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GENERAL PAPER

Wetland plant decomposition under different nutrient conditions: what is more important, litter quality or site quality?

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Abstract Plants in nutrient poor environments are often characterized by high nutrient resorption resulting in poor litter quality and, consequently, slow decomposition. We used oligotrophic, P-limited herbaceous wetlands of northern Belize as a model system, on which to document and explain how changes in nutrient content along a salinity gradient affect decomposition rates of macrophytes. In 2001 we established a nutrient addition experiment (P, N, and N&P) in 15 marshes of a wide range of water conductivities (200–6000 μS), dominated by *Eleocharis* spp. To determine what is more important for decomposition, the initial litter quality, or site differences, we used reciprocal litter placement and cellulose decomposition assay in a combined ''site quality'' and ''litter quality'' experiment. Our prediction of the positive effects of P-enrichment on decomposition rate due to both the quality of litter and the site was confirmed. The site effect was stronger than the litter quality although both were highly significant. Strong site quality effect was apparently the result of more active decomposer community in P-enriched plots as supported by finding of higher microbial biomass in litter decomposing there. The strong effect of site quality on decomposition was further confirmed by the cellulose assay. The cellulose decomposition was significantly slower at high salinity sites indicating lower decomposer microbial activity. Litter nutrient N and P content and nutrient ratios were well correlated with decomposition with the best fit found for log C/P. At C/P mass ratio of >4000 decomposition processes were extremely slow. We hypothesize that in a long run, the increased decomposition will compensate the increase in primary production resulting from increased nutrient loading and there will be no differences in accumulation of organic material between the controls and nutrient enriched plots.

Keywords *Eleocharis cellulosa* · Northern Belize · Litter bags · Cellulose · Nitrogen · Phosphorus · PLFA

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Introduction

Decomposition is a fundamental process in ecosystem carbon flux and nutrient cycling (Hoorens et al. 2003), especially so in ecosystems where little of primary production is consumed as a living tissue and

most ends up in the detritus food chain (Ayyappan et al. 1986; Menéndez et al. 2003). Wetlands are often characterized by low herbivory and, unless impacted by humans, they are often ecosystems with low nutrient input. In these limited nutrient environments, the continued availability of nutrient resources often depends on decomposition of organic material (Aerts and De Caluwe 1997; Shaver and Melillo 1984; Talling and Lemoalle 1998; Alvarez and Guerrero 2000).

Decomposition processes are regulated by three interacting sets of factors: physico-chemical environment, the quality or organic material, and the decomposing organisms (Coûteaux et al. 1995; Royer and Minshall 1997; Morris and Bradley 1999; Liski et al. 2003; Bünemann et al. 2004). In systems where temperature and moisture are not constraining, the most important determinants of decomposition rates are chemical properties of the decomposing material (litter quality), and nutrient availability and decomposer activity at the site where the decomposition occurs (site quality) (Vitousek 2004). Decomposition rates are usually related to litter quality indicators such as C:N, C:P, lignin:N and N:P ratios (Aerts 1997).

Plants in nutrient poor sites are often characterized by high nutrient resorption resulting in a poor litter quality and, consequently, low decomposition rates (Enriquez et al. 1993; Aerts and Chapin 2000; Rejmánková 2001). What happens with increased nutrient inputs? Nutrient enrichment increases primary productivity but also microbial activity and decomposition rate (Gulis and Suberkropp 2003). It also leads to shifts in composition of both plant and microbial communities (Paterson 2003). These shifts then have a potential to affect decomposition and nutrient dynamics (Hobbie and Gough 2004; Lovett et al. 2004). A thorough understanding of these processes can only be gained by long-term experiments providing data on ecological consequences of increased nutrient loading.

We have used the oligotrophic P-limited herbaceous wetland ecosystems of northern Belize as a model system, on which to document and explain how changes in nutrient limitation can be shifted through different constraints on individual components of plant communities along a salinity gradient. In 2001 we have established a long-term nutrient addition experiment, involving additions of nutrients to a set of 15 marshes covering the whole range of water conductivities and dominated by sparse macrophytes (*Eleocharis* spp.). In this paper, we report the effects of nutrient enrichment on decomposition rates and dynamics of C, N and P associated with litter and cellulose decay in controls and nutrient enriched plots in these 15 marshes. Nutrient loading to wetland ecosystems may increase decomposition rates as the nutrient conditions for the microorganisms improve (Holmboe et al. 2001). We hypothesized that the improved P balance in P enriched plots allows better development of the microbial decomposer community and thus faster decomposition, and that decomposition rates are slower at higher salinity as a result of salinity constraint on decomposing microbial community. We also hypothesized that better quality litter originating from nutrient enrichment plots decomposes faster. The objective of this study was to determine what is more important for decomposition: the initial litter quality differences or site differences. To sort out these differences, we used reciprocal litter placement and cellulose decomposition assay in a combined ''site quality'' and ''litter quality'' experiment (Vitousek 2004). In addition, we used the information on decomposition rates of nutrient enriched litter to predict if these rates are high enough to prevent accumulation of organic material. High organic material accumulation results from increased primary production under high nutrient loading. We also attempted to use nutrient ratios of decomposing litter as predictors of decomposition rates.

Methods

Study site

Our study sites are located in lowlands of northern Belize within a 50 km radius of 18°9′58″ N and 88°31′28″ W. This part of the Yucatan Peninsula is an uplifted marine platform composed of a 2–3 km thick sequence of Cretaceous and Tertiary limestone, dolomite, anhydrite, and gypsum (Weidie 1985). Marsh hydrology is closely linked to the ground water system, and water levels are controlled primarily by regional precipitation patterns. Most of the

coastal plain contains a fresh water lens many meters thick floating on seawater. Porous limestone aquifer allows intrusion of seawater far inland and, as a result, mixing of fresh and marine waters can occur in coastal aquifers. Furthermore, the ''fresh'' ground waters are nearly saturated with carbonate and sulfate, derived from dissolution of the limestone, dolomite, anhydrite, and gypsum in the platform rocks. The net result of these factors is that the conductivity of the inland wetlands varies by several orders of magnitude and chemical analyses of ion content revealed large differences in sulfate, bicarbonate and chloride, suggesting complex and varied sources of these waters. The climate of the Yucatan peninsula is tropical wet–dry in Koeppen's classification. The majority of wetlands in the study area remain flooded or water saturated year round, although the total flooded area may vary as water levels rise and fall (changes of <50 cm are typical).

Main primary producers in these systems are several species of emergent macrophytes (*Eleocharis cellulosa*, *E. interstincta*, *Cladium jamaicense* and *Typha domingensis*) and species rich communities of microphytes represented mostly by cyanobacteria (Rejmánková et al. 2004). Both macro- and microphytes in these wetlands are generally P limited. Phosphorus limitation has been experimentally confirmed in cyanobacterial mats (Rejmánková and Komárková 2000) and *Eleocharis* dominated marshes (Rejmánková 2001). No nitrogen limitation has been detected in any of the reported studies.

Until the mid-19th century, agriculture in Belize was rather insignificant (King et al. 1992). Sugar cane cultivation was established in the 1850's, but most expansion has occurred during the last 30 years and it is still rising. Fertilizer runoff from the sugar cane fields and other crops, and increased population density contribute to continuing water eutrophication.

Fifteen marshes, five in each low, medium and high salinity category, dominated by sparse macrophytes (*Eleocharis* spp.) have been studied as a part of a project aimed at the assessment of ecosystem response to nutrient addition along a salinity gradient. Briefly, four 10×10 m plots were established in each marsh in August of 2001, one represents a control, the remaining three received N, P and N&P addition once in August 2001 and the second time in August 2002. N was added as ammonium nitrate and P as triple super phosphate in the amounts corresponding to 20 and 10 g m^{-2} y^{-1}, respectively.

