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Endogenous versus exogenous nutrient control over decomposition and mineralization in North Carolina peatlands

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Abstract. We examined the relative importance of exogenous (pH, water table, soil nutrient and cation availability) and endogenous (carbon quality, nutrient and cation concentrations of litter) controls on litter decay over both the short term (1 yr) and intermediate term (3 yr) in four freshwater peatland communities that occur along a P and N availability gradient in the Coastal Plain of North Carolina. Four litter types were reciprocally transplanted into each community. Additionally, the effects of exogenous nutrient availability and low pH on decomposition dynamics were examined by fertilizing and liming plots in the most nutrient-deficient community, the short pocosin. Both exogenous and endogenous factors were important in controlling decay rates and nutrient mineralization-immobilization dynamics. The most important site factor controlling decay rates was water table, with greater rates of decomposition in drained sites. High initial soluble phenolic concentrations and a low holocellulose quotient (% holocellulose / % lignocellulose) in litter inhibited decay rates. Despite the extremely low nutrient availability in the pocosins and low soil pH in all three communities, both the cross-community comparison and the amendment experiment in the short pocosin demonstrated that exogenous nutrient availability, endogenous nutrient concentrations in litter, and low soil pH do not inhibit decomposition in these sites. In contrast, immobilization-mineralization dynamics of N and P were largely driven by a source-sink relationship, with greatest immobilization found with high exogenous nutrient availability and low initial endogenous nutrient concentrations. We suggest a conceptual model of nutrient control over decomposition as a function of carbon quality of litter.

Introduction

Decomposition dynamics determine such fundamental ecosystem properties as nutrient availability (and consequently biomass production), carbon storage, trace gas fluxes, and energy transfer. Factors that control decomposition rates, such as climate, substrate quality of the decaying material, and edaphic variables, have been well studied in a variety of ecosystems (Swift et al. 1979; Brinson et al. 1980; Cadisch and Giller 1997; Aber and Melillo 2001; Bridgham and Lamberti (in press)). However, the relative roles of exogenous versus endogenous nutrients as controls over decomposition remain unclear, where exogenous nutrients are defined as those in the environment exterior to the decaying material (litter) and endogenous nutrients refer to concentrations in the litter itself, along with its associated microbial microflora.

Numerous studies have shown that increasing initial endogenous N concentrations, a lower C:N ratio, and/or a lower lignin:N ratio of litter enhance short-term (months to a few years) decay rates (Coulson and Butterfield 1978; Pastor et al. 1987; Taylor et al. 1989; Aerts 1997; Berg and Matzner 1997; Heal et al. 1997). However, evidence of whether increasing exogenous N availability yields greater decomposition rates is contradictory, sometimes showing no effect (Coulson and Butterfield 1978; Pastor et al. 1987; Rochefort et al. 1990; Bridgham and Richardson 1992; Prescott 1995; Aerts et al. 2001), a stimulatory effect (Hunt et al. 1988; Berg and Tamm 1994; Hobbie 2000), a negative effect (McClaugherty and Berg 1987; Prescott 1995; Lockaby et al. 1996a, 1996b; Magill and Aber 1998), or a mixed, species-specific or site-specific effect (Aerts and de Caluwe 1997; Hobbie and Vitousek 2000).

Fewer studies have examined the role of exogenous P availability as a potential control over decomposition dynamics. However, as with N, increasing exogenous P availability has been found to have either no effect (Coulson and Butterfield 1978; Bridgham and Richardson 1992; Prescott 1995), a positive effect (Martin and Holding 1978; Berg and Tamm 1994; DeBusk and Reddy 1998; Qualls and Richardson 2000), or a mixed effect on decay rates (Hobbie and Vitousek 2000).

Such conflicting results concerning the role of endogenous and exogenous nutrients on decomposition suggest complicated controls and feedbacks. Heterotrophic microbial activity without growth (e.g., maintenance respiration) requires few nutrient resources, but active growth requires that the C:N:P stoichiometry of the microbial population be closely matched by the stoichiometry of resource uptake. It has been hypothesized that the initial stages of decomposition, when concentrations of labile carbon compounds in litter are often high, are nutrient limited (Taylor et al. 1989; Berg and Matzner 1997; Aber and Melillo 2001). This should lead to net immobilization of exogenous nutrients, and presumably to faster decay rates with both increased endogenous nutrient concentration and exogenous nutrient availability. However, in the later stages of decomposition, microbial activity is hypothesized to be limited by low carbon quality, typically best described by the lignin concentration or the holocellulose-lignin quotient (HLQ) of the litter (Taylor et al. 1989; Berg and Matzner 1997; Aber and Melillo 2001). Nitrogen inhibition of decomposition is often seen with humus (Bridgham and Richardson 1992; Berg and Matzner 1997) or during the later stage of decomposition of litter (Berg et al. 1996; Magill and Aber 1998). This effect has been hypothesized to be due to inhibition of lignolytic enzymes or enhancement of condensation reactions during humus formation (McClaugherty and Berg 1987; Berg et al. 1996).

Nutrients may also indirectly affect decomposition in a number of ways. High endogenous nutrient concentrations may be correlated with high concentrations of labile carbon compounds in litter, such as amino acids and DNA. Conversely, a frequent plant adaptation to low nutrient, acidic environments are high polyphenol concentrations, with consequent inhibition of nutrient mineralization and decomposition (Janzen 1974; Northrup et al. 1995; Richardson et al. 1999), and sclerophyllous, evergreen leaves (Bridgham et al. 1996; Jonasson and Shaver 1999; Aerts et al. 1999). In such cases, higher N availability would cause greater decomposition rates because of lower concentrations of inhibitory compounds or better carbon quality in plant litter.

Further complications may arise from edaphic controls over microbial activity, exogenous nutrient availability, and endogenous nutrient concentrations in litter. High soil acidity has often been thought to limit decomposer activity. However, studies that have manipulated pH in the field or laboratory have found conflicting results on its effect on decomposition and nutrient cycling (Farrish and Grigal 1988; Bridgham and Richardson 1992; Yavitt and Fahey 1996; Chapin 1998; Cirmo et al. 2000). These contradictory results may not be surprising considering that soil pH reflects a myriad of chemical reactions that consume and produce protons, and many of these reactions are directly related to carbon and nutrient cycling (Binkley and Richter 1987).

The effects of flooding on decay rates are dependent on its frequency and duration. Prolonged anaerobic conditions lead to substantially reduced rates of decomposition and soil respiration (Godshalk and Wetzel 1978; Updegraff et al. 1995; Bridgham et al. 1998). However, alternating flooded-dried conditions that are typical of many wetlands may cause enhanced rates of decomposition due to such factors as increased leaching, pulses of microbial activity, and amelioration of moisture limitation under drier conditions (Heal et al. 1978; Brinson et al. 1980; Day 1983; Mitsch and Gosselink 1993; Lockaby et al. 1996a, 1996b).

Peatlands are interesting ecosystems in which to examine questions of nutrient control over carbon cycling, as they are often characterized by an extreme soil environment with prolonged waterlogging, low pH, oligotrophic nutrient status, and a large, recalcitrant soil carbon reservoir. These soil conditions can have important negative feedbacks on plant production and substrate quality of litter (Small 1972; Coulson and Butterfield 1978; Bridgham et al. 1995b, 1998; Chapin 1998). Moreover, controls over carbon cycling in peatlands is of societal concern as they contain up to one third of the global soil carbon pool (Gorham 1991), and they may augment predicted climate change by enhancing trace gas fluxes (Bridgham et al. 1995a; Updegraff et al. 2001). The role of pH in decomposition in peatlands is particularly important, with large differences in pH being found among different wetland types. These differences are largely driven by the hydrological position of wetlands in the landscape and the geochemistry of the catchment (Bridgham et al. 1996, 2000). It is generally thought that low soil pH is at least partially responsible for the high soil carbon accumulation rates found in many peatlands (Mitsch and Gosselink 1993). However, the circumneutral to alkaline conditions found in many peatlands suggest that other factors must also control carbon accumulation (Craft and Richardson 1993).

Peatlands on the Coastal Plain of North Carolina are particularly useful areas to examine nutrient controls over decomposition, as different plant communities occur along P and N availability gradients in the landscape with correspondingly large differences in substrate quality of litter (Walbridge 1991; Bridgham and Richardson 1993). Additionally, soil pH tends to remain low ($\leqslant 4$) along the nutrient availability gradient, whereas in northern peatlands nutrient availability and pH are confounded in complicated ways (Bridgham et al. 1996, 2000, 2001; Chapin 1998).

