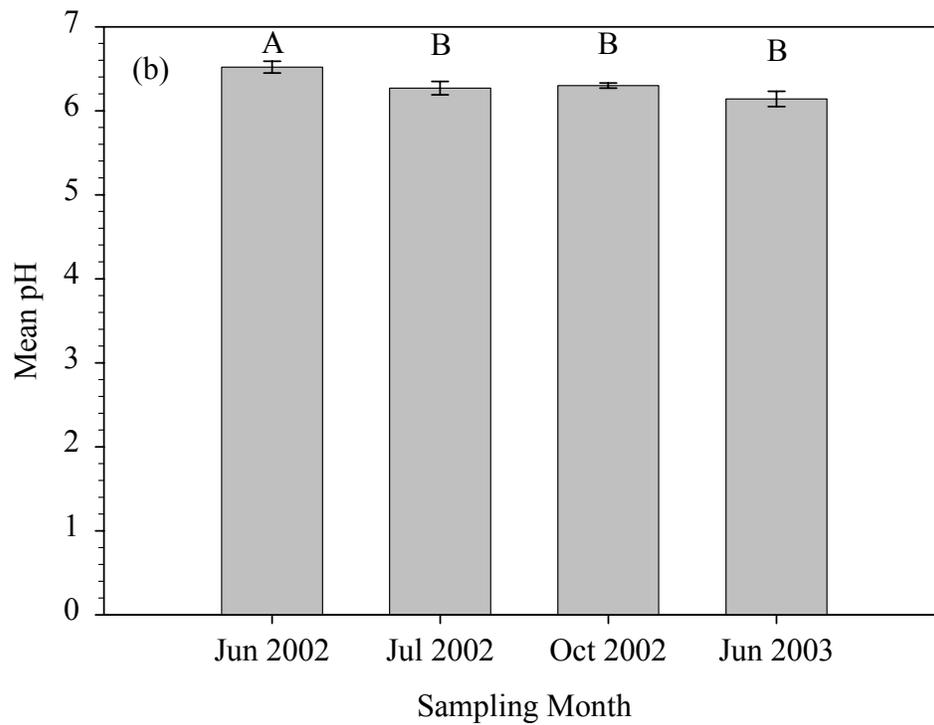
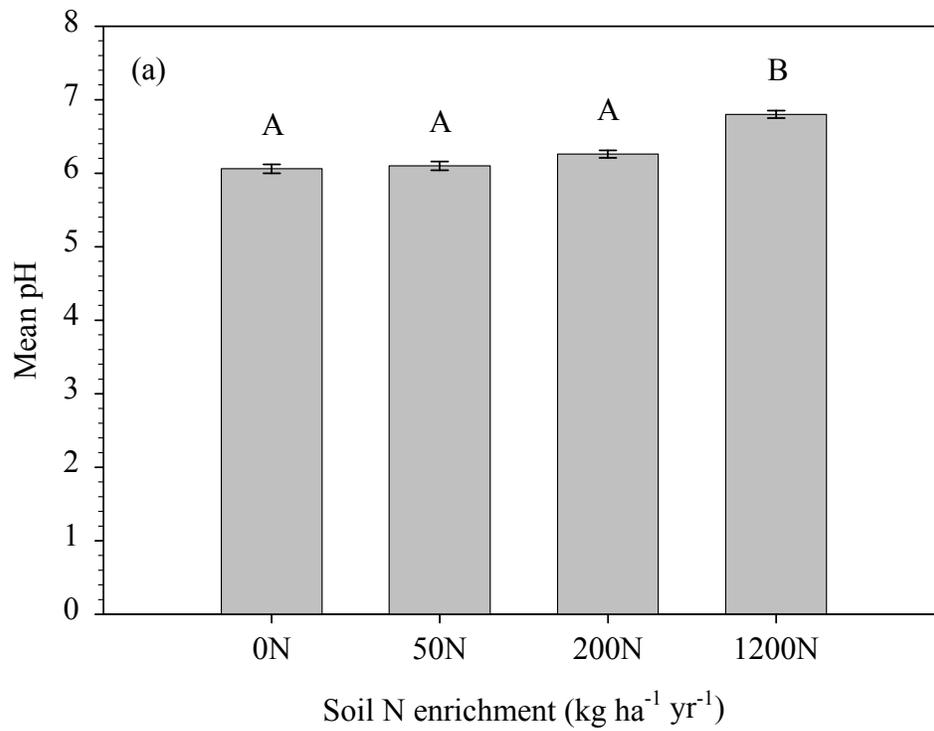


Fig. 12. The effects of (a) soil N enrichment and (b) sampling date on the mean pH of interstitial water. Error bars are standard errors; different letters indicate significant differences among means ($p \leq 0.05$).

conductivity ($p = 0.0143$) (Fig. 14). Lsmeans analysis of the N enrichment by P enrichment interaction indicated that $1200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ by $100 \text{ kg P ha}^{-1} \text{ yr}^{-1}$ had significantly higher conductivity levels than any of the other N by P treatment combinations except for $200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ by $100 \text{ kg P ha}^{-1} \text{ yr}^{-1}$, which was similar to all other treatment combinations. Further analysis of the N enrichment by P enrichment interaction revealed that the N by P effect was strongest during June 2002. Sampling time was highly significant ($p < 0.0001$) (Fig. 15); June and July 2002 conductivity results were similar to each other but higher than those for the other two sampling times. Neither October 2002 nor June 2003 was similar to any other sampling date.

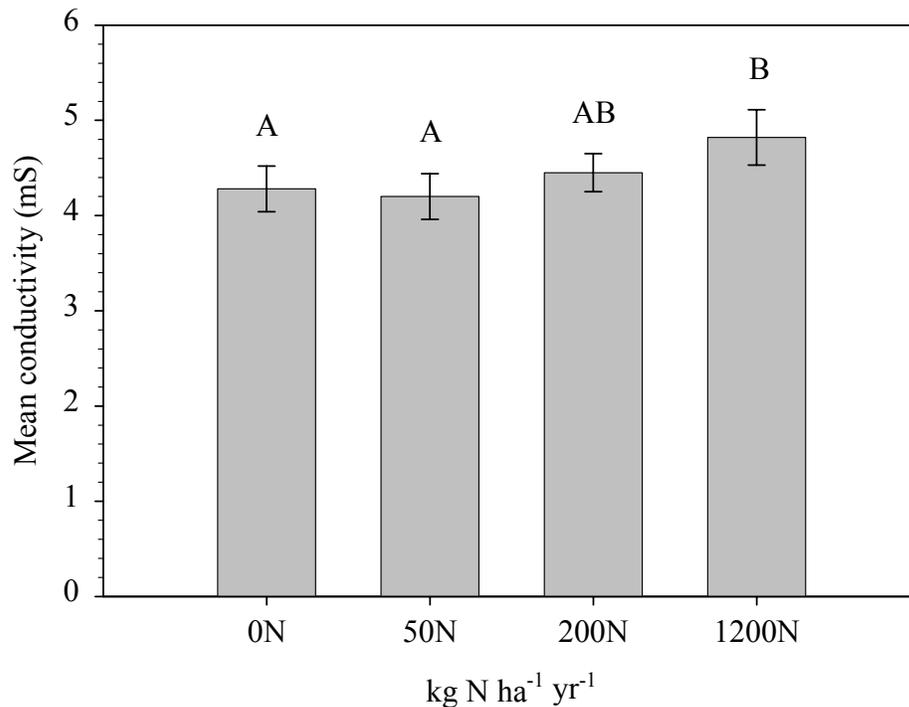


Fig. 13. The effect of soil N enrichment on mean conductivity in milli-Siemens (mS) of interstitial water. Error bars are standard errors; different letters indicate significant differences among means ($p \leq 0.05$).