Litter bags

In March and April of 2003 (dry season) we collected *Eleocharis* standing dead shoots in each of the four plots in 15 marshes. Five grams of air-dried plant material cut into approximately 3–5 cm long pieces were placed into 1-mm mesh litter bags (15×18 cm) to allow four replicates and five harvests in each plot. In addition to having plant litter from each plot decomposing in its ''home'' plot, we placed bags with litter from controls to NP plots and vice versa. The resulting six treatments were designated: control litter in control=C; NP litter in control = NP–C; P litter in P plot = P; N litter in N plot = N; NP litter in NP plot = NP; and control litter in NP plot = C–NP. We will use these abbreviations throughout the text. Subsamples from each plot were used to determine the air dry to oven dry (70°C) conversion and initial chemistry (see below). The bags were placed in the marsh plots on August 10–12, 2003 and they were loosely attached with dental floss to stakes that kept them close to the bottom. Four replicate bags were collected from each of the six treatments on day 27, 84, 149, 220, and 258. The experiment was terminated in late April (after less than a year), because by May, some of the marshes started drying up and we did not want to include different levels of desiccation as yet another factor. The cellulose decomposition assay (Ulehlová 1976; Kurka et al. 2000) was conducted in each plot using eight litter bags with cellulose filters (Whatman # 1; 12 cm diam.) to allow for two harvests. Cellulose filters were collected on day 28 and 84. Upon harvest, litter was removed from the bags, a composite subsample from all four replicates was immediately frozen for PLFA analysis, another subsample was kept refrigerated for the enzyme analysis (not shown here) and remaining material was dried, weighed, ground and used for nutrient analyses.

Nutrient analyses

Samples were analyzed for N and C content on a Carlo-Erba series 5000 CHN-S analyzer. Total phosphorus was analyzed using ascorbic acid reduc-

tion of phosphomolybdate complex (Hunter et al. 1993) after acid digestion. The total soluble phenolic content was determined colorimetrically using Folin–Ciocalteau reagent (SIGMA F9252) and *p*-coumaric acid as a standard (Waterman and Mole 1994). The concentration of lignin was determined according to Iiyama and Wallis (1989).

Leaching

To asses the amount of P leached from litter, 0.5 g of dry litter was placed in the acid washed 50 ml centrifuge tubes, filled with distilled water and let to shake on a slow shaker for 1 week. We used only a subset of litter from six control plots and six NP plots (two in each salinity category) for leaching assessment. The leachate was filtered through 0.45 μm milipore filter, frozen and later analyzed for soluble reactive phosphorus (SRP) using ascorbic acid reduction of phosphomolybdate complex (Hunter et al. 1993).

Phospholipid fatty acid (PLFA) analysis

Lipids for PLFA analysis were extracted for 2 h with a chloroform:methanol:phosphate buffer from 2 g of frozen litter. Phospholipids were then separated from neutral lipids and glycolipids on solid phase extraction column, 0.50 g Si (Supelco, Inc. Bellefinte, Penn.), and subjected to mild alkaline methanolysis to recover fatty acid methyl esters. Since the quantity of microbial PLFA is a function of microbial biomass (Hassett and Zak 2005), we used the total amount of all bacterial PLFA identified in the samples as an index of live microbial biomass.

Data analysis

Litter decomposition was expressed as the proportion of initial mass remaining at each harvest. We determined the exponential decay constant, k, from a single exponential decay model:

$$X_t = X_0 e^{-kt},$$

where X_t = litter mass at time t (days) and X_0 = initial mass.

Hierarchical (nested) ANOVA with location (marsh) nested within salinity level was used to test the effect of variables on decomposition rate. Treatment was used as within location factor, salinity as between location factor. To satisfy ANOVA model assumption, we log transformed some of the variables to normalize the data.

Results

Figures throughout the result section present combined means for individual treatments from all 15 marshes for those response variables that did not show any differences among the three salinity categories and separate means for individual salinity categories when a salinity effect was detected.

Litter quality and site characteristics

The initial N litter content, ranging from 0.42 to 1.08%, did not vary significantly among the three salinity levels but there were slight but significant differences between the treatment plots (C, P, N, N&P). At each salinity level, the litter from C and N plots had lower N content than litter from P and N&P plots (Table 1). Large differences were found in the initial P litter content among individual treatments with P and N&P litter having up to 23× more P than litter from C and N treatments. For initial P content we also detected a slightly significant effect of salinity ($P = 0.1$), with high salinity litter containing less P than litter from medium and low salinity plots. Lignin and soluble phenolic contents in the litter were low with means of 1.32 and 0.71%, respectively, and there were no differences between plants from nutrient enriched and control plots. There was no relationship between phenolic or lignin content or lignin/N ratio and decomposition (data not shown).

Means of water salinity expressed as specific conductivity, pH, soluble reactive phosphorus (SRP), and ammonium nitrogen for each treatment and each salinity class are given in Table 2. In addition to water characteristics, the table also lists the sediment P and N content and aboveground biomass value for macrophytes as an indicator of plant productivity. Only the sediment P and plant biomass differed significantly among treatments, both being higher in P and N&P treatments (Table 1). (Note, that sediment P values are from the upper 2 cm of the sediment; N values are from the upper 10 cm)

Table 1 Initial and final litter characteristics, remaining litter mass at the end of the experiment, and mean decay constants, k, for individual treatment and three salinity levels; $n = 5$, W = remaining biomas at the end of the experiment, %

Treat	Salinity	N init.%		N end%		P init.%		P end%		N/P init.	N/P end	C/N init.	C/N end	C/P init.	C/P end	W (%)		k (1/d)	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD							Mean	SD	Mean	SD
C	Low	0.60	0.15	0.88	0.19	0.009	0.002	0.011	0.005	65.2	82.8	74.5	51.6	4877.1	4882.7	58.3	5.1	0.0026	0.0004
NP in C	Low	0.70	0.13	1.34	0.23	0.099	0.035	0.0029	0.007	7.1	45.7	63.6	33.4	506.7	1578.2	39.7	8.9	0.0046	0.0009
N	Low	0.55	0.02	0.93	0.14	0.010	0.002	0.012	0.003	55.7	77.5	77.8	48.5	4438.8	3866.6	58.1	5.4	0.0026	0.0004
P	Low	0.75	0.21	1.99	0.35	0.093	0.046	0.099	0.049	8.1	20.1	60.3	23.3	625.4	589.5	25.7	9.7	0.0074	0.0024
NP	Low	0.70	0.13	1.89	0.29	0.099	0.035	0.121	0.072	7.1	15.7	63.6	23.3	506.7	435.4	22.5	7.9	0.0081	0.0019
C in NP	Low	0.60	0.15	1.65	0.54	0.009	0.002	0.077	0.061	65.2	21.4	74.5	30.2	4877.1	902.7	29.2	9.8	0.0071	0.0022
C	Med.	0.55	0.11	1.01	0.21	0.012	0.004	0.013	0.006	46.9	75.8	81.1	45.6	4020.4	4223.5	61.9	1.8	0.0024	0.0003
NP in C	Med.	0.70	0.08	1.41	0.23	0.069	0.020	0.027	0.003	10.3	53.2	62.4	31.6	687.7	1652.6	50.1	4.1	0.0035	0.0006
N	Med.	0.62	0.04	1.08	0.13	0.013	0.004	0.016	0.004	48.7	67.8	70.3	41.4	3649.3	2958.8	54.2	7.8	0.0031	0.0005
P	Med.	0.69	0.11	1.95	0.31	0.070	0.041	0.121	0.057	9.9	16.2	64.9	23.7	833.2	488.3	37.1	5.2	0.0051	0.0008
NP	Med.	0.70	0.08	2.08	0.31	0.069	0.020	0.163	0.087	10.3	12.7	62.4	21.9	687.7	429.5	32.1	9.8	0.0065	0.0031
C in NP	Med.	0.55	0.11	1.96	0.41	0.012	0.004	0.092	0.076	46.9	21.3	81.1	24.1	3406.2	1080.5	39.1	16.2	0.0057	0.0033
C	High	0.50	0.06	0.93	0.17	0.008	0.001	0.013	0.004	62.9	73.5	84.3	46.7	5451.7	3695.4	51.2	3.9	0.0032	0.0004
NP in C	High	0.70	0.16	1.38	0.30	0.043	0.018	0.024	0.005	16.5	58.2	63.1	32.2	1160.1	1870.7	47.9	11.1	0.0037	0.0011
N	High	0.57	0.05	1.15	0.32	0.009	0.003	0.012	0.003	63.6	93.2	76.7	39.6	5285.1	3730.1	49.9	11.4	0.0034	0.0009
P	High	0.67	0.17	1.71	0.43	0.050	0.023	0.044	0.013	13.5	38.9	67.9	25.8	1035.6	1021.4	35.7	15.1	0.0054	0.0021
NP	High	0.70	0.16	1.83	0.26	0.043	0.018	0.051	0.009	16.5	36.2	63.1	24.1	1291.2	762.7	35.7	7.1	0.0057	0.0012
C in NP	High	0.50	0.06	1.32	0.49	0.008	0.001	0.033	0.026	62.9	40.4	84.3	36.3	5451.7	2373.5	44.9	9.7	0.0045	0.0011
Salinity effect, S		ns		ns		0.100		0.029		0.150	0.023	ns	ns	0.05	0.042	0.125		0.18	
Treat. Effect, T		0.001		0.0001		0.0001		0.0001		0.0001	0.0001	0.0003	0.0001	0.0001	0.0001	0.0001		0.0001	
Marsh effect		0.050		0.0001		ns		0.003		ns	0.003	0.044	0.0001	0.077	0.0002	0.0002		0.0001	
S×T effect		ns		ns		ns		ns		ns	0.1	ns	ns	ns	0.1	0.002		0.01	