We report here the results from a 3-yr reciprocal decomposition study along a P and N availability gradient in three freshwater peatland communities (short pocosin, tall pocosin, and gum swamp) and in a drained short pocosin in the Coastal Plain of North Carolina. Additionally, the effects of exogenous nutrient availability and pH on decomposition dynamics were examined by fertilizing and liming plots in the most nutrient-deficient community, the short pocosin. Our overall objective was to determine the relative importance of edaphic factors (exogenous soil nutrient availability, pH, water table), endogenous nutrient concentrations in litter, and other litter quality factors in controlling decay rates and nutrient mineralization-immobilization dynamics in decomposing leaf litter in wetlands. Specific hypotheses were: (i) periodic flooding and drying should enhance decay, so in wetlands that normally experience only periodic periods of standing water (such as in our sites), drainage will decrease decomposition rates of surface litter; (ii) for the low carbon-quality litter typical of these sites, neither increasing endogenous nutrient concentrations nor exogenous nutrient availability will increase short-term (1 yr) or intermediate-term (3 yr) decay rates; (iii) the pH optima of the microbial populations reflect their native habitats, so decay rates will not increase with liming; and (iv) mineralization-immobilization dynamics (only measured at 1 yr) will reflect both endogenous nutrient concentrations and exogenous nutrient availability, with immobilization greatest in low-nutrient litters placed in habitats with high exogenous nutrient supply.

Study area

Distinct peatland communities occur in different topographic settings on the Coastal Plain of North Carolina because of differences in nutrient availability and hydrology (Bridgham and Richardson 1993). Short pocosins occupy the ombrotrophic center of domed bog complexes, are extremely P limited, and are characterized by stunted pond pine (*Pinus serotina*) and low (< 1.5-m height) shrubs, such as *Cyrilla racemiflora*, *Gaylussacia dumosa*, *Lyonia lucida*, and *Zenobia pulverulenta*. Peat depth ranges from 1 to 5 m. Tall pocosins occur on the fringes of short pocosins, with similar or slightly greater P availability, shallower peat (< 1.5 m), and a similar species mixture but of taller stature and greater aboveground biomass. Gum swamps occur along the outflows of lakes and along streams and have the greatest P and N availability. Vegetation is typical of southeastern bottomland hardwood swamps, with a canopy of black gum (*Nyssa sylvatica*), sweet gum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), and bald cypress (*Taxodium distichum*). Peat thickness is < 1 m.

Study sites were in the Croatan National Forest, North Carolina (34°55′ N, 77°5′ W) in a well developed peatland complex (see Bridgham and Richardson (1993) for a map of sites). We also chose drained short pocosin sites to examine the effects of water-table level on decomposition dynamics. These sites were similar in vegetation to the tall pocosin sites, although the visible effect of ditching only extended for 20 to 50 m from the ditch. Soils at all sites are dysic, thermic Typic Haplosaprists.

Methods

Treatments

In the first experiment, four replicate 0.1-ha sites were established in short pocosin, tall pocosin, gum swamp, and drained short pocosin communities (i.e., our 'cross-community comparison'). Drained plots were established 8–10 m from drainage ditches. In the second experiment, a fertilization-liming study was conducted in the short pocosin. Twenty 0.1-ha plots were established along a 700-m transect, and a 10 × 10-m subplot was randomly chosen within each plot to receive the treatments. All sampling took place in the inner 6 × 6-m area of each subplot to minimize edge effects. Treatments were applied shortly after placement of litter bags in December with 50 kg ha^{-1} of P and N as triple superphosphate and NH_4NO_3, respectively, and 4479 kg ha^{-1} of fine powdered dolomite limestone. Nitrogen and P fertilizers were applied with a grass spreader to ensure homogeneous coverage, while the limestone was applied by hand but the heavy application rate ensured complete coverage of the plots. Four replicate plots were established in the following treatments: control, P, P + N, lime, P + N + lime.

Soil chemistry

Three soil samples from each plot were taken with a stainless steel box corer and were composited. Roots were removed by hand. Samples for moisture content and total nutrient content were dried at 70 °C. Organic matter was determined by loss-on-ignition after combustion at 500 °C for 3 hr, and total C was estimated by assuming organic matter to be 63.7% C (Otte and Ingram 1979). A 1:1 wet soil mass/water slurry was used to determine pH.

Total soil nutrient (N, P, Ca, Mg, K) contents were quantified in dried samples after digestion with concentrated H_2SO_4 and 30% H_2O_2 (Lowther 1980). Extractable soil nutrients were measured in wet samples and adjusted to a dry-mass equivalent. Phosphate was extracted with 0.05 M HCl and 0.0125 M H_2SO_4 (Olsen and Sommers 1982), while NO_3-N and NH_4-N were extracted with 2 M KCl (Keeney and Nelson 1982). Nitrogen and P were measured with standard autoanalyzer techniques, and cations were measured with atomic adsorption spectrophotometry.

Decomposition

An initial study compared the chemical quality of litter of 21 site/species combinations (several species occurred in more than one community type). Based upon differences in N, P, and lignin concentrations, we subsequently chose four litter types that were used in both decomposition experiments: *Lyonia lucida* and a mix of *Gaylussacia dumosa* (ca. 70%) and *Cyrilla racemiflora* (ca. 30%) from the short pocosin, and *Liquidambar styraciflua* and *Nyssa sylvatica* from the gum swamp. The mix of *G. dumosa* and *C. racemiflora* (hereafter referred to as *G. dumosa*) resulted from the difficulty of discriminating in the large bulk litter samples the very similar leaves of the two species. *N. sylvatica* included the varieties *sylvatica* and *biflora* in approximately equal amounts, and the initial analysis indicated no differences in litter quality. Fresh litter was collected in September-November from litter traps, or litter ready to abscise was shaken from shrubs if enough could not be collected from litter traps. Litter was air dried and 2 g was placed in 10 × 10-cm fiberglass screen bags (1.5-mm mesh). Subsamples were taken to determine the air-dry:oven-dry (70 °C) ratio and for chemical analyses.

Three litter bags of each species were placed in each plot within the fresh litter layer in December. Litter bags were retrieved 1 and 3 yr later (768 total litter bags). In-grown roots and visible fungal mycelia were removed, and samples were dried at 70 °C. All results are expressed as ash-free dry mass.

The three litter bag from each plot were composited for chemical analyses, except that ash was determined separately in samples from the limed treatment due to the large and variable amount of mineral residue remaining. The initial litter samples were ground with a 40-mesh Wiley mill, whereas litter-bag samples were ground in a Spex shatterbox. Ash and nutrient concentrations were measured in the same manner as for soils.

Proximal organic fractions of the initial litter and the litter-bag residue in the gum swamp, tall pocosin, and short pocosin control plots were determined with a sequential fractionation scheme (Schlesinger and Hasey 1981). Lipids were extracted with diethyl ether, followed by extraction with 50% aqueous methanol. Soluble carbohydrates in the methanol extract were quantified with anthrone reagent based on glucose standards, and soluble phenolics were quantified based on the Folin-Denis reaction using tannic acid standards. The acid-insoluble fraction was measured by digestion of the methanol residue in 72% H_2SO_4, followed by digestion in 3% H_2SO_4 at 100 °C and weighing of the dried residue. Ash concentrations in the acid-insoluble residue were measured separately. The acid-insoluble fraction is typically defined as lignin, although this fraction often includes other recalcitrant compounds, particularly in the later stages of decay (Aber and Melillo 2001). The acid-soluble fraction was estimated by difference from the methanol residue and the acid-insoluble fraction. This fraction is typically defined as cellulose and hemicellulose (i.e., holocellulose), but it may also include other compounds. Carbon was assumed to be 50% of ash-free dry mass.

Statistics

Decomposition data were analyzed as % original mass remaining after 1 yr (short-term) and 3 yr (intermediate-term). We also examined our results with the often used simple exponential decay model: % remaining mass = e^{-kt}, where k is the decay rate constant and t is time (in yr). k values gave similar qualitative results to % remaining mass after 3 yr, but we wanted to examine treatment differences in short-term versus intermediate-term decomposition. Also, the exponential decay model did not always fit the data well, with 26% of the models having an $r^2 < 0.75$, typically because of a small difference in mass loss between years 1 and 3.

Treatment effects on % remaining mass were examined with repeated measure two-way ANOVAs (rmANOVA) with the three replicate bags within each plot nested to account for intra-plot variation. Simple two-way ANOVAs were also run within each year. As the replicates were composited for the chemical analyses, all other ANOVAs were not nested. All variables were log transformed as necessary to ensure normal distributions before performing ANOVAs. Pairwise comparisons used Fischer's Protected Least Significant Difference (FPLSD) with statistical significance assigned for $P < 0.05$. Forward stepwise regression analysis (with a P to enter of 0.05) was used to determine the best set of initial litter chemistry variables (endogenous variables) and soil chemistry variables (exogenous variables) for predicting remaining mass after 3 yr. Systat (SPSS Inc., Chicago, IL) was used for all analyses.