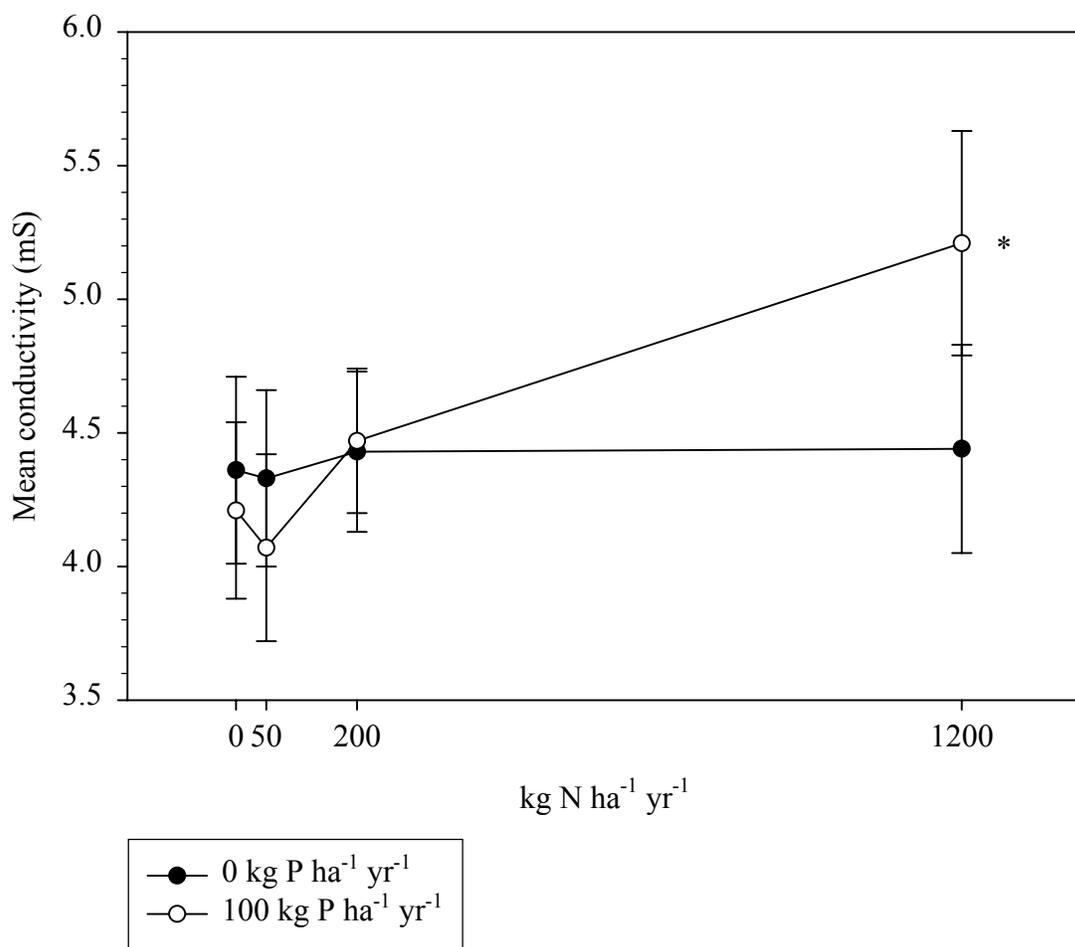


Fig. 14. The effects of N and P soil enrichment on the mean conductivity (mS) of interstitial water. *: Conductivity values in the treatment combination of 1200 kg N ha⁻¹ yr⁻¹ and 100 kg P ha⁻¹ yr⁻¹ were significantly higher than those for all other treatment combinations except for 200 kg N ha⁻¹ yr⁻¹ by 100 kg P ha⁻¹ yr⁻¹. Values are means ± standard errors.

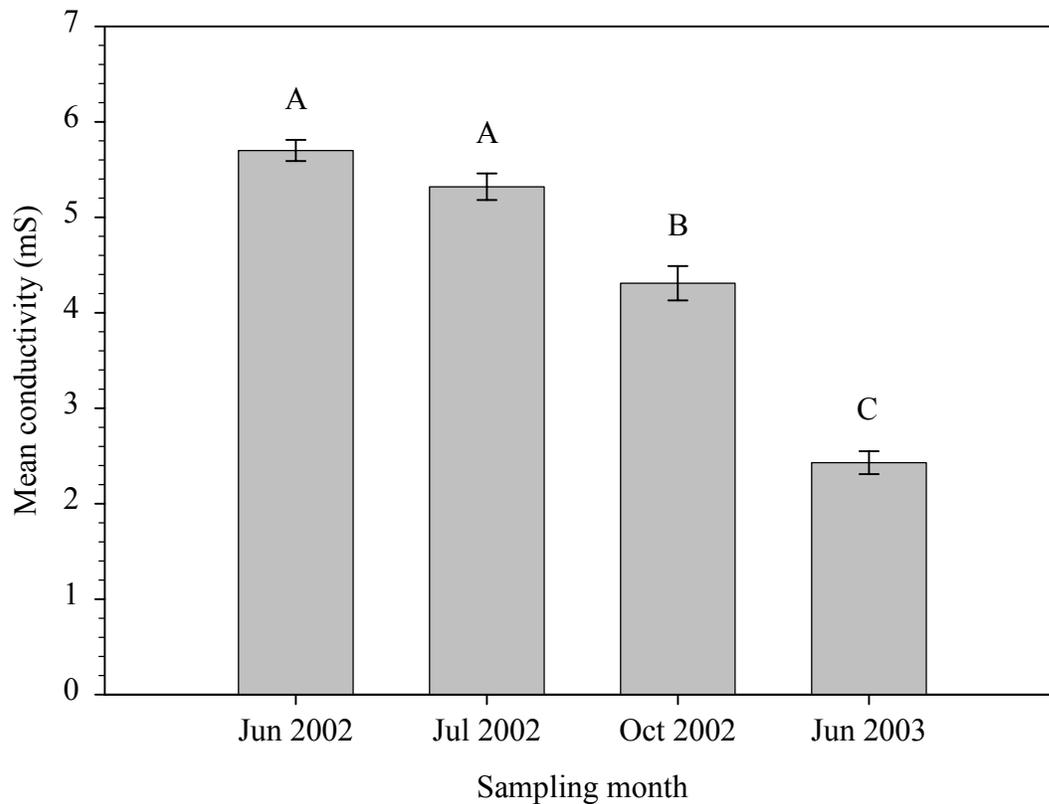


Fig. 15. The effect of sampling date on the mean conductivity (mS) of interstitial water. Error bars are standard errors; different letters indicate significant differences among means ($p \leq 0.05$).

Relationship between Cotton Strip Decomposition (CTSL d^{-1}) and Interstitial Variables

A stepwise multiple regression with forward selection of CTSL d^{-1} by interstitial NH_4-N , PO_4-P , pH, and conductivity indicated that pH and NH_4-N had the strongest effects on CTSL d^{-1} (Table 6). Interstitial pH was the strongest and first variable that entered the model ($p < 0.0001$) (Fig. 16). Interstitial N was the second and only other significant variable in the model ($p = 0.0453$) (Fig. 16), though PO_4-P also entered the model. I included sampling month as a variable in another regression because cotton strip measurements were taken at multiple times. In addition to identical results for pH and interstitial NH_4-N , this multiple regression indicated conductivity as a significant

variable ($p = 0.0169$). Correlation analyses revealed that CTSL d^{-1} was significantly correlated with pH ($r = 0.46182$, $p < 0.0001$) and interstitial NH_4-N ($r = 0.42676$, $p < 0.0001$), and also correlated with conductivity ($r = 0.21876$, $p = 0.0164$). Certain interstitial variables correlated with each other, such as conductivity and pH ($r = 0.34258$, $p = 0.0001$) and conductivity and interstitial NH_4-N ($r = 0.47798$, $p < 0.0001$). In addition, pH correlated with interstitial NH_4-N ($r = 0.65823$, $p < 0.0001$) and to a lesser degree with interstitial PO_4-P ($r = 0.27751$, $p = 0.0022$). Interstitial NH_4-N and PO_4-P also correlated ($r = 0.27331$, $p = 0.0025$).

Table 6. Multiple regression using forward selection relating cellulose decomposition (CTSL d^{-1}) to interstitial water characteristics. Coefficients of determination (R^2) and the significance (p) for each water characteristic entering the model are included.

| Variable Entered | Partial R^2 | Model R^2 | F-value | p |
|------------------|---------------|-------------|---------|------------------|
| pH | 0.2133 | 0.2133 | 31.99 | <.0001 |
| Ammonium | 0.0266 | 0.2399 | 4.09 | 0.0453 |
| Phosphate | 0.0071 | 0.2469 | 1.09 | 0.2993 |

Relationship between Litter Decomposition and Interstitial Factors

The decomposition of root tissues and shoot tissues associated differently with the interstitial water characteristics in the multiple regressions and correlations. None of the interstitial variables related significantly to root decomposition rates. For the rates (b1) in the more rapid phase of decomposition, interstitial ammonium accounted for the greatest percentage of the variability in root decomposition, though its p-value was not significant ($p = 0.1310$) and it had a low partial R^2 value ($R^2 = 0.0606$). Correlation analysis did not reveal any interstitial variables significantly correlated with b1 root decomposition rates.