Table 2 Mean values of water (soluble reactive phosphorus, SRP, NH_4–N), sediment (total P and total N) and plant (aboveground biomass) characteristics in the experimental plots in each salinity category; $n = 5$

Plot	Salinity	Conductivity (μS cm^{-1})		pH		SRP (ppb)		NH_4–N (ppb)		Sediment P (mg g^{-1})		Sediment N (mg g^{-1})		Plant*W* (g m^{-2})	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
C	Low	254	85	7.1	0.6	7.5	4.9	43.1	49.3	0.331	0.055	12.53	4.51	242.7	331.6
N		242	93	6.5	1.7	12.4	8.7	38.6	30.9	0.305	0.104	11.04	10.01	249.3	252.3
P		241	146	6.9	0.9	32.7	40.4	65.6	63.1	6.222	2.914	15.88	13.81	828.2	464.5
NP		259	98	6.9	0.6	19.9	29.1	64.1	60.2	2.396	0.7	12.11	10.84	811.7	351.7
C	Med.	1308	490	7.1	0.1	6.1	1.5	33.1	23.4	0.459	0.083	9.76	3.84	223.4	102.9
N		1273	680	7	0.1	5.2	1.1	19.4	16.5	0.411	0.065	13.76	6.61	220.1	78.5
P		1221	510	7.1	0.3	11.1	5.1	34.9	30.3	2.254	0.712	15.27	7.31	757.8	269.6
NP		1177	331	7.1	0.4	11.3	7.1	23.1	8.7	2.19	0.219	16.61	7.73	673.1	165.4
C	High	4580	795	7.6	0.2	12.6	9.6	21.1	12.3	0.356	0.116	7.41	3.38	143.8	83.5
N		5150	919	7.7	0.1	6.8	5.2	29.5	12.1	0.284	0.036	6.44	3.55	168.7	88.3
P		4900	590	7.5	0.3	8.1	5.9	25.9	16.3	1.562	0.426	7.14	4.24	498.3	248.7
NP		5125	827	7.7	0.3	6.6	4.7	19.8	12.9	1.192	0.521	7.73	3.04	442.1	149.3
Salinity effect		0.0001		ns		ns		ns		0.11		ns		ns	
Treatment effect		ns		ns		0.1		ns		0.0001		ns		0.0001	
Marsh effect		0.0001		ns		0.0001		0.001		ns		0.001		0.1000	
Interaction		ns		ns		0.07		ns		0.002		ns		ns	

Litter bags biomass changes

Decomposition of litter measured as dry mass loss showed a clear differentiation between P un-enriched plots and P-enriched plots (Fig. 1). Strong effect of treatment as well as time was detected in the repeated measure ANOVA (Table 3). The significant interaction of the two allowed us to calculate posthoc significance test for individual dates. As shown in Fig. 1, at the first sampling date there was no difference in the litter mass decrease among individual treatments, but starting the second sampling date, the remaining litter in N and C plots was significantly higher than in P and NP plots. In reciprocally placed litter bags, both litter quality and site had significant effect on decomposition (Fig. 2) but the effect of the site was stronger (Table 4).

Decay constant

Decomposition coefficients expressed from the negative exponential model ranged from 0.0024 to 0.0081 per day (Table 1, Fig. 3). The decay rates were 2–3 times higher in the P enriched plots than in C and N plots. When all treatments were included in the analysis, no salinity effect was detected (see Table 5) but when only P enriched treatments (P, NP, C–NP and NP–C) were analyzed, then a significant effect of salinity was found.

Cellulose

Decomposition of cellulose provided a measure of the activity of decomposers at individual sites. It proceeded significantly faster in litter-bags in P and NP fertilized plots than in the control and N plots. Results showed significant effect of both salinity and treatment plot (Fig. 4, Table 6). The values of cellulose decomposition at day 84 (the 2nd sampling period) correlated well with the litter decomposition during all but the 1st sampling period (R^2 = 0.062, 0.692, 0.765, 0.729, and 0.718 for the 1st, 2nd, 3rd, 4th, and 5th sampling period, respectively). This indicates that cellulose could be used as a predictor of *Eleocharis* litter decomposition in this wetland system. Cellulose decomposition was positively correlated with substrate P (R^2= 0.755) and this correlation was somewhat closer than the correlation between substrate P and litter decomposition (R^2 = 0.625; data not shown).

Changes of N and P in decomposing litter

N increased in all treatments but the increase was sharper in P and NP plots (Fig. 5). During the first sampling interval, P content dropped substantially in all samples except for those from C–NP treatment that showed increase in P content. The decrease in P litter content during the first exposure is apparently

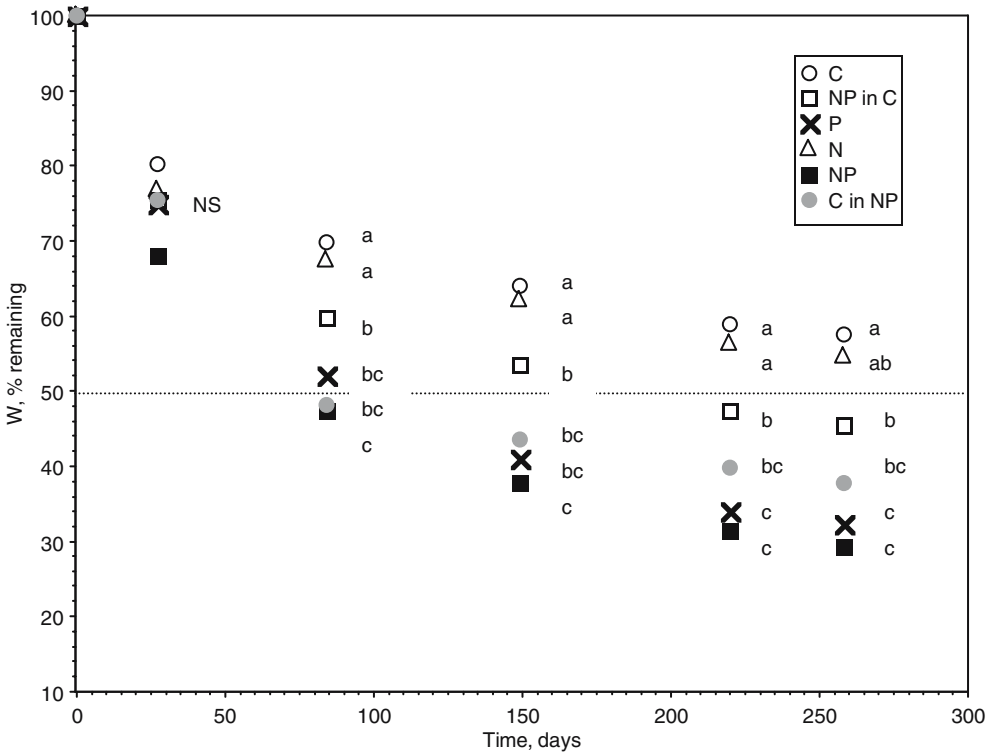

Fig. 1 Decomposition expressed as % of remaining mass (*W*, %) over 258 days of the experiment. C = litter from control in control; NP–C = litter from NP plot decomposing in control; P=litter from P plot decomposing in P plot; N = litter from N plot decomposing in N plot; NP=litter from NP plot decomposing in NP plot and C–NP = litter from control decomposing in NP plot. Values are means from all 15 marshes; same letters indicate no statistical significance among treatment; Scheffe, 0.05