Results

Soil chemistry

Total soil P and PO_4-P contents and N:P ratios showed a P-availability gradient, with larger soil P pools in the gum swamp, smaller soil P pools in the short pocosin, and soil P pools in the tall pocosin that were similar or slightly larger than in the short pocosin (Table 1). Total soil N and NO_3-N contents were also greater in the gum swamp than in the other communities, although NH_4-N contents did not differ. The lower organic matter concentration and higher Mg, Ca, and K contents in the gum swamp than in the short pocosin and tall pocosin reflect the minerotrophic (i.e., influenced by groundwater and overland flow) status of the gum swamp. Despite the clear minerotrophic status of the gum swamp based upon most soil chemical variables and its landscape position, it had a low pH similar to the pocosin sites. In contrast to most northern peatlands, degree of minerotrophy and pH may be unrelated in peatlands along the North Carolina Coastal Plain because of the underlying sandy mineral substrata with low cation exchange capacity (Bridgham and Richardson 1993; Bridgham et al. 2000). Drained pocosin sites retained soil chemistry characteristics that were quite similar to the short pocosin in

Table 1. Soil characteristics of the four peatland communities in the Croatan National Forest, North Carolina, USA.

Variable	Short Pocosin	Tall Pocosin	Gum Swamp	Drained Pocosin
pH[1]	3.94 (0.01)^{a}	3.71 (0.04)^{b}	3.92 (0.05)^{a}	3.89 (0.10)^{a}
%Organic matter[1]	95.2 (0.6)^{a}	91.5 (4.1)^{a}	75.8 (7.1)^{b}	95.5 (0.4)^{a}
N (g m^{-2})[2]	401 (17)^{b}	376 (42)^{b}	802 (40)^{a}	367 (12)^{b}
P (g m^{-2})[2]	8.56 (0.26)^{c}	11.8 (0.4)^{b}	82.9 (10.1)^{a}	7.69 (0.26)^{c}
N:P ratio[2]	46.9 (1.8)^{a}	31.8 (3.2)^{b}	10.1(1.2)^{c}	47.9 (1.9)^{a}
Mg (g m^{-2})[2]	30.1 (0.7)^{b}	25.7 (4.5)^{b}	51.7 (7.3)^{a}	33.1 (2.4)^{b}
Ca (g m^{-2})[2]	6.86 (0.64)^{b}	8.41 (2.32)^{b}	18.8 (3.3)^{a}	14.9 (2.7)^{a}
K (g m^{-2})[2]	6.38 (0.31)^{c}	14.3 (1.8)^{b}	128 (19)^{a}	6.98 (0.58)^{c}
PO_4-P (ug cm^{-3})[3]	0.075 (0.013)^{b}	0.053 (0.012)^{b}	0.865 (0.243)^{a}	0.031 (0.005)^{b}
NH_4-N (ug cm^{-3})[3]	0.610 (0.442)^{a}	0.100 (0.063)^{a}	0.440 (0.349)^{a}	0.610 (0.442)^{a}
NO_3-N(ug cm^{-3})[3]	0.042 (0.013)^{b}	0.005 (0.002)^{b}	0.449 (0.136)^{a}	0.000 (0.000)^{b}
Ca (ug cm^{-3})[3]	32.4 (6.5)^{b}	30.8 (3.6)^{b}	25.9 (5.2)^{b}	86.2 (13.8)^{a}
Mg (ug cm^{-3})[3]	32.5 (6.6)^{b}	26.0 (1.0)^{b}	13.7 (2.1)^{a}	32.8 (4.9)^{b}

Mean ± (SE), n = 4. Different letters within a row indicate significant differences among communities.

[1] To 10-cm depth.

[2] Total nutrient content to 30-cm depth.

[3] Extractable nutrient content to 10-cm depth.

Table 2. Extractable nutrient contents (ug cm^{-3}) and pH from 0–10 cm soil depth for treatment plots in the short pocosin.

Treatment	pH	PO_4-P	NH_4-N	NO_3-N	Ca	Mg
Control	3.94 (0.01)	0.0751 (0.0130)	0.610 (0.442)	0.0420 (0.0128)	32.4 (6.5)	32.5 (6.6)
Lime	5.37 (0.18)	0.0790 (0.0214)	0.813 (0.449)	0.0571 (0.0458)	169 (21)	109 (12)
P	3.81 (0.03)	3.93 (0.80)	0.750 (0.157)	0.0326 (0.0126)	55.1 (11.1)	32.8 (1.6)
P + N	3.84 (0.04)	2.87 (0.47)	1.55 (0.15)	0.0360 (0.0055)	52.1 (4.7)	36.2 (4.7)
P + N + Lime	5.03 (0.21)	4.62 (1.60)	2.14 (0.38)	0.0300 (0.0138)	191 (22)	97.5 (4.1)

Mean ± (SE), n = 4. Measured in May, 5 months after treatment application.

all aspects other than somewhat higher Ca content. Thus, our natural sites reflect a gradient of N, P, and cation availability under low soil pH conditions.

The treatments imposed upon the short pocosin had their desired effects in changing soil pH and nutrient content (Table 2). Five months after application, liming had raised soil pH in the short pocosin from 3.9 to approximately 5.2, and also increased extractable Ca content by 5 to 6 fold and extractable Mg content by 3 fold. Phosphorus fertilization increased P content by 38 to 62 fold, and N fertilization increased NH_4-N content by 2.5 to 3.5 fold, with no change in NO_3-N content.

Table 3. Initial litter quality of the four species in the litterbag experiment.

Variable	*N. sylvatica*	*L. styraciflua*	*L. lucida*	*G. dumosa*
%P	0.060 (0.004)^{b}	0.079 (0.004)^{a}	0.015 (0.000)^{c}	0.021 (0.003)^{c}
%N	0.857 (0.061)^{a}	0.808 (0.032)^{a}	0.397 (0.005)^{b}	0.504 (0.030)^{b}
%Mg	0.541 (0.035)^{a}	0.361 (0.029)^{b}	0.109 (0.008)^{c}	0.374 (0.044)^{b}
%Ca	1.03 (0.14)^{a}	1.07 (0.08)^{a}	1.30 (0.03)^{a}	0.97 (0.06)^{a}
%K	0.138 (0.028)^{b}	0.251 (0.008)^{a}	0.164 (0.015)^{b}	0.177 (0.012)^{b}
N:P	14.5 (0.9)^{b}	10.4 (0.9)^{b}	26.7 (1.0)^{a}	25.7 (2.3)^{a}
%Ash	3.77 (0.47)^{b}	5.34 (0.18)^{a}	3.64 (0.09)^{b}	3.57 (0.20)^{b}
%Methanol	13.5 (1.8)^{b}	14.5 (0.6)^{b}	27.4 (1.0)^{a}	26.9 (1.7)^{a}
%Carbohydrate	3.03 (0.44)^{c}	3.13 (0.18)^{c}	13.6 (0.4)^{a}	12.2 (0.4)^{b}
%Phenolic	1.93 (0.14)^{c}	2.37 (0.11)^{b}	2.00 (0.02)^{c}	3.27 (0.05)^{a}
%Ether	1.52 (0.91)^{b}	1.01 (0.84)^{b}	0.13 (0.13)^{b}	4.21 (0.72)^{a}
%Acid insoluble	40.1 (1.2)^{b}	50.2 (1.0)^{a}	41.9 (0.8)^{b}	34.6 (1.1)^{c}
%Acid soluble	45.0 (1.1)^{a}	33.8 (0.8)^{bc}	30.6 (0.8)^{c}	34.2 (1.1)^{b}
Acid insol.:P	686 (64)^{c}	588 (19)^{c}	2850 (100)^{a}	1810 (310)^{b}
Acid insol.:N	47.4 (3.0)^{c}	66.0 (4.9)^{b}	106 (2)^{a}	69.6 (5.5)^{b}
HLQ	0.529 (0.014)^{a}	0.402 (0.010)^{b}	0.422 (0.011)^{b}	0.497 (0.015)^{a}

Mean + (SE), n = 4. %Methanol = %methanol extractable; %Carbohydrate = %soluble carbohydrates; %Phenolic = %soluble phenolics; %Ether = %lipids; Acid insol. = % acid insoluble; HLQ = holocellulose quotient. Different letters within a row indicate significant differences among litter types.