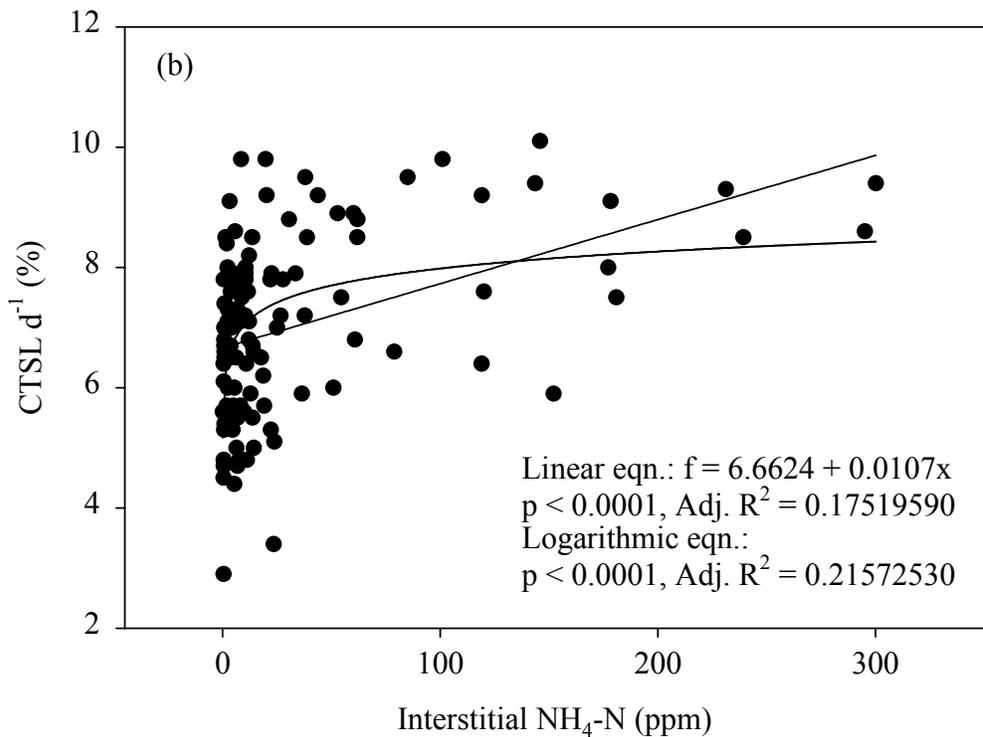
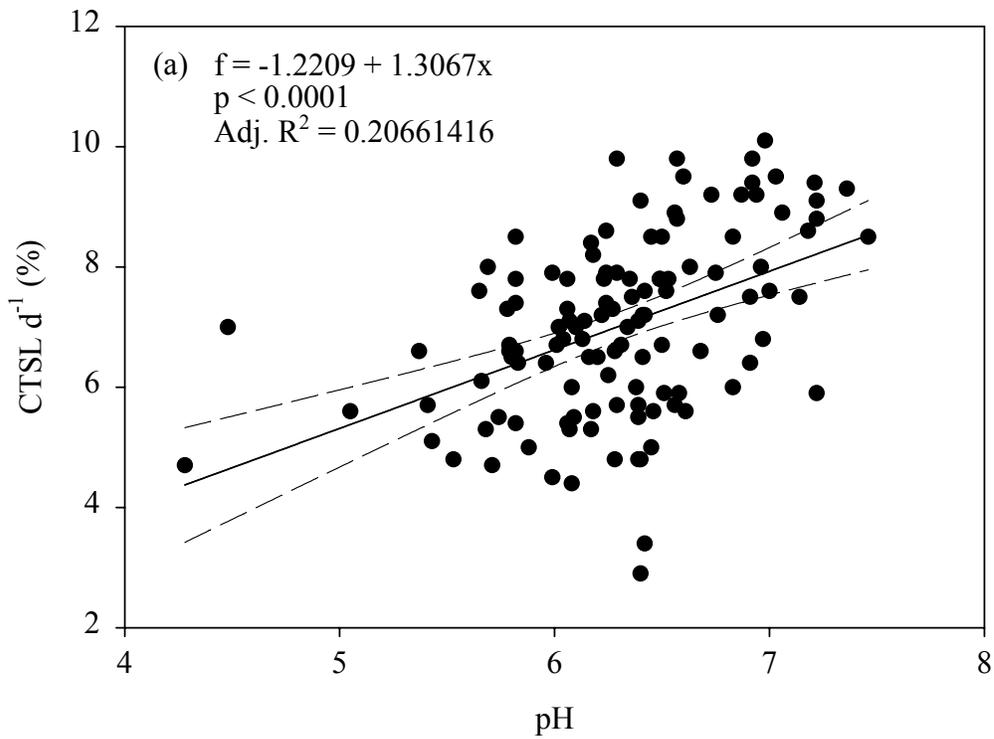


Fig. 16. The relationships between (a) pH and (b) interstitial ammonium and cellulose decomposition (CTSL d^{-1}). Equations of the simple linear regression lines are included, as are p-values and coefficients of determination (adjusted R^2). Confidence intervals set at 95%.

However, conductivity and pH positively correlated with interstitial $\text{NH}_4\text{-N}$ ($r = 0.51841$, $p = 0.0007$ and $r = 0.60918$, $p < 0.0001$, respectively). In addition, the pH variable and the interstitial P variable were positively correlated at $p = 0.0613$ ($r = 0.30241$).

Interestingly, the slower rates for the decomposition phase involving more recalcitrant tissues (b2), was significantly related to pH (partial $R^2 = 0.1046$, $p = 0.0417$) and interstitial $\text{NH}_4\text{-N}$ (partial $R^2 = 0.1231$, $p = 0.0202$) in the multiple regression. However, in the correlation analysis b2 correlated positively with pH ($r = 0.32347$, $p = 0.0417$) but not with interstitial $\text{NH}_4\text{-N}$ ($r = -0.08125$, $p = 0.6182$).

Shoot decomposition also varied with interstitial parameters. An ANCOVA analysis indicated that the slopes for the regression of each tissue enrichment type (control, moderately enriched, or highly enriched) with pH were similar to each other. As such, the tissue types did not need to be analyzed separately for the effects of pH. Regressing the percent mass remaining for the control, moderately enriched, and highly enriched shoot tissues together with interstitial factors showed a significant relationship between pH and decomposition ($R^2 = 0.1276$, $p < 0.0001$), but no other interstitial factors related to decomposition (Table 7). Similarly, percent mass remaining for all tissue types correlated only with pH ($r = -0.35726$, $p < 0.0001$) (Fig. 17). Conductivity and pH positively correlated with interstitial $\text{NH}_4\text{-N}$ ($r = 0.51783$, $r = 0.60900$, respectively, and $p < 0.0001$ for both). A significant positive correlation also existed between pH and interstitial $\text{PO}_4\text{-P}$ ($r = 0.30378$, $p = 0.0007$).

The multiple regression of control shoot tissue by the interstitial variables revealed no further relationships between shoot tissue % mass remaining and the interstitial variables. As in the root analyses and the overall shoot analysis, interstitial

Table 7. Multiple regression using forward selection relating interstitial water characteristics to the decomposition of control, moderately enriched, and highly enriched shoot tissues (% mass remaining). The table includes the significance (p) and the coefficient of variation (R^2) for each interstitial water characteristic that entered the model.

| Variable Entered | Partial R^2 | Model R^2 | F-value | p |
|------------------|---------------|-------------|---------|--------|
| pH | 0.1276 | 0.1276 | 16.97 | <.0001 |
| Conductivity | 0.0122 | 0.1398 | 1.63 | 0.2046 |

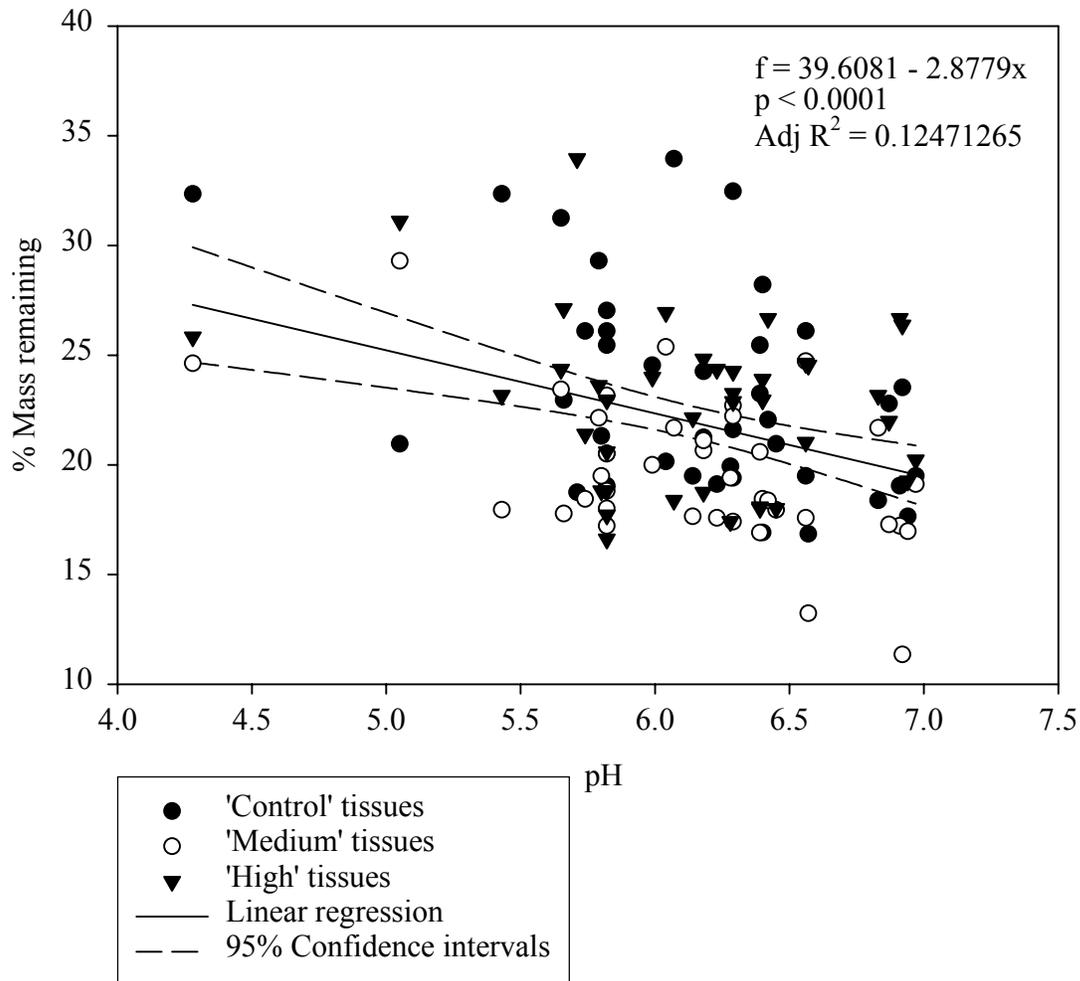


Fig. 17. The relationship between interstitial pH and the decomposition (% mass remaining) of shoot tissues. Decomposition rates are slower at higher percent mass remaining values. The equation of the simple linear regression is included, as are the p-value and coefficient of determination (adjusted R^2). Confidence intervals set at 95%.