Table 3 Results of repeated measures ANOVA comparing the effect of treatment and time on the remaining litter mass

Source of variation	DF	MS	*F*-value	*P*-value
Treatment, *T*	5	6051.5	22.8	<0.0001
Repeated Time, *R*	4	13442.5	395.6	<0.0001
T×*R*	20	201.8	5.9	<0.0001

due to leaching. Leaching experiment conducted with litter from control and NP plots resulted in significant differences between the two treatments with the average of 11.3% P leached from controls and 25.6% from NP ($n = 24$; $t = -3.727$; $P = 0.0005$) (Fig. 6). Similarly, in the decomposition experiment, more P leached from the litter from P-enriched plots. In the consecutive dates the P content increased in all treatments, again, more so in P and NP (Fig. 5). Carbon proportion in the litter did not change significantly and averaged 43.2 (range 41–44.7) and 43.9 (range 37.3–48) at the beginning and at the end, respectively (data not shown).

To explore how the changes in the decomposition relate to changes in N, P, and mass ratios of C/N, C/P and N/P we calculated simple regressions and found that the best predictor of the decomposition expressed as remaining W was log P or log C/P (Table 7). Regressions of decomposition on log N/P, log C/N and N were also highly significant ($P < 0.0001$). Figure 7 clarifies why the log C/P gives the best fit. Essentially, decomposition is linearly dependent on C/P, C/N and N/P mass ratios up to a critical ratio after which there are no changes. These ratios are 50:1, 4000:1, and 80:1 for C/N, C/P and N/P, respectively.

Over time a strong correlation developed between N and P, first both increasing linearly but after the second sampling date and P content >0.15%, the N content leveled off at ~2.3% and did not increase any more (Fig. 8). At the 4th sampling date, the N/P ratio of control and N treatments (86.8 and 79.8, respectively) was about 3–4 times higher than N/P of litter

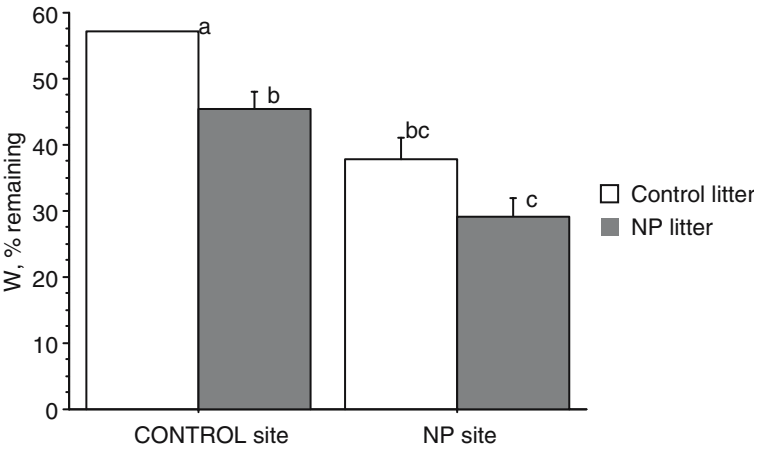

Fig. 2 The effect of litter quality and site on decomposition expressed as % of remaining mass (*W*, %; open bars litter from controls, dark bars litter from NP plots). Same letters indicate no statistical significance among treatments; Scheffe, 0.05

Table 4 Results of 2-way ANOVA comparing the effect of site quality (control plots versus NP plots) and litter quality (litter from controls versus litter from NP plots) on the remaining litter mass

Source of variation	DF	MS	*F*-value	*P*-value
Site, *S*	1	3573.3	49.2	<0.0001
Litter quality, *L*	1	872.3	12.1	0.0012
$S \times L$	1	139.2	1.9	0.1731

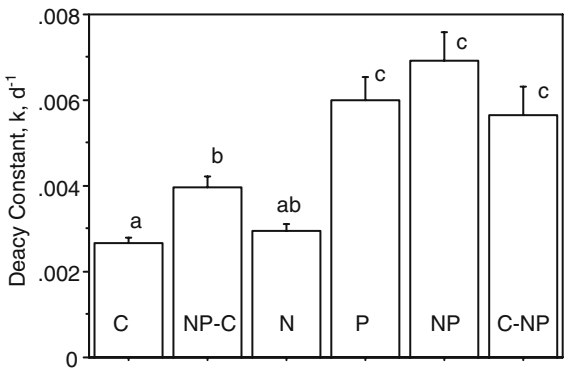

Fig. 3 Decay constants (k, day^{-1}). For symbol explanation see Fig. 1. Bars indicate means with standard error, same letter indicate that the values are not significantly different from each other; Sheffe, 0.05

from NP and P treatments (22.2 and 25.9, respectively). The C/N ratio showed a consistent decrease after the first sampling date in all treatment with a significantly smaller decrease in litter from control and N treatment as compared to the rest. The C/P ratio, after the initial increase probably caused by P leaching, stayed about the same for P, NP, C–NP and NP–C and decreased in control and N treatment (Fig. 9).

Correlation with PLFA

We analyzed the total phospholipids fatty acid (PLFA) content in litter samples from the second sampling period as a measure of live microbial biomass present in litter. PLFA content was closely correlated with decomposition (R^2 = 0.412, 0.478. 0.456, and 0.464 for the 2nd, 3rd, 4th, and 5th sampling period). In reciprocally placed litter bags, both litter and site quality had significant effect on PLFA content with the site effect being stronger than litter quality effect (Table 8). The salinity did not have any significant effect on the PLFA, while there was a highly significant effect of treatment and location (Table 9; Fig. 10). There was a close correlation between PLFA content and both N and P litter content (R^2 = 0.597 and 0.609, respectively).

Discussion

The decomposition experiment started with large differences in litter quality, especially in P content, in litter originating from different long-term nutrient addition plots. It is important to point out that experimental N addition did not have any effect on litter N content, on the contrary, litter originating in P and N&P plots had slightly higher N content. This supports our previous finding that the system is strongly P deficient and rich enough in N, apparently due to N input through N-fixation by cyanobacteria (Rejmánková and Komárková 2000; Rejmánková 2001). Differences in site quality, specifically in P

Table 5 Results of hierarchical nested ANOVA comparing the effects of treatment, (C, NP–C, P, N, NP and C–NP), salinity (low, medium, high) and marsh on decay constant, *k*

Source of variation	DF	MS	*F*-value	*P*-value
(a) All treatments				
Treatment, *T*	5	0.3182	34.3	<0.0001
Salinity, *S*	2	0.0733	1.9	0.1835
Marsh in salinity	12	0.0411	4.4	0.0001
Treatment×salinity	10	0.0243	2.6	0.0118
(b) Only treatment with P addition				
Treatment, *T*	3	0.1130	12.3	<0.0001
Salinity, *S*	2	0.1504	3.2	0.0754
Marsh in salinity	12	0.0494	5.4	0.0001
Treatment×salinity	6	0.0013	0.1	0.9879

Marsh nested within salinity level. The effect of treatment used as within plot (marsh) factor, salinity as between plot factor. (a) All treatments and (b) only treatment with P addition