Initial litter quality

The four litter types were chosen to represent a range of initial litter quality (Table 3). The greater soil P and N availability in the gum swamp relative to the pocosins (Table 1) was reflected in higher P and N concentrations in litter. No consistent differences in Mg, Ca, and K concentrations occurred among the litter types.

There were much higher concentrations of methanol-extractable compounds and soluble carbohydrates in the short pocosin species (*L. lucida* and *G. dumosa*) than in the gum swamp species (*N. sylvatica* and *L. styraciflua*) (Table 3). It appears that in the highly nutrient-deficient short pocosin vegetation non-structural carbohydrates are in excess relative to the demands of the plant (cf. Chapin (1980)). Other organic fractions varied significantly among litter types, but not in ways that reflected the nutrient availability gradient. The sclerenchymatous nature of the vegetation was reflected in the high acid-insoluble concentration of all four litter types. *L. styraciflua* had the highest acid-insoluble concentration at 50%, and *G. dumosa* had the lowest concentration at 35%. The holocellulose quotient (HLQ) is the acid-soluble fraction divided by the acid-soluble plus acid-insoluble fractions and approximates that portion of the structural carbon compounds that are relatively easily decomposable (McClaugherty and Berg 1987; Melillo et al. 1989). *N. sylvatica* and *G. dumosa* had the highest HLQ ($\sim$0.50).

Mass loss: cross-community comparison

When % remaining mass was examined at both 1 and 3 yr in the cross-community comparison (Figure 1), there were significant community and litter-type effects (rmANOVA, both $P < 0.001$), the expected time effect ($P < 0.001$), and a significant interaction between time and community ($P = 0.001$). There was also a suggestion of a three-way interaction among time, litter-type, and community ($P = 0.076$). When individual years were examined, there were significant community and litter-type main effects (both years, $P < 0.001$) and significant community-litter type interactions (yr 1 $P = 0.050$, yr 2 $P = 0.034$). Despite the significant interactions, a general picture is evident in relative treatment effects. At both time points, relative rates of decay among communities were drained pocosin $\geqslant$ tall pocosin $\geqslant$ gum swamp $\geqslant$ short pocosin, and relative rates of decay among litter types were *N. sylvatica* $\geqslant$ *L. lucida* $\geqslant$ *L. styraciflua* = *G. dumosa*. The most evident time-treatment interactions were relatively greater remaining mass of *N. sylvatica* and *L. lucida* litter in the gum swamp compared to the other communities in yr 3 than in yr 1 (Figure 1). The most evident litter type-community interaction in yr 1 was the relatively fast decay of *N. sylvatica* in the drained pocosin and the relatively slow decay of *L. styraciflua* in the gum swamp. The most evident litter type-community interaction in year 3 was relatively greater remaining mass of *G. dumosa* in the tall pocosin, such as it was not different than the short pocosin and gum swamp.

We used a stepwise regression to examine the combined effects of exogenous (i.e., variables in Table 1) and endogenous factors (i.e., variables in Table 3) in control over % remaining mass after 3 yr in the cross-community comparison. Results from a stepwise regression on % remaining mass after 1 yr are not shown, but were qualitatively similar. The final regression equation explained 70% of the variance in % remaining mass, and carbon quality of the litter and soil cation content were important in the equation (Table 4). Soluble phenolics were the most important litter quality variable in the multiple regression model. However, the individual effect of soluble phenolic concentration on % remaining mass was moderate (yr 1: $r = 0.40$, $P = 0.001$; yr 3: $r = 0.42$, $P = 0.001$). The holocellulose quotient was also significant in the stepwise regression, although its individual effect was insignificant (yr 1: $r = -0.23$, $P = 0.07$; yr 3: $r = -0.14$, $P = 0.26$). The acid-insoluble fraction alone was unimportant ($r \leqslant 0.04$ in both yr).

Total soil Ca content was negatively correlated with % remaining mass, with high contents (Table 1) in the drained pocosin with its fast decay rates. Total soil K was positively correlated with remaining mass because it was quite high in the gum swamp with its moderate rates of decay. Although extractable soil NH_4-N contents were individually poorly correlated with % remaining mass ($r = 0.01$), both it and extractable soil NO_3-N contents entered into the multiple regression equation.

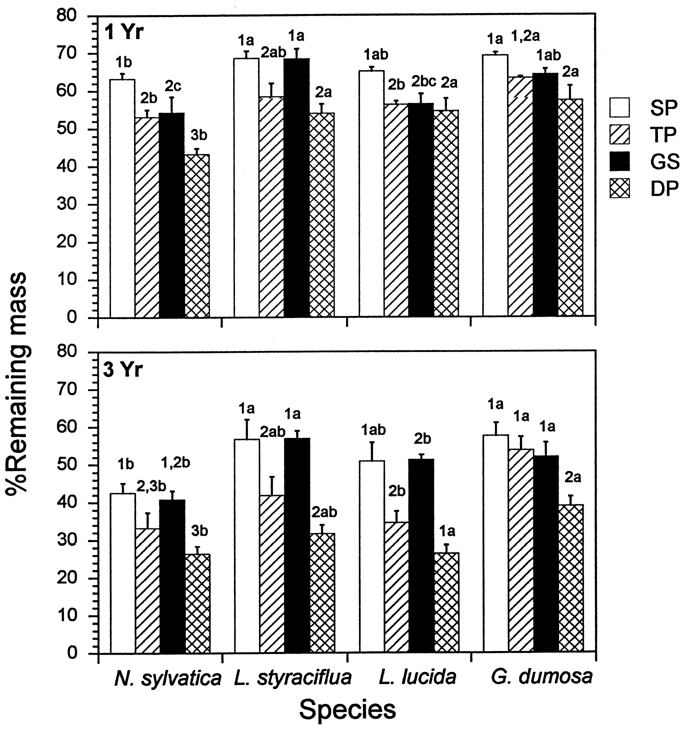

Figure 1. Percent remaining dry mass of litter after 1 and 3 years of decomposition in untreated short pocosin (SP), tall pocosin (TP), gum swamp (GS), and drained pocosin (DP) plots for four litter types: *Nyssa sylvatica*, *Lyonia lucida*, *Liquidambar styraciflua*, and *Gaylussacia dumosa*. Significant differences ($P < 0.05$) among communities within a litter type are shown by different numbers, whereas significant differences among litter types within a community are shown by different letters. Error bars indicate 1 standard error.

Mass loss: fertilization and liming experiment

When % remaining mass was examined for the fertilization and liming treatments in the short pocosin, there were significant litter-type and time effects (rmANOVA, both $P < 0.001$) and significant time-litter type ($P < 0.001$) and time-treatment ($P = 0.004$) interactions in both yr 1 (Figure 2) and yr 3 (Figure 3). The time-treatment interaction was evident in the significant treatment effect in yr 1 ($P < 0.001$) but not in yr 3. Even in yr 1, differences among treatments were small (< 5%), and only the limed treatment differed from the control, with liming decreasing the decay rate (Figure 2). Decay in treatments where both P and N were added was faster than when only P was added. The time-litter type interaction was apparent in *L. styraciflua* having slower decay than *G. dumosa* in yr 1 (Figure 2), but these two litter types had similar, slow decay in yr 3 (Figure 3). At both time points, *N. sylvatica* had the greatest mass loss, followed by *L. lucida*.

Table 4. Results from step-wise multiple regression models that examine the effect of initial litter quality and soil nutrient contents on mass loss after 3 years and nutrient immobilization-mineralization after 1 year. Pearson r shows the correlation of each independent variable, whereas the incremental R^2 shows the progressive increase in predictive power as each variable is entered into the model. Data are included for the short pocosin control plots, tall pocosin, gum swamp, and drained pocosin.