conductivity and pH correlated positively with interstitial NH₄-N ($r = 0.51783$, $p = 0.0006$ and $r = 0.60900$, $p < 0.0001$), while pH also correlated positively with interstitial PO₄-P at $p = 0.0567$ ($r = 0.30378$). These relationships between interstitial variables were present with the control as well as the moderately and highly-enriched shoot tissue analyses.

Tissues that grew in the medium soil fertility level (200 kg N ha⁻¹ yr⁻¹ by 66 kg P ha⁻¹ yr⁻¹) behaved somewhat similarly to the control tissues. As with the control tissues, no additional interstitial variables were significantly related to percent mass remaining in the multiple regression. However, correlation analysis indicated that interstitial NH₄-N negatively correlated with percent mass remaining of medium tissues ($r = -0.38227$, $p = 0.0179$) (Fig. 18).

Highly enriched shoot tissue regressed by interstitial variables exhibited different results than control and medium tissues. Neither of the interstitial variables that entered the multiple regression model was significant; the closest was conductivity ($p = 0.0772$) (Table 8). No interstitial factors significantly correlated with the percent mass remaining of highly enriched shoot tissues.

Table 8. Multiple regression using forward selection relating interstitial water characteristics to the decomposition (% mass remaining) of highly enriched shoot tissue. The table includes the significance to the model (p) and the coefficient of variation (R^2) for each interstitial characteristic that entered the model.

| Variable Entered | Partial R^2 | Model R^2 | F-value | p |
|------------------|---------------|-------------|---------|--------|
| Conductivity | 0.0799 | 0.0799 | 3.30 | 0.0772 |
| pH | 0.0420 | 0.1219 | 1.77 | 0.1916 |

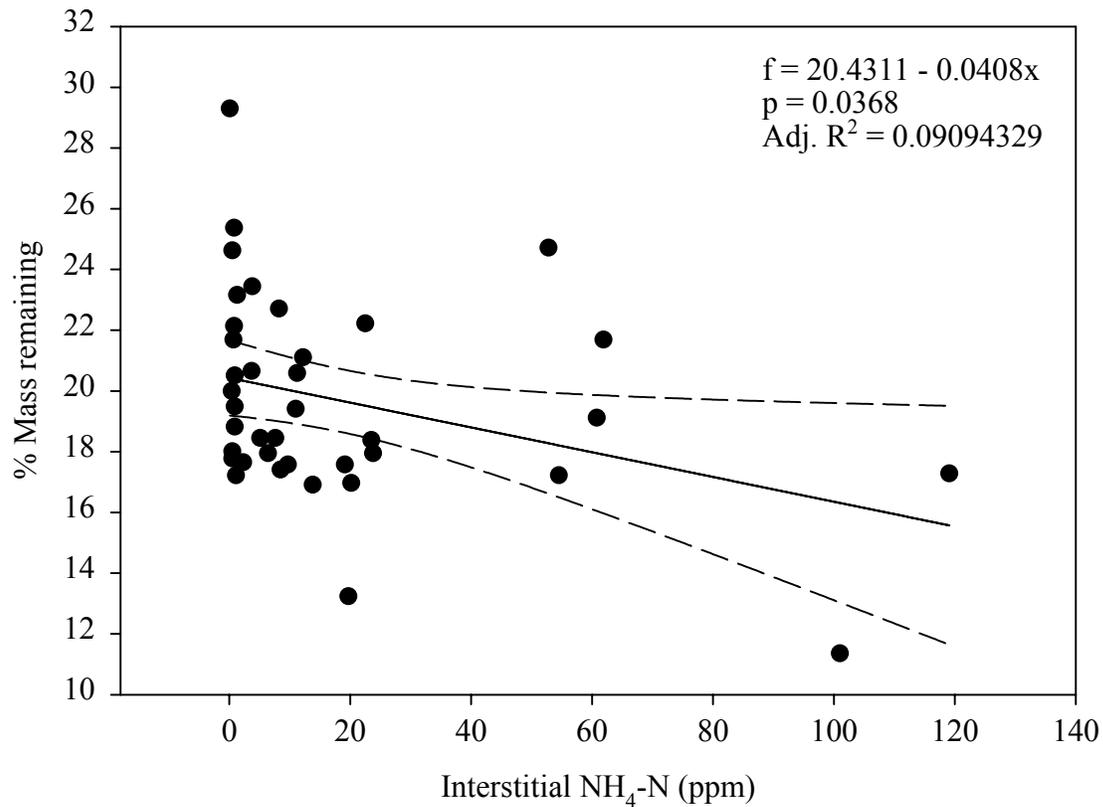


Fig. 18. The relationship of interstitial water ammonium concentration to the decomposition (% mass remaining) of moderately enriched shoot tissue. The rate of decomposition is lower at higher values of % mass remaining. The equation is that for the simple linear regression; the p-value and adjusted coefficient of determination (R^2) are also included. Confidence intervals set at 95%.

Redox

Soil N enrichment and sampling date had significant effects on soil redox potential (both at $p < 0.0001$). Soil Eh was less reducing at 50 kg N ha⁻¹ yr⁻¹ than the other N enrichment levels. The most strongly reducing conditions (most negative mean redox) existed at 1200 kg N ha⁻¹ yr⁻¹ (Fig. 19). Reducing conditions were weakest on July 3 and August 15, 2003 (Fig. 20). The strongest mean reducing conditions existed on August 1, 2003 (Fig. 20).

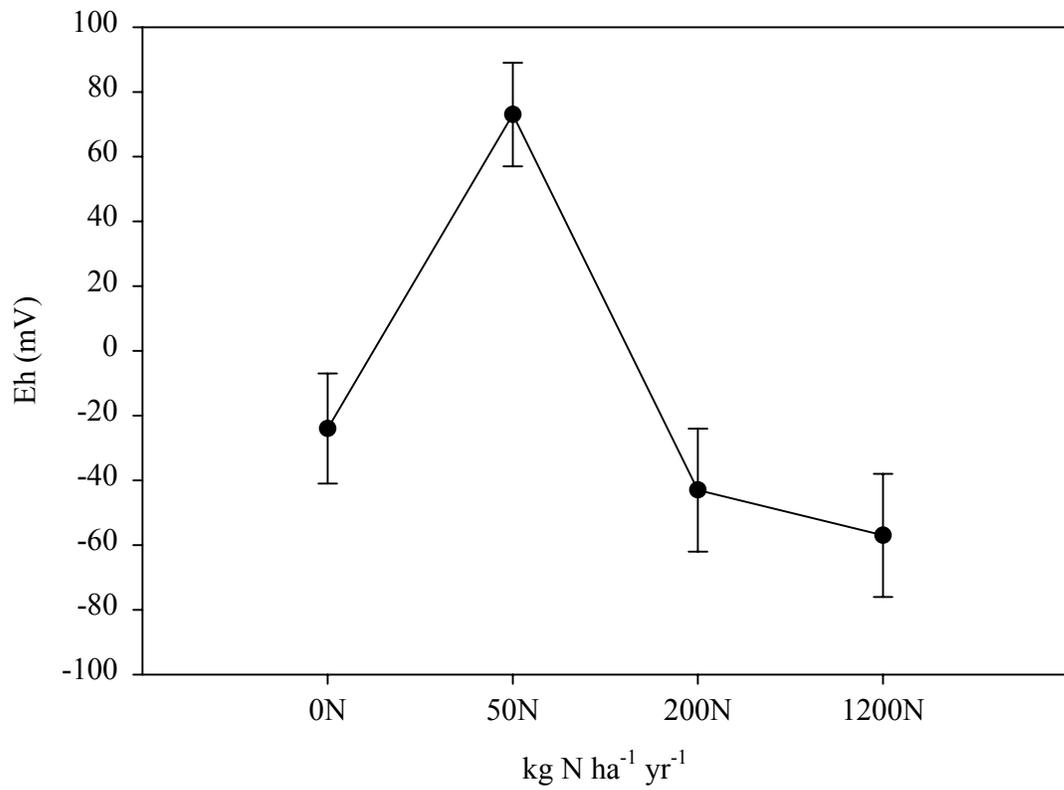


Fig. 19. The effects of soil N enrichment on mean Eh. Values are means \pm standard errors.