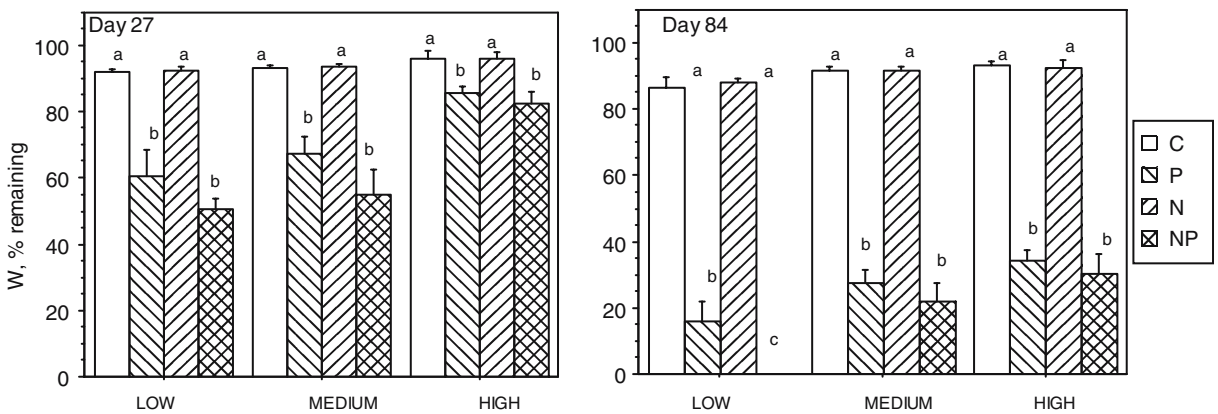

Fig. 4 Means for low, medium and high salinity category of cellulose decomposition expressed as % of remaining mass after 27 and 84 days of exposure in C, P, N, and N&P plots. Same letters indicate no statistical significance among treatments; Scheffe, 0.05

Table 6 Results of 2-way ANOVA comparing the effect of salinity and treatment (C, P, N, NP) on the cellulose decomposition after 27 days (a) and 84 days (b) of exposure

Source of variation	DF	MS	*F*-value	*P*-value
(a) 27 days				
Salinity, *S*	2	4313	13.01	<0.0001
Treatment, *T*	3	15054	45.42	<0.0001
S×*T*	6	686	2.07	0.05
(b) 84 days				
Salinity, *S*	2	4156	17.71	<0.0001
Treatment, *T*	3	83628	356.51	<0.0001
S×*T*	6	671	2.86	0.01

content of the upper 2 cm of the sediments, were not as pronounced as in the litter. This can be explained by the fact that soil nutrients are slower to respond to nutrient additions than biota as documented from the Everglades by Newman et al. (2001). The fact that our site characteristics showed less difference than litter characteristics may indicate that the site characteristics we have the information on were not the

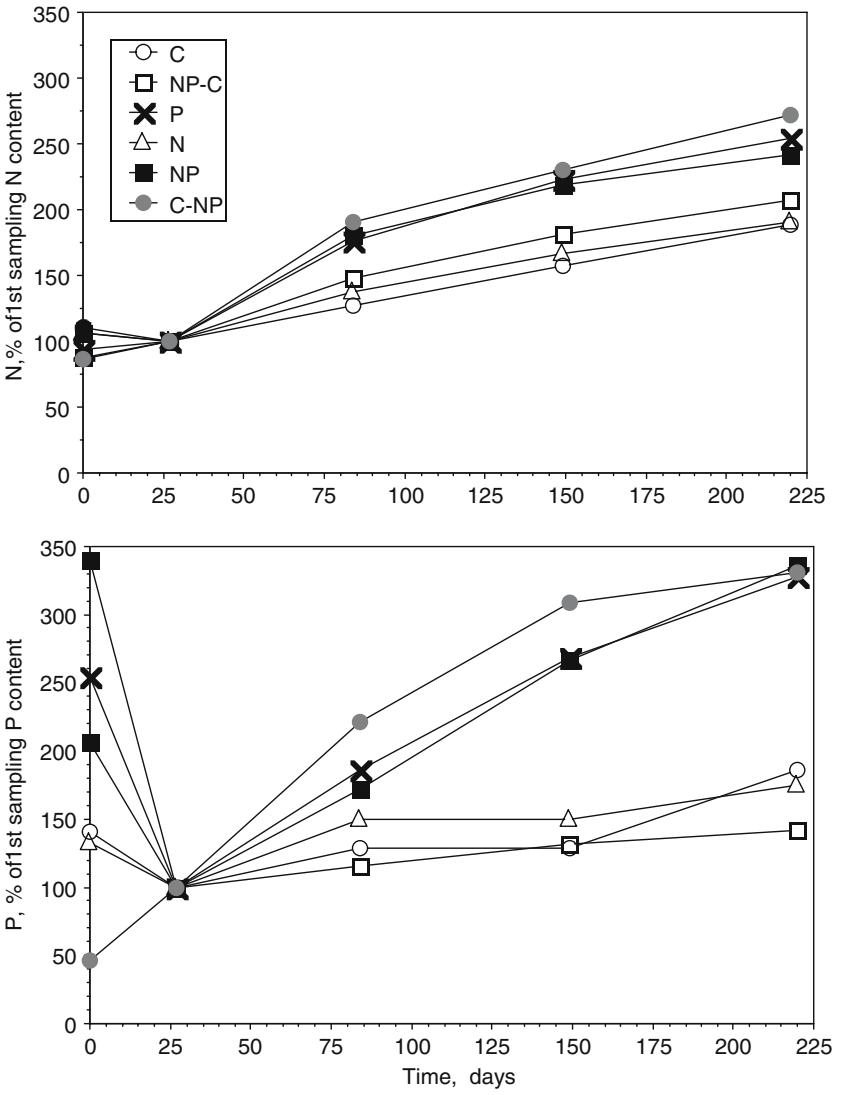

Fig. 5 Relative changes in N and P content in the course of the decomposition. The first sampling values (day 27) are equaled to 100%. For symbol explanation see Fig. 1

most suitable ones. The salinity effect was superimposed on differences in litter and site quality. Soon in the time course of decomposition, the litter and site quality differences resulted in consistent and distinctly different decomposition changes. That confirmed our prediction of the positive effects of P-enrichment on decomposition rate due both the quality of litter material as well as at the site. The site effect tested with the reciprocally placed litter bags was stronger than the litter quality effect, although both were highly significant. Strong site quality effect is expected to be a result of more active decomposer community in P-enriched plots, which is supported by our finding of higher microbial biomass, expressed as PLFA, associated with litter decomposing in P-enriched plots. The literature reports on relative importance of litter versus site quality vary. Hobbie and Vitousek (2000) found both substrate quality and site quality to increase decomposition rates, but the substrate quality effect was stronger. On the contrary, Hobbie and Gough (2004) demonstrated a strong effect of site quality on decomposition rate in the Alaskan tundra, where the limiting nutrient was not P but N. Clearly these processes are specific for individual ecosystems and we do not have enough data to explain why in some cases the litter quality and while in others site characteristics are stronger determinants of decomposition rates. Kourtev et al. (2002) stated

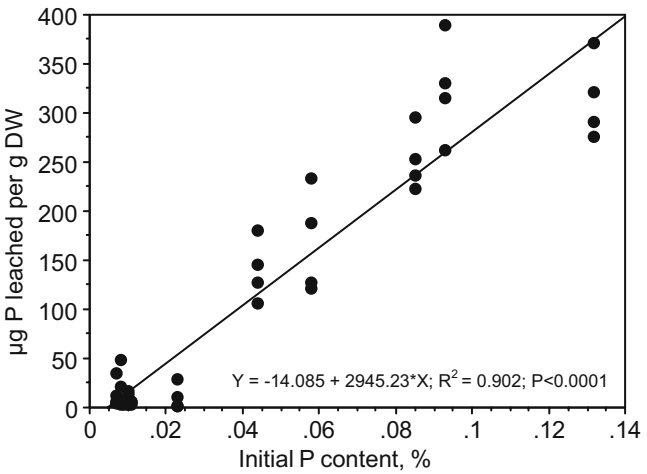

Fig. 6 Relationship between the initial litter P content (*x*-axis) and the amount of leached P

Table 7 Simple linear regression of decomposition against nutrients (3rd sampling date)

Factor	*r*	R^2	*n*	*P*
Litter N%	−0.903	0.815	80	<0.0001
Log litter P%	−0.91	0.827	80	<0.0001
Log litter N/P	0.876	0.767	80	<0.0001
Log litter C/N	0.895	0.801	80	<0.0001
log litter C/P	0.912	0.831	80	<0.0001

that litter quality is the major determinant of enzyme activities in decaying litter, with soil physical and chemical parameters significantly modifying enzymatic activities by affecting function of soil microbial communities. Extracellular enzyme activities in our samples were also more significantly affected by site quality than by litter quality (Rejmánková, unpublished data).