Dependent variable	Independent variable	Pearson r	Incremental R^2
%Mass	Litter phenolic	0.421	0.24^{***}
Remaining	Total soil Ca	–0.43	0.34^{***}
	Ext. soil NH_4-N	0.01	0.44^{***}
	Litter HLQ	–0.14	0.54^{**}
	Ext. soil NO_3-N	0.31	0.64^{***}
	Total soil K	0.24	0.70^{***}
ln P Mineralization	Litter P	–0.71	0.51^{***}
	Total soil P	0.53	0.79^{***}
	Ext. soil Mg	–0.45	0.82^{**}
N mineralization	Total soil N	0.60	0.35^{***}
	Litter N	–0.48	0.58^{***}
	Litter ether	0.28	0.64^{**}
	Ext. soil Mg	–0.50	0.68^{**}
ln Mg mineralization	Total soil K	–0.54	0.29^{***}
	Litter acid soluble	–0.49	0.53^{***}
	Total soil Ca	0.34	0.65^{***}
	Ext. soil NH_4-N	0.06	0.72^{***}
	Ext. soil Mg	0.34	0.75^{*}
	Litter ether	–0.20	0.77^{*}
Ca mineralization	Total soil P	–0.58	0.33^{***}
	Total soil Ca	0.44	0.48^{***}
	Ext. soil NH_4-N	–0.05	0.54^{**}
	Total soil K	–0.55	0.59^{**}
	Ext. soil Ca	0.49	0.63^{*}
K mineralization	Litter acid soluble	0.77	0.59^{***}
	Ext. soil Ca	0.35	0.71^{***}
	Total soil Ca	0.26	0.73^{***}
	Ext. soil NH_4-N	0.08	0.79^{***}

*** $P \leqslant 0.001$, ** $P \leqslant 0.01$, * $P \leqslant 0.05$

Units as in Tables 1 and 3. Ext. = extractable, HLQ = holocellulose quotient.

Immobilization-mineralization: cross-community comparison

Immobilization and mineralization are defined as the increase or decrease, respectively, in the absolute amount of a nutrient in decaying litter over time. For clarity, our data are presented as a percentage of the initial amount of a nutrient in the litter, with immobilization being a positive value and mineralization a negative value. Nutrient contents of the litter bags were only measured after 1 yr. This should be a period of active immobilization if it is going to occur, as leaching of initial

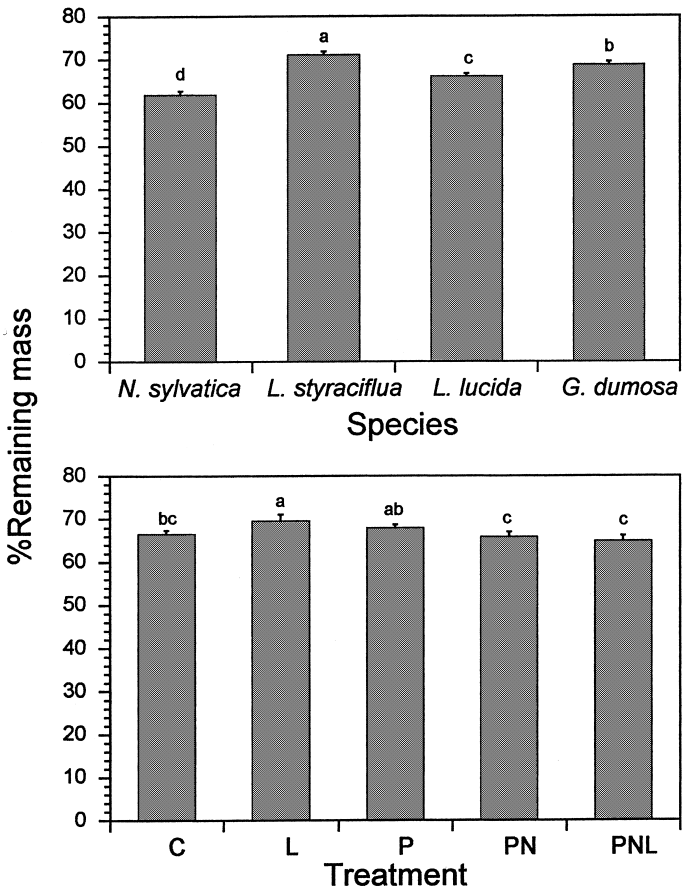

Figure 2. Percent remaining dry mass of litter after 1 year of decomposition in fertilization and liming treatments in the short pocosin. Litter types as in Figure 1. Treatments were control (C), + lime (L), + phosphorus (P), + phosphorus and nitrogen (PN), and + phosphorus, nitrogen, and lime (PNL). Significant differences ($P < 0.05$) among litter types or treatments are shown by different letters. Error bars indicate 1 standard error.

soluble compounds should be completed and maximum immobilization occurs in the early stages of decomposition (Aber and Melillo 2001).

In the cross-community comparison, P dynamics showed a range of responses from large immobilization gains to small mineralization losses (Figure 4). A very strong interaction was evident between community and litter type ($P < 0.001$ for main effects and interaction term). For all litter types, the greatest immobilization, or smallest mineralization, of P occurred in the gum swamp with its high exogenous nutrient supply. In the two litter types with the lowest initial endogenous P concentration, *L. lucida* and *G. dumosa*, P immobilization occurred in all communities except in the extremely P-deficient short pocosin. Phosphorus was mineral-

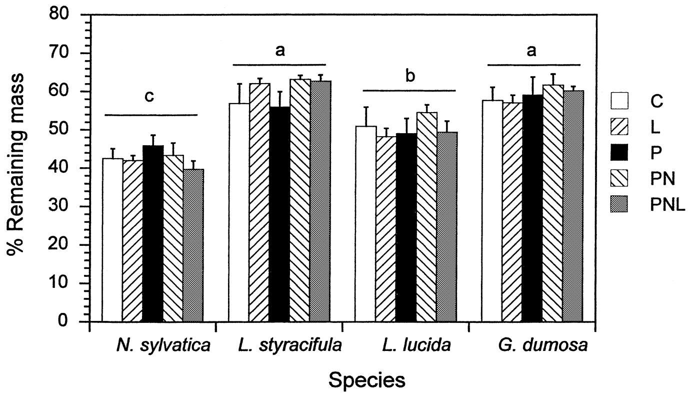

Figure 3. Percent remaining dry mass of litter after 3 years of decomposition in fertilization and liming treatments in the short pocosin. Litter types and treatments as in Figures 1 and 2. Significant differences ($P < 0.05$) among litter types are shown by different letters. Error bars indicate 1 standard error.

ized in *L. styraciflua* and *N. sylvatica*, except for a small immobilization (4%) in *N. sylvatica* in the nutrient-rich gum swamp.

When exogenous and endogenous factors were combined in a stepwise regression, 82% of the variation in P immobilization-mineralization was explained by only three factors, initial litter P concentration, total soil P content, and extractable soil Mg content (Table 4). The first two factors explained 79% of the variation, suggesting the dominant influence of exogenous P availability and endogenous P concentration on P immobilization-mineralization dynamics.

Nitrogen immobilization-mineralization dynamics in the cross-community comparison were qualitatively similar to those for phosphorus ($P < 0.001$ for main effects, $P = 0.003$ for interaction; Figure 4). The greatest immobilization of N occurred in the N-rich gum swamp in all litter types. The two litter types with the lowest initial N concentration, *L. lucida* and *G. dumosa*, had greater N immobilization in all communities, except for the short pocosin where significant differences did not occur among litter types. In the stepwise regression, 68% of the variation in N dynamics was explained by total soil N content, initial litter N and ether-extractable concentrations, and extractable soil Mg content (Table 4). Thus, as with P, exogenous N availability and endogenous N concentration were of primary importance in explaining N mineralization-immobilization dynamics (explaining 58% of the variance alone).

Magnesium, Ca, and K had large mineralization losses in all communities (Table 5). For all three cations, there was a significant or marginally significant effect of both community and litter type on mineralization rates ($P < 0.001$; except litter-type effect for Ca, $P = 0.09$), but the interaction between the two factors was always insignificant ($P > 0.49$), suggesting exogenous and endogenous factors acted independently. For both Ca and Mg, mineralization was greatest in the gum swamp and lowest in the drained pocosin. For K, mineralization was greatest in the short pocosin and lowest in the drained pocosin. Thus, drainage appears to impede min-

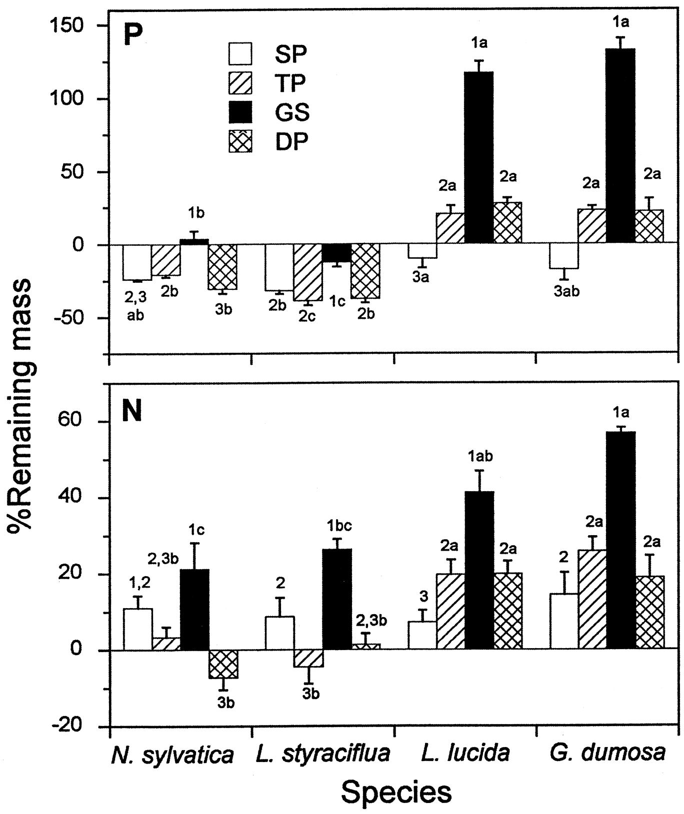

Figure 4. Percent mineralization (negative) or immobilization (positive) of P and N in litter after 1 year of decomposition in untreated short pocosin (SP), tall pocosin (TP), gum swamp (GS), and drained pocosin (DP) plots for four litter types. Significant differences ($P < 0.05$) among communities within a litter type are shown by different numbers, whereas significant differences among litter types within a community are shown by different letters. Error bars indicate 1 standard error.