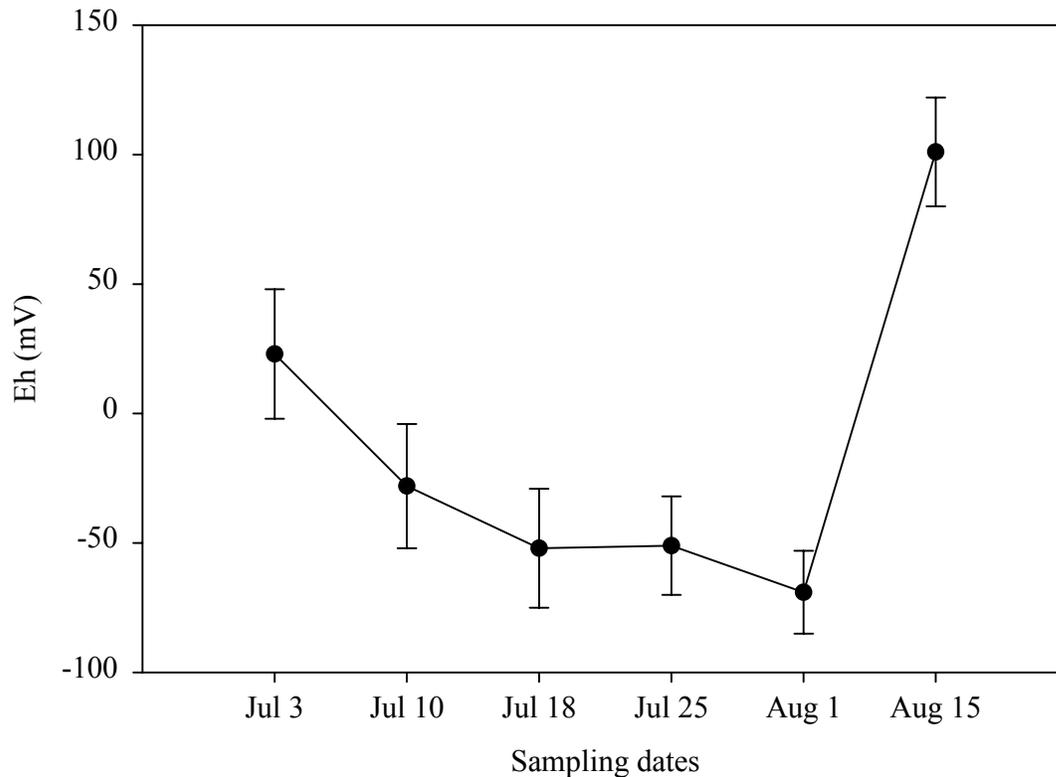


Fig. 20. The effect of sampling date on mean Eh. All sampling occurred in Summer 2003. Values are means \pm standard errors.

Temperature

The average temperature at 15 cm below soil surface during the 2002 growing season (May - August 2002) was 25°C, and measurements ranged between 23 and 27°C. The average temperature for the 2003 growing season (May - September 2003) was again 25°C with measurements ranging between 23 and 27°C. Cotton strips were in the field from June 12 to June 21, 2002, July 24 to August 2, 2002, and June 24 to July 3, 2003. All three sets of strips experienced similar belowground temperatures, as the average temperatures for each test period were 26°C, 25°C, and 25°C, respectively.

Chemical Composition of Litter Material

C and N Content of Tissues

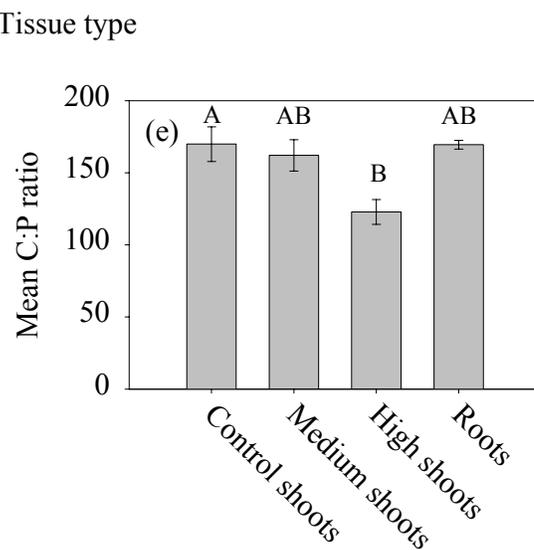
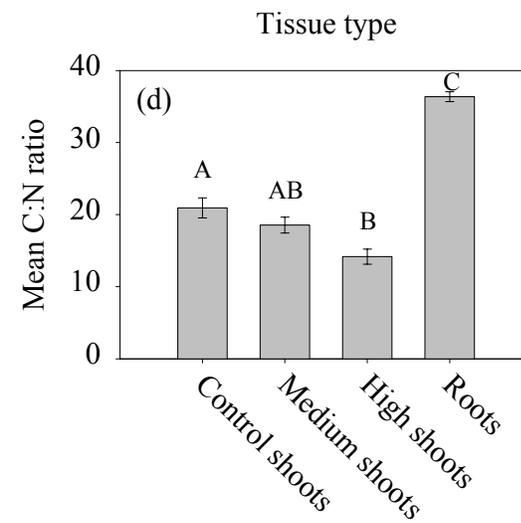
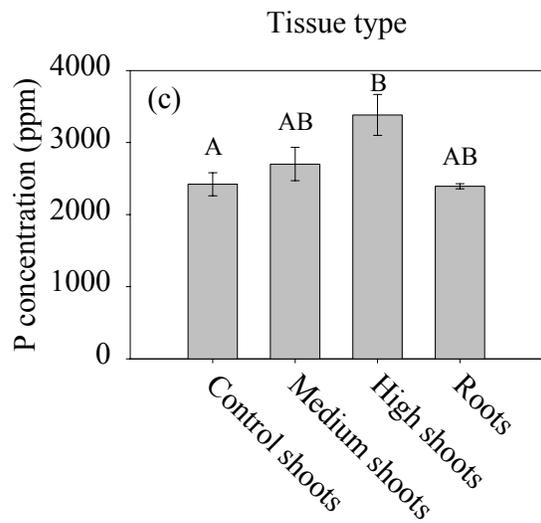
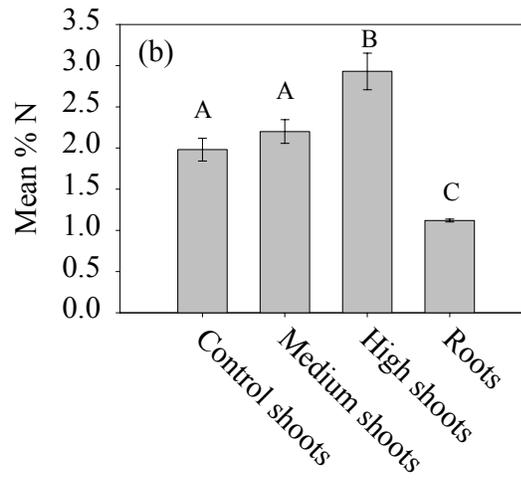
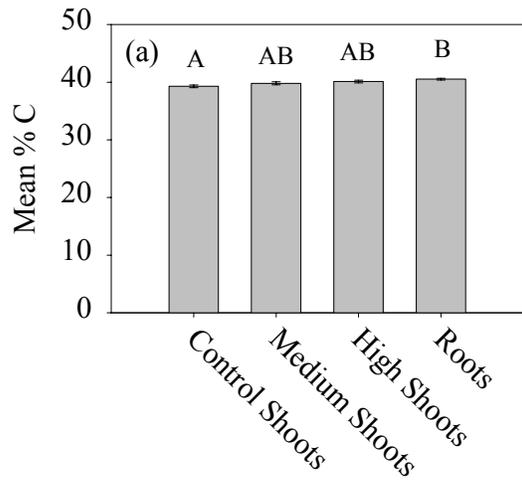
Tissue type significantly affected the percent of carbon content present in the litter ($p = 0.0139$). Percent carbon was significantly higher in roots than in the control shoot tissues. However, moderately and highly enriched tissues contained carbon percentages that were statistically similar to both roots and unenriched shoots (Fig. 21). No difference in % C appeared between the shoot tissues when analyzed separately from root tissues.

Tissue types significantly differed in regards to percent nitrogen content ($p < 0.0001$) (Fig. 21). Highly enriched shoot tissues had significantly higher % N content than the roots or the control or moderately enriched shoots. Conversely, roots had significantly lower % N content than any of the shoot tissues. Unlike the trend for percent carbon, tissue type significantly affected % N content ($p = 0.0021$) when roots were not included. In this case, there was a greater % N for the highly enriched tissues as opposed to the moderately enriched and control tissues, which remained similar to each other.