The effect of P-enriched site on decomposition rate was further confirmed by the cellulose decomposition assay. Measuring the decomposition of cellulose is expected to estimate the relative rate of soil microbial activity as a function of environmental factors (Kurka et al. 2000; Newman et al. 2001). Faster decomposition of the cellulose in the P-enriched plots confirmed that P availability in control and N plots was limiting the microbial population of decomposers. This is in agreement with Maltby (1985) who showed that just a small increase of N and P promoted cellulose decay in Everglades soil columns, and Verhoeven et al. (1996), Feller et al. (1999), and Newman et al. (2001) who found faster decomposition of cellulose strips in wetland sediments with higher P content.

We did not find consistently significant effect of salinity on decomposition rate of litter when all treatments were included, but when we only considered litter from nutrient enriched litter/site (P, NP, C–NP, NP–C), the effect of salinity became stronger. The same applied to PLFA content. Apparently in the unfertilized plots the decomposition is so slow (and PLFA content so low) that the salinity effect is hard to detect. The cellulose decomposition proceeded significantly slower at high salinity sites. This indicates that decomposer microbial activity may be lower in high salinity marshes. ''High'' salinity in our study system is actually quite low in comparison to coastal salt marshes. While there is a general consensus that decomposition decreases at high salinities (Mendelssohn and Slocum 2004 and references therein), higher salinities than those in our system may be required for a significant decrease to take place. Mendelssohn and Slocum (2004) suggest that there may be a salinity threshold that needs to be surpassed for a significant reduction of decomposition and it appears that our high salinity sites may be just near that threshold. Since the primary production of macrophytes is also lower at higher salinities (Table 1 and Rejmánková, unpublished data), the net result of balancing primary production with decomposition may come out even for high and low salinity marshes.

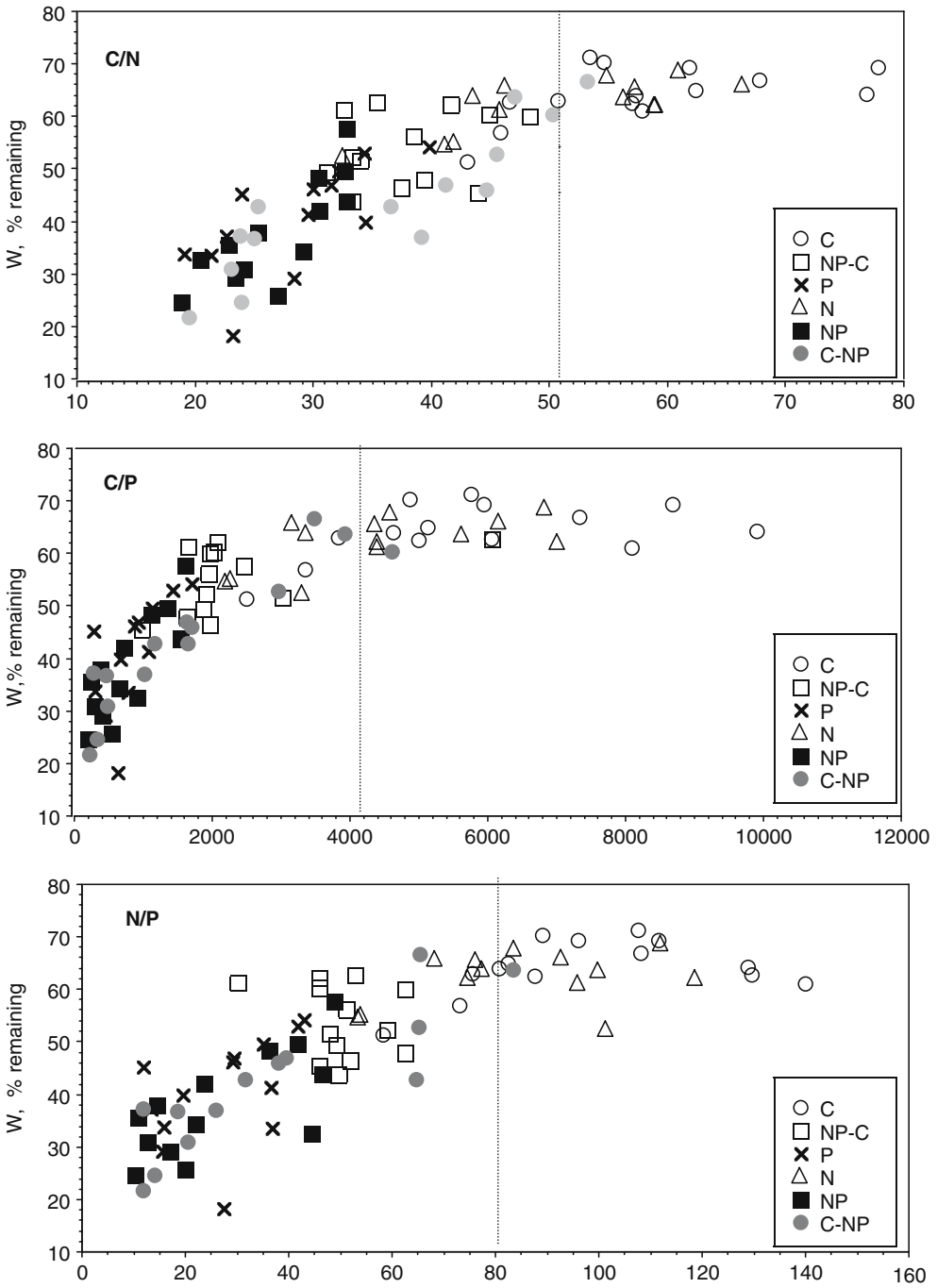

Fig. 7 Relationship between litter C/N, C/P and N/P mass ratios (*x*-axes) and decomposition expressed as % of remaining mass (*W*, %) during the 3rd sampling period. For symbol explanation see Fig. 1

Prediction of relationships between primary production and decomposition

One of our goals was to use the information on decomposition rates of control and nutrient enriched litter to predict if these rates are high enough to prevent accumulation of organic material. High organic material accumulation results from increased primary production under high nutrient loading. The annual aboveground primary production of *Eleo-*