eralization of these cations from litter. Mineralization of Mg among litter types was in the order *N. sylvatica* > *G. dumosa* > *L. styraciflua* > *L. lucida* (Table 5). Although the overall litter type effect for Ca mineralization was weak ($P = 0.09$), pairwise comparisons suggested Ca mineralization was greater in *N. sylvatica* than in *L. styraciflua* (FLSD $P = 0.015$). Litter-type effects were quite different for K mineralization, with fastest mineralization in *L. styraciflua* and *L. lucida* and slowest in *N. sylvatica*.

The stepwise regressions explained from 63 to79% of the variance in the mineralization dynamics of the three cations (Table 4). A variety of factors entered into the equations, without any necessary obvious cause-effect relationship. Perhaps most pertinent, endogenous concentrations of the cations never entered into their own mineralization equations, although exogenous availability appeared to be important for Ca and Mg mineralization. The majority (59%) of the variation in K

Table 5. Mineralization rates (% loss) for Mg, Ca, and K of four litter types in four different communities after 1 year.

Main effects	Mg	Ca[1]	K
Site			
Short pocosin	−76.2 (3.1)^{b}	−53.1 (4.1)^{b}	−78.7 (1.8)^{a}
Tall pocosin	−66.7 (3.3)^{c}	−42.9 (2.6)^{bc}	−75.2 (1.9)^{b}
Gum swamp	−84.0 (2.6)^{a}	−75.0 (5.3)^{a}	−76.5 (1.8)^{ab}
Drained pocosin	−60.3 (3.5)^{d}	−32.5 (2.9)^{c}	−70.3 (1.8)^{c}
Species			
N. sylvatica	−82.6 (1.4)^{a}	−53.5 (3.4)^{a}	−62.9 (1.4)^{d}
L. styraciflua	−65.9 (2.9)^{c}	−36.1 (4.8)^{b}	−77.6 (0.9)^{a}
L. lucida	−60.7 (3.0)^{d}	−48.4 (4.3)^{ab}	−79.4 (1.2)^{a}
G. dumosa	−74.9 (2.2)^{b}	−42.0 (5.1)^{ab}	−74.8 (1.1)^{c}

Means ± (SE). Different letters within a column indicate significant differences among communities or litter types.

[1] ANOVA P-value for species effect was 0.088.

mineralization was explained by the initial acid-soluble fraction of the litter, suggesting a strong carbon quality control over K mineralization.

Immobilization-mineralization: fertilization and liming experiment

Similar effects of exogenous P availability and endogenous P conconcentration of litter on P immobilization-mineralization were evident in the fertilizer and liming treatments in the short pocosin (Figure 5). Much greater P immobilization occurred in the P, P + N, and P + N + lime treatments, especially for *L. lucida* and *G. dumosa* ($P < 0.001$ for main effects and interaction term). The particularly high immobilization values obtained in the P + N + lime treatment is likely due to the formation of Ca-P complexes.

There were also significant treatment and litter-type effects on N immobilization ($P \leqslant 0.001$), but the interaction effect was insignificant ($P = 0.42$). Nitrogen fertilization enhanced N immobilization with the highest values in the P + N and P + N + L treatments (Figure 5). *G. dumosa* had the greatest N mineralization (Figure 5), although it had moderate initial endogenous N concentrations (Table 3).

Discussion

Mass loss: exogenous factors

Our results show that both site conditions and initial litter quality provide strong controls over the decomposition of wetland leaf litter. We examine the relative strength of these exogenous and endogenous controls over litter decay over both

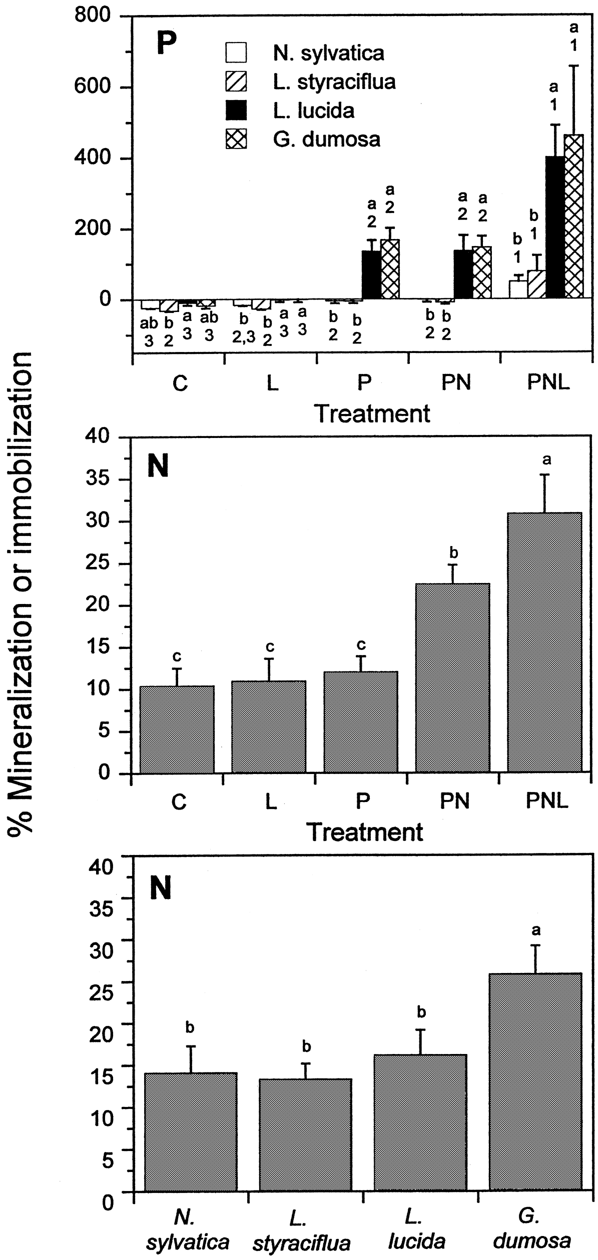

Figure 5. Percent mineralization (negative) or immobilization (positive) of P and N in litter after 1 year of decomposition in fertilization and liming treatments in the short pocosin. Treatments and litter types as in Figures 1 and 2. In the top panel (with significant interactions), differences ($P < 0.05$) among treatments within a litter type are shown by different numbers, whereas differences among litter types within a treatment are shown by different letters. For N, only the main effects were significant, so interaction effects are not shown. Error bars indicate 1 standard error.

the short term (1 yr) and intermediate term (3 yr) below. We consider first exogenous factors (pH, water table, soil nutrient and cation availability) and secondly endogenous factors (carbon quality, nutrient concentrations of litter).

In the cross-community comparison, despite the significant interactions among time, community, and litter type, it was clear that greatest mass loss occurred in the drained pocosin plots after both 1 and 3 yr and lowest mass loss occurred in the short pocosin (yr 1 and 3) and the gum swamp (yr 3) (Figure 1). The soil chemistry of the drained pocosin and short pocosin are very similar (with the exception of Ca—but see below), suggesting that exogenous nutrient availability and pH were not important factors in explaining the differences in decay rates between these two sites. Surface soil moisture content, water-table level, and the proportion of the soil profile that was anaerobic were highest in the short pocosin and lowest in the drained plots during the incubation period (Bridgham and Richardson 1993). The gum swamp had the most seasonally variable hydrology, with wet conditions in the winter and a water table often > 1 m from the surface during the growing season. However, there was only occasionally standing water in any site, so the litter bags experienced aerobic conditions during the majority of the time. Other studies have found that alternating flooded/dry conditions maximized decomposition (Brinson et al. 1980; Day 1983; Mitsch and Gosselink 1993; Lockaby et al. 1996a, 1996b), on which we based hypothesis 1 (see *Introduction*), but in this study we found a significant positive effect of drainage on the decomposition of surface litter.