P Content of Tissues

Tissue P content varied significantly with litter tissue type ($p = 0.0152$) when comparing roots with control, medium, and highly enriched shoot tissues (Fig. 21). Highly enriched shoots had significantly greater concentrations of P in their tissues than control shoots, while roots and moderately enriched shoots had similar levels to both high and control shoots. When comparing the shoot tissues alone, high and control tissues

Fig 21. The effects of tissue type on (a) mean percent carbon content of tissues, (b) mean percent nitrogen content of tissues, (c) mean phosphorus content ($\mu\text{g/g}$) of tissues, (d) mean carbon:nitrogen ratio of tissues, and (e) mean carbon:phosphorus ratio of tissues. Phosphorus content was converted to a percentage for use in the C:P ratios. Control shoots were grown in non-fertilized plots. Medium shoot tissue was grown in plots receiving $200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ and $66 \text{ kg P ha}^{-1} \text{ yr}^{-1}$. High shoots were grown in plots receiving $1200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ and $396 \text{ kg P ha}^{-1} \text{ yr}^{-1}$. Error bars are standard errors, and different letters indicate significant differences among means ($p \leq 0.05$) in each graph.



Tissue type

continued to differ while medium tissues remained intermediate between the two ($p = 0.0174$).

C:N and C:P Ratios in Litter

C:N ratios significantly differed among the root and shoot tissues ($p < 0.0001$) (Fig. 21). Roots had significantly higher C:N ratios than any shoot tissue type. Highly enriched shoots had significantly lower C:N ratios than control tissues, while moderately enriched tissues had intermediate C:N ratios; similar to both control and highly enriched tissues. Significant differences between C:N ratios in the shoot tissues remained when analyzed separately from the root tissues ($p = 0.0037$).

C:P ratios differed significantly ($p = 0.0213$) between the litter types. C:P ratios for control shoot tissues were significantly higher than those for the highly enriched shoots, which had the lowest C:P ratios (Fig. 21). Roots and moderately enriched shoots had intermediate C:P ratios that were similar to both the control and highly enriched shoots.

Cellulose, Lignin, Hemicellulose, and Ash Content of Tissues

Cellulose, hemicellulose, lignin, and ash contents of root tissues were compared to shoot tissues grown in the $0 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ by $0 \text{ kg P ha}^{-1} \text{ yr}^{-1}$ enrichment. These shoots served as a proxy for the shoot tissue used in the litter bags because insufficient litter remained from the original tissue to run the tests after constructing the litter bags. As the shoot tissues are not identical to those from the litter bag assay, this is a general comparison of percent cellulose, lignin, and hemicellulose content between roots and shoots of *S. lancifolia*. These structural carbohydrate amounts varied between roots and shoots. Roots had a significantly higher percentage of hemicellulose in their tissues than

did shoot tissues ($p = 0.0438$). Roots also had significantly higher cellulose content than shoots ($p = 0.0149$). In addition, roots had greater lignin content at a highly significant level ($p < 0.0001$). In contrast, ash content was significantly higher in shoots than in roots ($p < 0.0001$) (Fig. 22). However, the total sum percentage including both the fiber contents and the ash content was significantly greater in root tissues than in shoot tissues ($p = 0.0016$). The mean total sum of the components for roots was 81.12% (SE = 1.33%) and for shoots was 70.35% (SE = 1.78%). Roots and shoots were also qualitatively different during the digestion process. The filtered hydrolysate samples were two distinct shades of amber, and the dried lignin samples from the roots and shoots were of two different colors and textures. In addition, ash from roots was light tan, whereas ash from shoots was grey-white.

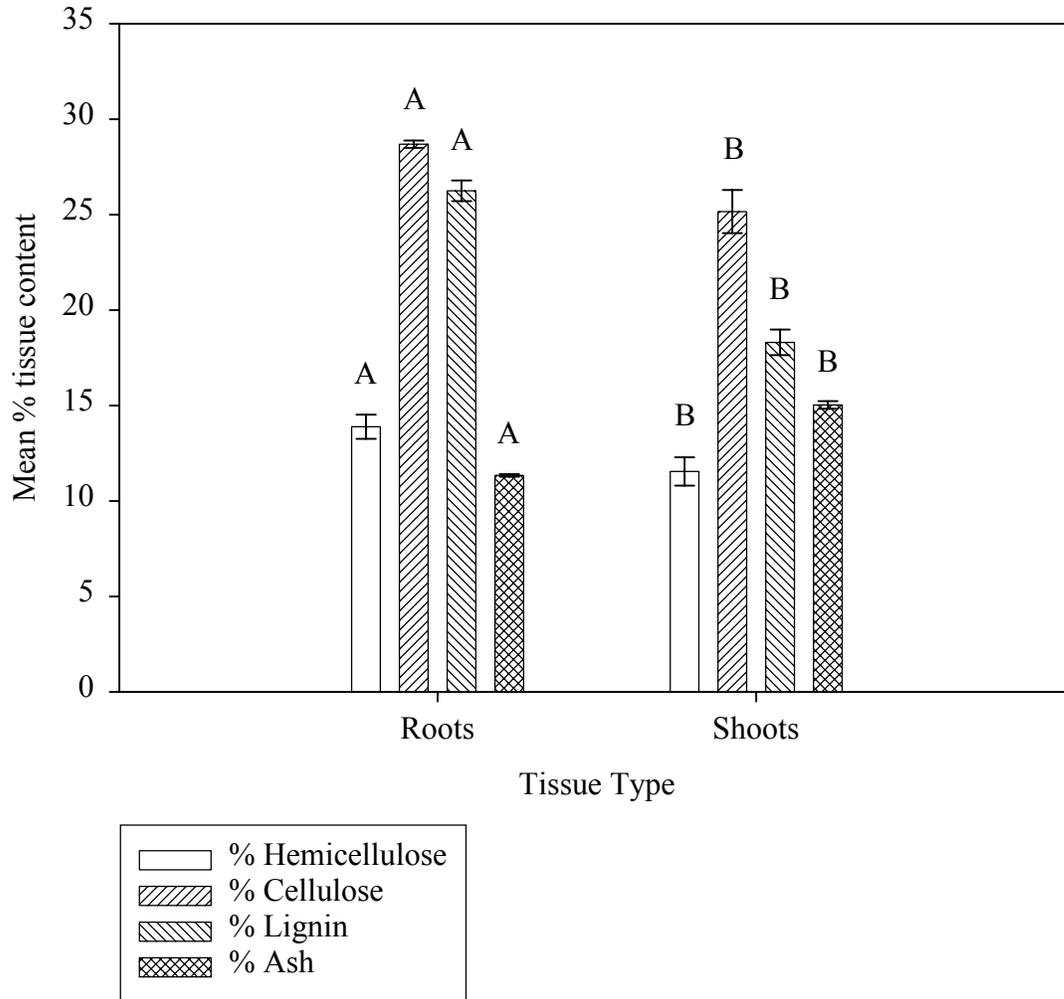


Fig. 22. A comparison between root and shoot tissues of mean % tissue content of hemicellulose, cellulose, lignin, and ash components. Significant differences existed between roots and shoots for all components. Shoot tissues for these tissue content analyses were grown in the experimental plots receiving no N or P soil enrichments. Different letters indicate significant differences among means for a given tissue component ($p \leq 0.05$), for example, between lignin amounts for roots and shoots. Values are means \pm standard errors.

DISCUSSION

This research investigated the effects of nitrogen and phosphorus enrichments on belowground decomposition in an oligohaline, subtropical marsh. I analyzed decomposition using three different tissue types; these were cotton strips, *Sagittaria lancifolia* shoot tissues grown at three nutrient levels, and uniformly treated *Sagittaria lancifolia* root tissues. These tissues comprised a range of tissue structural compositions, including a standard composed primarily of cellulose and natural tissue that included more recalcitrant lignin. The study was designed to address several different questions. First, I asked whether nitrogen and phosphorus enrichments affect belowground decomposition and whether the decomposition of different tissues under similar circumstances responds to soil enrichment differently. I also examined which of the nutrients, N or P, had the primary effect on belowground decomposition in the study marsh and whether abiotic factors in the soil itself changed in response to enrichment. In addition, this experiment was useful for comparison of two methods of analyzing decomposition, the cotton strip and litter bag assays.

The decomposition process can be split into three phases. In a description of the decomposition process (Rybczyk et al. 1996), leaching of very labile compounds from the litter occurs rapidly in the first phase. Microbial decomposers break down the less labile portion of the remaining tissue in the second phase, which is less rapid than the first. Finally, decomposition of the refractory portion of the tissue, which is slow in comparison to the preceding phases, occurs in the third phase (Rybczyk et al. 1996). The current study addressed the phases of decomposition involving the more labile components and the first portion of the slow phase of decomposition.

Cotton Strips

The cotton used in this study consisted primarily of cellulose (Latter and Howson 1977), and as such decomposed at a greater pace than the more complex tissues, which contained refractory lignin, used in the litterbag portion of this study. Mean CTSL d^{-1} ranged with depth between 6.3% and 8.1% loss of tensile strength per day. These values were higher than those found in some previous studies. For example, Mendelsohn et al. (1999) found values ranging from 1.8-5.5% per day. Though higher than some, the tensile strength losses found in this study are reasonable. In other studies, Mendelsohn and Slocum (2004) found values ranging between 5.4 and 7.4%, and Maltby (1988) found values ranging between 0.403 and 7.004% in the Everglades. Elevated decomposition in the current study may be partly due to environmental factors such as differences in temperature, ambient nutrient concentrations, soil redox potential, microbial communities present, or other variables.