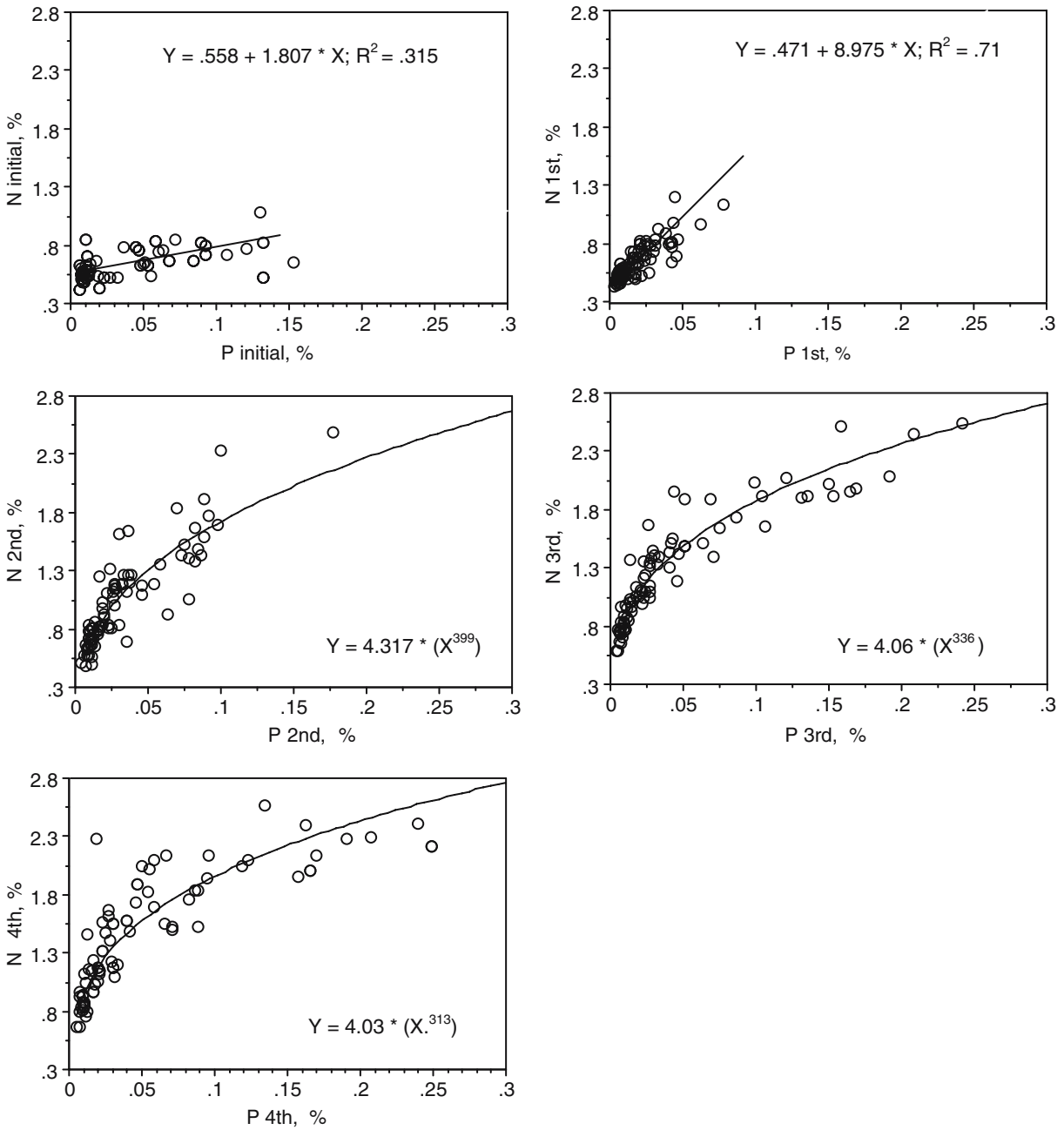

Fig. 8 Correlation between N and P in decomposing litter. After log transformation of the *x*-axis, R^2 was 0.757, 0.893, and 0.802 for 2nd, 3rd, and 4th sampling date, respectively

charis in Belizean marshes can be estimated as double the biomass of the full developed stand (Rejmánková 2001). We used biomass data from August 2003 (see Table 2) multiplied by 2 as the annual NPP and calculated remaining W after 1, 2 and 3 years using the corresponding decay constants (Table 1). The predicted outcome is summarized in Fig. 11 showing that after 1 year of decomposition, there would be no differences in the remaining W among treatments while after 2 and 3 years, there would be actually significantly less litter left in P-enriched plots. This estimate does not consider a

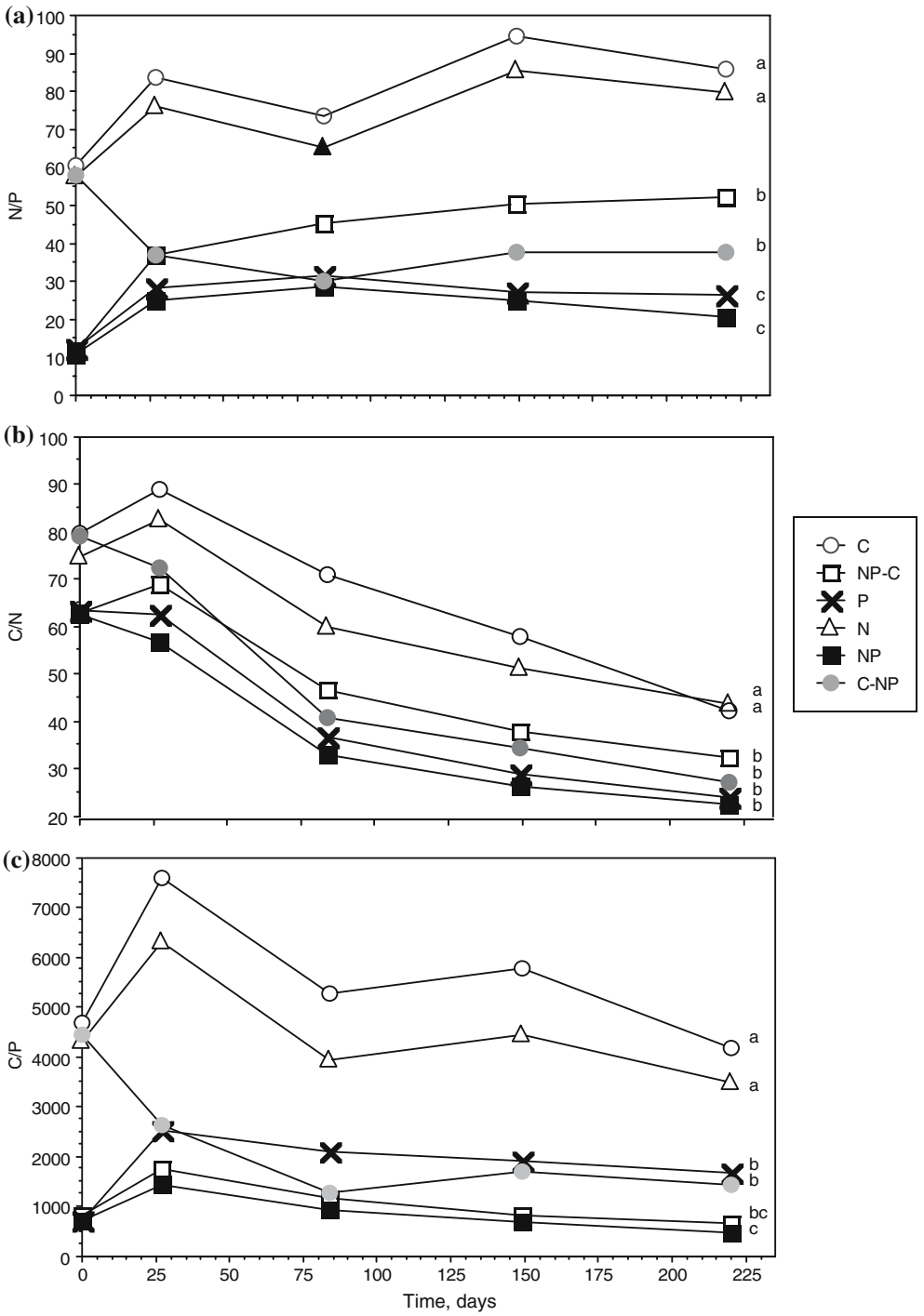

Fig. 9 Time course of changes in N/P, C/N and C/P mass ratios in litter from individual treatments during the decomposition. For symbol explanation see Fig. 1. Values are means from all 15 marshes; same letters indicate no statistical significance among treatment; Scheffe, 0.05

Table 8 Results of 2-way ANOVA comparing the effect of site quality (control plots versus NP plots) and litter quality (litter from controls versus litter from NP plots) on the PLFA content

Source of variation	DF	MS	*F*-value	*P*-value
Site, *S*	1	1.431	25.14	<0.0001
Litter quality, *L*	1	0.488	8.58	0.0052
$S \times L$	1	0.012	0.21	0.6471

Table 9 Results of hierarchical nested ANOVA comparing the effects of treatment (C, NP–C, P, N, NP and C–NP), salinity (low, medium, high) and marsh on the PLFA content

Source of variation	DF	MS	*F*-value	*P*-value
Treatment, *T*	5	0.4067	15.6	<0.0001
Salinity, *S*	2	0.1400	0.8	0.4829
Marsh in salinity	12	0.1728	6.6	<0.0001
Treatment × salinity	10	0.0610	2.3	0.0240

Marsh nested within salinity level. The effect of treatment used as within plot (marsh) factor, salinity as between plot factor

refractory fraction, estimated for some wetland macrophytes to be as high as 18–22% (Morris and Bowden 1986; Davis et al. 2003). Our experiment did not last long enough to allow for estimates of this fraction, but based on the observational data it is probably lower than 18–22%, at least at the nutrient enriched sites. After 3 years of duration of the nutrient addition experiment our observations of the amount of decomposing litter in P and NP plots compared to C and N plots indicate that there is not a substantial increase in organic matter accumulation. *Eleocharis* spp. seem to be decomposing faster than macrophytes from similar marshes, specifically *Cladium jamaicense* from the Everglades where decay constant were found to be as low as 0.000274–0.00042/d (Newman et al. 2001) compared to our lowest values of 0.0024/d.