The fertilization treatments in the short pocosin reinforce the results from the cross-community comparison that exogenous nutrient concentrations do not inhibit decomposition in these wetlands, in support of hypothesis 2. There were only significant fertilization effects in yr 1, with lower mass loss in the + P treatment relative to treatments where P and N fertilization were combined (N + P, N + P + L) (Figure 2). Additionally, treatment differences were small (< 5% difference among means).

In support of hypothesis 3, there was only a significant lime effect on mass loss in yr 1, and then lime actually inhibited decay in the short pocosin, although the soil pH was initially < 4. High soil acidity in wetlands has been shown to inhibit microbial activity (Benner et al. 1985; Kok et al. 1990; Cirmo et al. 2000). However, others have found that peatland microflora are optimally adapted to low pH conditions (Williams and Crawford 1983; Goodwin and Zeikus 1987; Bridgham and Richardson 1992; Chapin 1998). Our results support this latter conclusion.

However, basic soil cation availability could directly limit microbial activity, apart from any correlative relationship with pH. Total soil Ca content was negatively correlated with the remaining mass of litter in the stepwise regression model (Table 4) because of the high soil Ca content in the drained pocosin (Table 1) with its high decay rates. However, one needs to be cautious in ascribing cause-effect to correlations, and we suggest that this result was spurious. The negative (yr 1) or neutral (yr 3) effect of liming on mass loss in the short pocosin plots and the large mineralization losses of Ca in the litter bags (Table 5) suggest that low soil Ca content was not limiting decay rates.

Mass loss: endogenous factors

The stepwise regression results indicated that litters with low initial soluble phenolic concentrations decayed faster (Table 4). Despite its apparent importance in determining decay rates, initial concentrations of soluble phenolics were < 4% of dry mass (Table 3). Soluble phenolics in litter are easily leached, but they also may slow decomposition by directly inhibiting microorganisms, binding proteins and polysaccharides, and inactivating enzymes (McClaugherty 1983; Palm and Sanchez 1990). Phenolics have been shown to inhibit decomposition (Nicolai 1988; Palm and Sanchez 1990), nitrification (Baldwin et al. 1983), and N mineralization (Northrup et al. 1995). Phenolic concentrations in vegetation are often higher in more acidic and nutrient-deficient environments (Nicolai 1988; Northrup et al. 1995; Richardson et al. 1999).

The holocellulose quotient (acid-soluble fraction/acid-soluble + acid insoluble fractions) was also significant in the stepwise regression (Table 4), although its individual effect was insignificant. The holocellulose quotient represents the portion of the structural carbon compounds that are relatively easily decomposable and has been found to be a powerful predictor of decay in other studies (McClaugherty and Berg 1987; Melillo et al. 1989; DeBusk and Reddy 1998).

Either the initial N concentration in litter or the lignin:N ratio have been found to be important in determining decay rates in many studies (see *Introduction*). Despite the low initial nutrient concentrations in the short pocosin litter, endogenous nutrients were not important in explaining differences in decay rates in this study. Thus, our results support hypothesis 2 that neither endogenous nutrient concentrations nor exogenous nutrient availability are important in controlling decay rates in these sites.

Aber and Melillo (2001) suggested a general model of decomposition with the initial stages of decomposition limited by nutrients and the later stages limited by the low carbon quality of the remaining litter because of the progressive microbial consumption of labile carbon substrates. In this study, we found no initial period of nutrient limitation of decomposition (as measured by mass loss at 1 yr) due to the very low initial carbon quality of the four litter types used in this study, particularly as indicated by the high initial acid-insoluble concentrations (Table 3). Others have also shown a greater stimulatory effect of either endogenous or exogenous N on the decay of litter with low lignin concentrations than on litter with high lignin concentrations (Taylor et al. 1989, 1991; Hobbie 2000).

Qualls and Richardson (2000) suggested that the N:P ratio of the litter determines if P limits decay rates. They demonstrated that sawgrass (*Cladium jamaicense*) and cattail (*Typha domengensis*) litter, with initial N:P ratios of 73 and 37 respectively, had faster decay rates with exogenous P additions. Furthermore, DeBusk and Reddy (1998) obtained litter of these two species from a P-fertilization gradient and showed that decomposition was faster in litter with higher endogenous P concentrations. A N:P ratio of 10:1 has been suggested as the cut-off point for P-limited decomposition (Alexander 1977). However, in our study litter had initial N:P ratios ranging from 10 to 27, and we found no evidence of P limitation of decomposition. We suggest that any theory of the effects of N:P ratios of litter on decay rates must also consider litter carbon quality.

Immobilization-mineralization

As we only examined immobilization-mineralization dynamics after yr 1, our results only reflect the short-term period of decomposition when immobilization would be expected to be greatest. As opposed to mass loss dynamics, immobilization-mineralization dynamics of N and P depended heavily on the interaction between endogenous nutrient concentrations and exogenous nutrient availability and support hypothesis 4. Within the cross-community comparison, greatest P and N immobilization occurred in the litter from the short pocosin (*G. dumosa* and *L. lucida*) when placed in the gum swamp (Figure 4). Similarly when considering the short pocosin treatments, greatest P immobilization occurred in short pocosin litter placed in the P fertilized plots, with small changes in total P content in litter from the gum swamp, irrespective of treatment (Figure 5). Greatest N immobilization occurred in the *G. dumosa* litter in the N fertilized plots. Thus, we demonstrate that N and P immobilization-mineralization dynamics are dependent on both source and sink terms, with the source term being exogenous nutrient availability and the sink term being endogenous nutrient concentration (i.e., low initial nutrient concentrations in litter lead to a large sink term). When the source and sink terms were large, we observed substantial nutrient immobilization.

Endogenous nutrient concentrations in litter often have been expressed as a C:nutrient ratio. This ratio is typically examined within the context that the decomposing microbial community immobilizes nutrients from the surrounding environment until the C:nutrient ratio of the organic substrate approximates their internal ratio (Swift et al. 1979). The litter in this study had high initial C:N and C:P ratios (58 to 126 and 633 to 3333, respectively), and immobilization of N and P often occurred (Figures 4 and 5). The initial C:N and C:P ratios of the litter used in our experiment were much higher than the ratios found by Tezuka (1990) to be the maximum for N and P mineralization to occur in bacteria cultures (i.e., the critical ratio, C:N ratio $< 15:1$, C:P ratio $< 60:1$). Tezuka (1990) cautioned that in substrates with high concentrations of complex structural carbon compounds, the effective maximum C:nutrient ratios for mineralization could be much higher. Stevenson (1986) suggested a critical C:P ratio for soil organic matter of 200 to 300:1 and a critical C:N ratio of 20 to 30:1. Phosphorus mineralization in our experiment occurred with C:P ratios less than about 820:1, while N was generally immobilized. Thus, our data demonstrate the difficulty of using C:nutrient ratios to predict mineralization-immobilization dynamics in litter because of the heterogenous lability of different organic compounds, and the importance of also considering exogenous nutrient availability.

As opposed to N and P mineralization-immobilization dynamics, the stepwise regression results suggest that mineralization of Mg, Ca, and K were not controlled by endogenous concentrations of these cations. Exogenous concentrations of Mg and Ca were important in their mineralization dynamics, whereas K mineralization appeared to be primary controlled by the initial holocellulose concentration of the litter.

The relative magnitude of mineralization for the short pocosin species, *L. lucida* and *G. dumosa*, was K $\geqslant$ Mg > Ca >> N $\geqslant$ P. Losses of K and Mg were large, losses of Ca were moderate to small, and N and P showed small mineralization losses to large immobilization gains. For the gum swamp species, *L. styraciflua* and *N. sylvatica*, the relative magnitude of mineralization was K > Mg > Ca > P > N. Loss of Mg was greater than K from *N. sylvatica*. The relative magnitudes of mineralization (or immobilization) of *L. styraciflua* and *N. sylvatica* were similar to the short pocosin species. Other studies have found that N and P are often immobilized, rapid leaching of K, and moderate rates of loss for Ca and Mg (Chamie and Richardson 1978; Schlesinger and Hasey 1981; Waring and Schlesinger 1985; O'Connell 1988; Qualls and Richardson 2000).