The additions of nitrogen and of phosphorus separately increased the decomposition of cotton strips in this study, as found in past research. For example, Mendelsohn et al. (1999) found that natural increases in nitrogen and phosphorus concentrations when considered separately both positively correlated with the decomposition of cotton strips. Increased nutrient availability also increased the cellulose decomposition rate in studies in the Florida Everglades and the Mississippi floodplain (Maltby 1988). In addition, Rybczyk et al. (1996) reviewed 24 studies and found that nitrogen enrichment often increased the rate of decomposition, as did the combination of nitrogen and phosphorus. Phosphorus by itself also increased decay rates in some of the papers examined, but this was less common. However, Feller et al. (2002) found that the

addition of phosphorus to a calcareous mangrove island greatly increased cellulose decomposition, indicating that P can limit belowground decomposition in some cases. In addition, Sundareshwar et al. (2003) found that though nitrogen enrichments increased plant production in coastal wetlands, microbial decomposer activity was limited primarily by phosphorus availability.

In addition to the nitrogen and phosphorus enrichments, depth below soil surface affected CTSL d^{-1} in the current study. The highest mean tensile strength loss values were located 1 cm below the surface, indicating that greater oxygen availability and higher temperatures may have hastened decomposition at that depth. Other researchers have also found higher cellulose decomposition near the soil surface (Maltby 1988, Mendelssohn and Slocum 2004). A second peak in decomposition existed between 13 and 19 cm, centered around 15 cm depth. N and P enrichments were placed at approximately 15 cm depth, which could have increased decomposition there. In conjunction with the depth effect, a significant interaction existed between nitrogen enrichment and depth, in which the CTSL d^{-1} by depth increased with each higher level of N. This effect was especially apparent at $1200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. Increases in N enrichment also tended to increase the spread along the depth gradient of the second peak at 15 cm, indicating that nutrient enrichment increased decomposition at depth. However, this secondary peak in decomposition also occurred in the control plots. The relative magnitude of this peak to the rest of the depth profile in the control treatment was fairly similar to those for $50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ and $200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ but smaller than that for $1200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, though the actual rates of decomposition within the peaks rose with increasing N enrichment. Lawson (1988) found a similar peak in decomposition between 8 and 14 cm

and explained it as potentially due to greater populations of microbes at that depth, which could be the case in this study. Microbial activities may have been greater at 15 cm due to the concentration of roots at this depth and the activities of roots. Roots produce labile organic exudates that microbes can use towards growth and activity (Howarth and Hobbie 1982, Moriarty et al. 1986). Another potential source of the peak could have been the gelatin capsule used to enclose the fertilizer and also placed empty in the control plots. They may have been sufficient by themselves to slightly increase decomposition at their insertion depth.

Multiple regression models and correlation analyses indicated that higher pH was related to higher CTSL d^{-1} . Mendelssohn and Slocum (2004) found a similar effect of pH on cotton decomposition, as did Maltby (1988) in the Mississippi floodplain. A study of the effects of liming on cellulose tensile strength loss also found that raising pH tended to increase decomposition (Vickery and Floate 1988). In addition, several other researchers have found that higher acidity paired with lower decomposition rates, as in the examination of leaf litter decomposition by Hoisve and Blanc (1993) and that of *Carex aquatilis* tissue by McKinley and Vestal (1982).

Shoot Tissues

Shoot tissue percent mass remaining ranged from 11% to 34% after 291 days of exposure, or 66 to 89 percent mass lost. As comparison, Wrubleski et al. (1997) found in a study of four species that *Phragmites australis* roots lost between 59.2 and 85.5% mass in 112 days, while Gessner (2000) found that leaves and leaf sheaths of *P. australis* lost approximately 80% of their mass in eight months.

Both nitrogen soil enrichment and the interaction of N and P enrichments tended to increase shoot tissue decomposition. These results generally agreed with several other studies of decomposition. For example, Thormann and Bayley (1997) found that decomposition of *Carex aquatilis* litter as standard plant tissue was increased by NH_4^+ concentrations, though phosphorus also increased the decomposition of *Carex* and of filter paper samples included in the study. The addition of N to forest floor also increased the rate of microbial respiration in loblolly pine stands in North Carolina (Allen and Schlesinger 2004). The results of the current study indicated that phosphorus enrichment increased decomposition in combination with elevated levels of nitrogen (200 and 1200 $\text{kg N ha}^{-1} \text{ yr}^{-1}$), especially at 200 $\text{kg N ha}^{-1} \text{ yr}^{-1}$. However, the addition of P did not increase decomposition at 0 or 50 $\text{kg N ha}^{-1} \text{ yr}^{-1}$. This indicates that for *Sagittaria* shoot tissues, P may co-limit decomposition with N after a certain amount of N is present in the system. Studies have reached mixed conclusions on the cumulative effects of N and P. In a review by Rybczyk et al. (1996), several cases examined indicated that the addition of N and P together increased decomposition rates, and on occasion the addition of N may have caused P to become limiting. This leads to higher decomposition rates with the inclusion of P as well (Rybczyk et al. 1996), as occurred in the current study. However, other studies within and outside of the review found that the addition of N and P to the sediments had no effect on decomposition rates (Rybczyk et al. 1996, Holmboe et al. 2001).

The nutrient level of the shoot tissues themselves and the interactions of tissue nutrient content with soil N enrichment affected *Sagittaria lancifolia* shoot tissue decomposition. Interestingly, the greatest decomposition was present for the medium

shoot tissues, i.e., those that grew at the moderate soil fertility levels, both when considering the effects of shoot tissue nutrients alone and in combination with soil nitrogen. This occurred though the medium tissues had C:N ratios intermediate between control and high tissues. C:N ratios indicate tissue quality and the usefulness of the tissue as an energy source for decomposers; higher ratios tend to pair with lower decomposition rates (Enríquez et al. 1993, Lee and Bukaveckas 2002). In concurrence with the effects of this ratio, N and P concentrations in litter have been related to elevated decomposition rates (Enríquez et al. 1993). In addition, Neely and Davis (1985) found that litter decomposition related to the initial nutrient levels in the tissue though it did not relate to N and P enrichment of the water column. These findings illustrate the importance of tissue nutrients, but they do not fully explain why the medium tissue in this experiment decomposed faster than the high tissue. The medium tissues tended to experience increased decomposition with increased soil N, excepting the 50 kg N ha⁻¹ yr⁻¹ treatment that showed a slight decrease in decomposition. In contrast, decomposition of the high nutrient tissues decreased through 200 kg N ha⁻¹ yr⁻¹ and then remained at fairly similar levels for 1200 kg N ha⁻¹ yr⁻¹. At 200 and 1200 kg N ha⁻¹ yr⁻¹, decomposition in control tissues were intermediate between the medium and high tissues. This pattern between tissue types may exemplify an interaction between N enrichment and tissue components. Similarly, Scheu and Schauer mann (1994) found slower decomposition in small beech roots and shoots that contained more nitrogen than larger roots and shoots, though the trend did not hold for ash tree samples. They suggested that tissue quality (e.g. nitrogen content) might restrict decomposition in some circumstances, especially in conjunction with higher lignin concentrations. The authors postulated that this could occur through

the inhibition of ligninolytic enzymes at higher levels of nitrogen or through the formation of compounds of lignin and nitrogen that are more difficult to decompose. In contrast, other studies found a reduced proportion of refractory compounds present in tissues with increased levels of enrichment (Enríquez et al. 1993, Rybczyk et al. 1996). Due to a limited quantity of tissues available, the shoot tissues used in the litterbags for this study were not analyzed for refractory compounds. However, the combination of higher tissue nutrient concentrations with high levels of soil N enrichment may have reduced litter decomposition in the high shoot tissues, either through interactions with tissue carbon to form resistant compounds or, more likely, by limiting the production of microbial enzymes that decompose lignin.

Decomposition of control and medium tissues correlated positively with pH. This agrees with the positive relationship found between pH and decomposition discussed above for the cotton strips. In contrast, the decomposition of highly enriched tissue did not correlate with pH. In this case, it may be that the addition of nitrogen influenced decomposition rates more strongly than pH, masking its potential impact.

Root Tissues

Root tissue decomposition rates ranged between 0.0719 and 0.18191 % day⁻¹ in the faster (b1) portion of the decay curve. These rates compared to those for the aquatic plant *Eichhornia crassipes*, which ranged between 0.047 day⁻¹ and 0.099 day⁻¹ (Xie et al. 2004). However, the rates for *E. crassipes* were calculated using a single exponential decay model, which did not separate the rates for the labile and recalcitrant fractions. As such, the b1 rates found in the current study and representing the labile fraction only are higher than rates combining all phases of decomposition. Rates (b2) in the slow portion

of the curve ranged between 0.000454 and 0.001919 % day⁻¹. These rates were slightly slower than those from a single exponential decay model of *Phragmites australis* roots and rhizomes, which ranged from 0.0014 to 0.0032 day⁻¹ (Wrubleski et al. 1997), and *Spartina patens* shoot tissues, which averaged 0.0007 day⁻¹ over two locations (Foote and Reynolds 1997). The b2 rates represented the decomposition of the more recalcitrant litter; hence these rates were slower than the b1 rates (Wieder and Lang 1982) and the rates from single exponential curves.