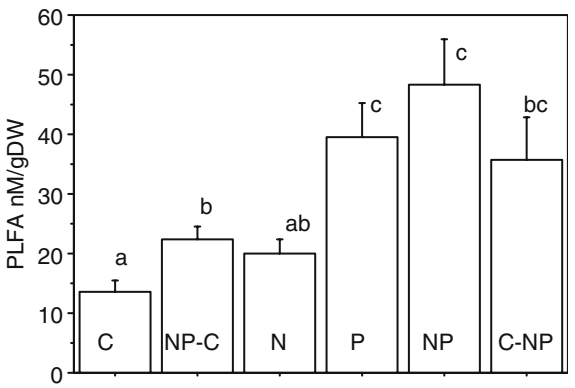

Fig. 10 The phospholipid fatty acid content (PLFA, nM g^{-1} dry mass). For symbol explanation see Fig. 1. Bars indicate means with standard error, same letter indicate that the values are not significantly different from each other; Sheffe, 0.05

Mass loss and changes in nutrient ratios

Mass loss during decomposition has been correlated with the N and P content and/or their ratios, and with various indicators of secondary compounds content, mainly lignin/N (Vitousek et al. 1994; Aerts and de Caluwe 1997; Hoorens et al. 2003; Xuluc-Tolosa et al. 2003, and others). Litter C/N and C/P mass ratios were found to be excellent predictors of decomposition rate, sometimes explaining ~90% of its variation (Enriquez et al. 1993). In our case the best predictors of the decomposition rate were litter P or C/P, but litter N content was also highly significant (Table 7). With the litter C/P mass ratio > 4000, decomposition proceeded extremely slowly. When we divided the whole data set (excluding reciprocal transplants) into two groups with C/P < 4000 and C/P > 4000, there was a highly significant difference between the two groups in decomposition rate in all sampling intervals (DF 51, t=−5.06 to −6.13, $P < 0.0001$). We believe it is safe to use this ratio for prediction of high versus low decomposition rates for *Eleocharis* spp.

As decomposition proceeded the C/N and C/P mass ratios gradually decreased as a result of C mineralization (Fig. 9). According to Paul and Clark (1989), the ratio of C/N of 25 divides net mineralization (<25) and immobilization, i.e., retention by microbes (>25). Our litter had the initial C/N ratios in the range of 60–80, which is a range found for macrophytes of a similar growth form (Kuehn and Suberkropp 1998). Except for the litter in P-enriched plots on the last sampling date, the ratio never dropped below 25, thus N immobilization was to be expected. The initial C/P ratio in litter from P-unenriched plots ranged from 2237 to 6410, which is much higher than is generally found in plant litter, with the exception of macrophytes from P-limited systems (e.g., the un-impacted Everglades, C/P 3700; Newman et al. 2001). C/P ratio dividing immobilization×mineralization processes for P is 80 according

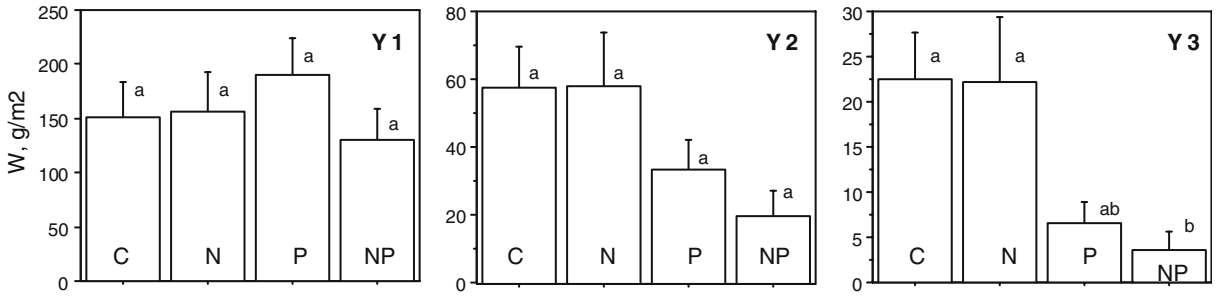

Fig. 11 The estimated amounts of remaining W (g m^{-2}) after 1, 2, and 3 years of decomposition. Bars indicate means with standard error, same letter indicate that the values are not significantly different from each other; Sheffe, 0.05

to Canfield et al. (2005). Clearly the discrepancy between microbial demand and litter P in our system was very high (much higher than for N), which made P more profoundly limiting. Figure 5 shows well how N increased steadily in litter from all treatments, because N is not limiting in this system. On the contrary to N, there was a significant difference in low P increase in litter decomposing in P-limited plots versus high P increase in litter decomposing in P-enriched plots.

Importance of leaching

In all our treatments except for C–NP, we saw a substantial drop in P during the initial exposure period, while there was almost no change in N. Higher initial loss of P from decomposing litter compared to N is believed to be due to a relatively large water soluble fraction of P in plant tissue as opposed to N (Davis et al. 2003) and has been reported by numerous authors (Kwabiah et al. 2001; Qualls and Richardson 2003). Litter from P-enriched plots lost more P due to leaching than litter from controls. We agree with the suggestion of Davis et al. (2003) that leachate from surrounding decomposing litter could be a source of enriching P for microbial decomposers leading to the positive feedback. If this is the case, then there should be differences in availability of this leachate P throughout the year. During the early rainy season when gradually more and more standing (or lodged) dead material is being flooded, the P release would be expected to be the greatest. Our experiment was not set up to answer this, but the litter bags were exposed at the beginning of the rainy season and the water levels during the first sampling period were quite low. They increased until about the third sampling date and then started decreasing.

PLFA

We was measured the PLFA content to provide an estimate of live microbial population associated with various treatments. It was measured only once after 84 days of litter bags exposure. According to Gulis and Suberkropp (2003), bacterial C associated with leaf litter of maple and rhododendron increased rapidly in first ~30 days of decomposition, it then reached a plateau and stayed stable for next 200 days. If their results represent a general trend, then our one time measurement was sufficient. There is not a great deal on information on PLFA content in decomposing samples, but the available data are in agreement with our finding of higher PLFA content in P-enriched litter/plots (Gulis and Suberkropp 2003; Poll et al. 2003; Bünemann et al. 2004).

Conclusion

Nutrient, specifically P, addition results in higher primary production, but also changes in nutrient composition and microbial environment at the site. Both litter quality and site environment have significant effect on decomposition and results from reciprocally placed litter bags indicate a stronger effect of site than the litter quality. Because decomposition proceeds much faster at P-enriched sites we predict that there will be no differences in accumulation of organic material between the controls and nutrient enriched plots. Litter nutrient content, N and P, and nutrient mass ratios, C/N, C/P and N/P are well correlated with decomposition with the best fit found for log C/P. At C/P ratio of >4000 decomposition processes are extremely slow. Microbial biomass

expressed as PLFA is closely positively correlated with decomposition.

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