Synthesis

We found that both exogenous and endogenous factors were important in controlling decay rates and nutrient mineralization-immobilization dynamics of litter in North Carolina peatlands. The most important site factor controlling decay rates was water table, with greater rates of decomposition in drained sites. High initial soluble phenolic concentrations and a low holocellulose quotient in litter also inhibited decay rates. Despite the extremely low nutrient availability in the pocosins and low soil pH in all three communities, both the cross-community comparison and the amendment experiment in the short pocosin demonstrated that exogenous nutrient availability, endogenous nutrient concentrations in litter, and low soil pH do not inhibit litter decomposition in these sites. Probably because of the low initial carbon quality of the litter, we did not observe a change from nutrient limitation to carbon limitation of decomposition over time, as has been suggested by others as a general model of decomposition dynamics (Taylor et al. 1989; Berg and Matzner 1997; Aber and Melillo 2001). Immobilization-mineralization dynamics of N and P were largely driven by a source-sink relationship, with greatest immobilization with high exogenous nutrient availability and low initial endogenous nutrient concentrations.

Based on our results and the literature, we suggest the following conceptual model of factors that control decomposition and nutrient cycling in litter as a function of endogenous and exogenous nutrients (Figure 6). There is substantial theoretical and empirical evidence to suggest that plants adapted to low-nutrient environments have foliage with low nutrient concentrations and low carbon quality, e.g., greater sclerophylly, specific leaf area (leaf mass per area), concentrations of structural compounds such as cellulose and lignin, and concentrations of inhibitory compounds such as phenolics (Northrup et al. 1995; Reich et al. 1997; Richardson et al. 1999; Aerts et al. 1999; Jonasson and Shaver 1999). Plants adapted to low-nutrient environments also have a number of adaptations in terms of growth, with generally higher nutrient-use efficiency, longer leaf life-span, low maximal photosynthetic rates, low growth rates, and low physiological ability to respond to nutrient additions (Chapin 1980; Chapin et al. 1986; Chapin 1998; Aerts and Chapin 2000). Plants adapted to nutrient-rich environments tend to have the opposite set of traits. These physiological trends in plant response to nutrient availability have been related to herbivory (Coley et al. 1985; Grime et al. 1996), but here we extend this theory to consider direct and indirect effects of nutrients on decomposition (Figure 6).

In an initially low nutrient environment, fertilization often causes an increase in nutrient concentration in plants, whether accompanied by an increase in growth (i.e., a limiting nutrient) or due to luxury uptake (Chapin 1980; Chapin et al. 1986). However, we have found no increase in foliar nutrient concentrations of many northern peatland plants even after prolonged fertilization (Chapin (1998); Iversen and Bridgham, unpublished data). There may also be an accompanying increase in litter nutrient concentrations, as seen in Table 3, but there may be little change in litterfall mass if the plants are inherently slow growing and have low physiologically ability to respond to greater nutrient availability (Chapin 1980; Chapin et al. 1986). Because plants from low nutrient environments have low carbon-quality litter, decomposition rates will be unaffected by the increase in either endogenous nutrient concentrations or exogenous nutrient availability. If greater nutrient availability leads to better litter carbon quality, for example through increased amino acid or soluble carbohydrate concentrations or decreased lignin or phenolic concentrations (Northrup et al. 1995), then there should be an increase in decay rates. However, this change in carbon quality will likely be minimal unless continued fertilization leads to replacement by species adapted to more nutrient-rich environments with their correspondingly higher carbon-quality litter. Thus, the net effect of fertilization on decay rates should be minimal in an initially low nutrient environment, until plant species replacement occurs.

The increase in endogenous nutrient concentrations in litter should suppress nutrient immobilization and possibly even cause a shift to net nutrient mineralization. In contrast, increasing exogenous nutrient availability will enhance nutrient immobilization. It is the balance between these two processes, plus any increase in litter mass from a nutrient effect on productivity, that will determine ecosystem nutrient retention in the litter layer.

In contrast, fertilization of a moderate-to-high nutrient environment should lead to greater plant growth, litterfall mass, and nutrient concentrations of litter. As plants adapted to such environments typically have high carbon-quality litter, decay rates should be enhanced in the initial phases of decomposition with carbon-limitation occurring in later phases of the decay continuum (Taylor et al. 1989; Berg and Matzner 1997; Aber and Melillo 2001).

Hobbie and Vitousek (2000) suggested that nutrient control over ecosystem production and decomposition are decoupled. Whereas addition of a limiting nutrient may enhance net primary production and increase the nutrient content of vegetation, this often is not accompanied by a corresponding increase in decay rates, potentially resulting in carbon and nutrient accumulation within the ecosystem. Nu-

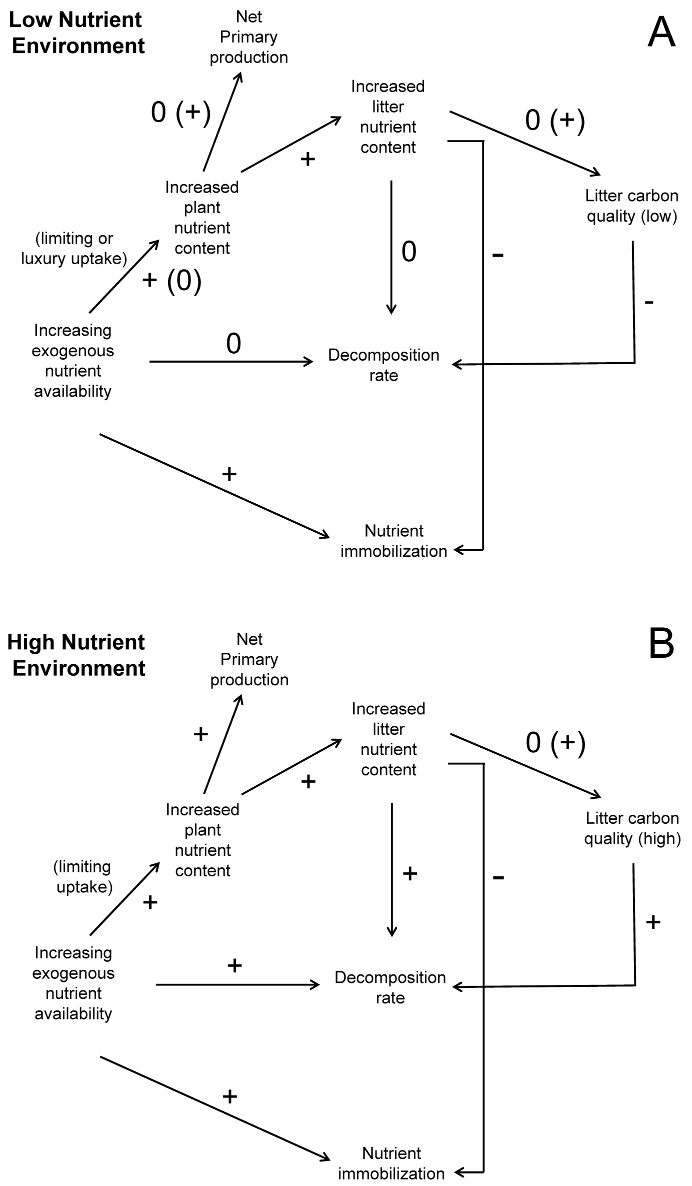

Figure 6. A conceptual model of how changes in exogenous nutrient availability affects decomposition rates and nutrient immobilization in low nutrient and high nutrient environments. Positive effects are shown by '+', negative effects by '–', and neutral effects by '0'. Effects in parentheses indicate alternative possibilities based upon inconsistent results among previous studies.

trient retention is further enhanced if increasing exogenous nutrient availability leads to greater nutrient immobilization in litter without an accompanying increase in decay rates. Our decomposition results partially support their hypothesis in initially low-nutrient environments. However, increasing exogenous nutrient availability may lead to increasing endogenous litter nutrient concentrations, which will decrease immobilization in litter and provide a negative feedback on ecosystem nutrient retention. Thus, nutrient retention in the litter layer of a fertilized ecosystem may be primarily driven by changes in litter inputs, with little long-term change in immobilization-mineralization dynamics on a mass-specific basis.

Finally, we wish to emphasize that our conceptual model encompasses only plant-litter-nutrient interactions over the short-to-intermediate phases of decomposition. Fertilization effects on nutrient retention in soils below the litter layer may be quite different, including inhibitory effects of N on humus decomposition (Berg and Matzner 1997; Fenn et al. 1998; Magill and Aber 1998), stabilization by organic-mineral complexes in mineral soil, and geochemical sinks and sources (Richardson 1999; Richardson and Quin 1999). However, Qualls and Richardson (2000) suggest that nutrient immobilization during the first year of decomposition is a critical, and perhaps the dominant, step in long-term nutrient storage in soil from agricultural run-off in the Everglades.

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