The interaction of the N and P soil enrichments affected the decomposition rates corresponding to the decay of the more labile root tissue components. It appeared from the graph of the interaction that the addition of either N or P by itself decreased decomposition to some extent, though the addition of N and P enrichments together tended to result in greater decomposition. As discussed above, several studies found this positive relationship between N and P enrichments and decomposition. In addition to those studies mentioned previously, N and P were required in combination to hasten decomposition of yellow poplar leaves in one creek, though decomposition was not affected by combined N and P enrichments more than P enrichments alone in another creek (Grattan and Suberkropp 2001). This illustrates that the impact of nutrient enrichment can vary with different circumstances. In addition, Sundareshwar et al. (2003) found that though marsh plant growth was limited by nitrogen, phosphorus limited the bacteria that decomposed the tissues. This phosphorus effect could partially explain why there were low and similar decomposition rates at all N enrichment levels starting at 50 kg N ha⁻¹ yr⁻¹, while the addition of P in concert with N increased the decomposition rate at these levels. An exception to this relationship was for the 1200 kg N ha⁻¹ yr⁻¹

enrichments with and without P enrichment. These two treatment levels had relatively low and similar decomposition rates. It is possible that this reduced decomposition at high soil N enrichment indicated an inhibitory effect of increased nitrogen on the decomposition of lignin. Roots had significantly higher C:N ratios than any of the shoot tissues, which indicated that roots had lower tissue quality than the shoots. In addition, roots contained a higher percentage of lignin than shoots. Nitrogen enrichments can affect microbial activity in contrasting ways depending on whether the decomposing substrate is higher in cellulose or lignin. Carreiro et al. (2000) found that enzymes used to break down cellulose were stimulated by the addition of N, while phenol oxidase, an enzyme used by white rot fungi to degrade lignin, was reduced. Alternatively, some researchers postulate that nitrogen and lignin may complex to form stable derivatives (Camiré et al. 1991), while others found no evidence of these reactions (Sjöberg et al. 2004). As such, N enrichment may have affected decomposition in this study by altering enzyme activity or other facets of decomposition.

In one interpretation of decomposition, Berg and Staaf (1980) presented a two phased process based on Scots pine litter. The first phase consisted of decomposition dependent on the level of nutrients in the plant, corresponding to the faster rate (b1) in this experiment's double exponential analysis. In the second phase of decomposition, lignin levels in the plant dominated decomposition processes. This may correspond to the lower (b2) rates for the slower portion of the decay curve, which were not greatly affected by the N and P enrichments. This lack of an effect is likely due to the recalcitrant nature of the tissue present in the slow phase of the decay process. The variation in the initial, faster root tissue decomposition rates (b1) was not explained by

any of the interstitial variables. Similarly to the high shoot tissue, pH did not correlate with the b1 root decomposition rates. As above, this may indicate that another factor such as nitrogen enrichment may have played a greater role than pH in the decomposition process. Interestingly, the rates corresponding to the slower phase of decomposition (b2) was significantly associated with interstitial pH in the multiple regression. This may indicate that acidic conditions could further slow decomposition of the more recalcitrant portions of the litter. Interstitial $\text{NH}_4\text{-N}$ also accounted for part of the variation in the b2 decomposition rates in the multiple regression, though they did not significantly relate in the correlation analysis. This may indicate a slight influence of $\text{NH}_4\text{-N}$ availability on decomposition, though the soil enrichment levels showed no effect on b2 decomposition rates.

Cotton Strip Assay as Compared to the Litter Bag Assay

As exhibited by this study and others, cotton strips can show effects on decomposition that differ from effects found in other tests such as the litter bag assay. This is because cotton strips are primarily composed of cellulose, as opposed to the more complex combination of organic compounds in plant litter. The simple composition of the strips does, however, allow their use as standardized material that is also sturdier than other standards such as filter paper (Latter and Howson 1977). In addition, it allows comparison of decomposition across multiple locations (Maltby 1988). However, due to the simplified nature of cotton as compared to natural tissues, the assay may be more useful as a measure of cellulolytic microbial activity, to make relative comparisons between treatments, and/or in pilot studies. In contrast, litter bags containing more complex tissues local to the study area may be more appropriate for site-specific or

detailed examinations of how factors identified as important by a cotton strip assay affect tissues that are native to a given system. In addition, quantitative examinations of decomposition in relation to accretion require analysis of plant tissue decomposition, whereas cotton strips provide a relative examination of decomposition.

As they are structurally different, the litter tissues and cotton strips reacted differently to soil nitrogen and phosphorus enrichments. Cotton strips, composed primarily of cellulose, decomposed far more rapidly than either the shoot or root tissues. Cellulose decomposition increased with nitrogen and phosphorus enrichments. Shoot tissue decomposition increased with nitrogen, and was also affected by the interaction of the N and P enrichments. Root tissues decomposed more slowly than shoots or cotton strips. However, the root decomposition rates for the more labile tissue fraction (b1) was affected by the interaction of N and P enrichments in a similar fashion to the shoot tissues. In contrast to the litter tissues, cellulose decomposition was not significantly related to the interaction of N and P enrichments. This may indicate that interactions between nutrients are best observed through use of more complex litter tissues rather than the structurally simpler cotton strips.

Future Research

This examination revealed several other topics that could be explored to more fully address the effects of nitrogen and phosphorus enrichment of oligohaline, subtropical marshes. First, a direct analysis of the microbial community and its activity in relation to nitrogen and phosphorus enrichments would be useful in addressing how this enrichment alters the biological diversity of the community and its actions. A general survey of decomposers in the unenriched system would help discern whether N

and P enrichments change the community structure. These together would help to identify whether fungi or bacteria are dominant decomposers in the system and to describe the exact relationship between nitrogen, lignin, and microbes in this system. Another point of interest would be the effects of the soil enrichments on the above- and belowground productivity of the dominant *Sagittaria lancifolia* and other species in the marsh. In conjunction with this information, it would be useful to discern the relative abundance of root versus shoot detritus in the organic component of the soil. Changes in the plant contribution to the soil may affect accretion rates, so an elevation change study could also be interesting. Finally, pH and N appear to be related, as pH was highest in the highest level of N enrichment and the two factors strongly correlated. As such, an examination of the effects of N enrichment on soil pH would be useful, as would further studies of how pH affects decomposition under constant N levels.

Conclusions

This study examined the effects of several combinations of nitrogen and phosphorus enrichment on the belowground decomposition of *Sagittaria lancifolia* shoots, roots and a cellulose source in a marsh system. Roots, shoots, and cotton strips varied in their structural components and tissue quality, which allowed factors affecting decomposition of these tissues to vary. Nitrogen and phosphorus appeared important to decomposition of tissues proportionally higher in cellulose. In addition, N and P effects were important in the initial decay phase of more recalcitrant tissues. However, tissue quality appeared to more strongly affect decomposition in tissues that were proportionally higher in lignin. Based on the information gathered in this study, it seems that nitrogen may limit belowground decomposition of cellulose and shoot tissues in the

study marsh. However, after a certain amount of nitrogen is added, phosphorus can become limiting to decomposition. Interstitial pH was important in the decomposition of both cotton strips and shoots. Other studies found pH to be important as well, so a further examination of the effects of pH on decomposition in subtropical marshes may be useful. This study illustrates that nitrogen and phosphorus content both in the soil and in decomposing tissues can interact with the carbon quality of the tissues and with abiotic variables such as pH to control decomposition rates of belowground organic matter in a marsh system.

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APPENDIX: FIELD SITE LOCATION



Fig. A1. Location of field site. The site was located in a Louisiana marsh bordered to one side by the Tchefuncte River (see DOQQ image) and another by the north shore of Lake Pontchartrain (at the base of the DOQQ image). •: Location of field site. DOQQ source: <http://www.atlas.lsu.edu/doqq/>.

VITA

Kristen Raye Laursen was born on August 22, 1979, in Overland Park, Kansas, to William and Marjorie Laursen. She has one brother, Erik, and a sister-in-law, Elizabeth. Kristen attended high school at Blue Valley North High School in Overland Park, Kansas, and at Langley High School in McLean, Virginia, where she graduated in 1997. Kristen then attended the College of William and Mary in Williamsburg, Virginia, as a Monroe Scholar. While there, she conducted an electron microscopic study of sporogenesis in the coralline red algal genus *Metagoniolithon* as an undergraduate research project, which attained high honors. She completed a Bachelor of Science degree in biology *cum laude* with the class of 2001. Following this, she enrolled at Louisiana State University in Baton Rouge and worked as a graduate assistant for her advisor, Dr. Irv Mendelssohn, where she learned much about wetland plant ecology and advanced her scientific training. She is completing her Master of Science degree in the Department of Oceanography and Coastal Sciences and plans to graduate in December 2004.