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ORIGINAL ARTICLE

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Response of nutrient dynamics of decomposing pine (*Pinus massoniana*) needles to simulated N deposition in a disturbed and a rehabilitated forest in tropical China

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Abstract The effects of simulated N deposition on changes in mass, C, N and P of decomposing pine (*Pinus massoniana*) needles in a disturbed and a rehabilitated forest in tropical China were studied during a 24-month period. The objective of the study was to test the hypothesis that litter decomposition in a disturbed forest is more sensitive to N deposition rate than litter decomposition in a rehabilitated forest due to the relatively low nutrient status in the former as a result of constant human disturbance (harvesting understory and litter). The litterbag method and N treatments (control, no N addition; low-N, 5 g N m^{-2} $year^{-1}$; medium-N, 10 g N m^{-2} $year^{-1}$) were employed to evaluate decomposition. The results revealed that N addition increased (positive effect) mass loss rate and C release rate but suppressed (negative effect) the release rate of N and P from decomposing needles in both disturbed and rehabilitated forests. The enhanced needle decomposition rate by N addition was significantly related to the reduction in the C/N ratio in decomposing needles. However, N availability is not the sole factor limiting needle decomposition in both disturbed and rehabilitated forests. The positive effect was more sensitive to the N addition rate in the rehabilitated forest than in the disturbed forest, however the reverse was true for the negative effect. These results suggest that nutrient status could be one of the important factors in controlling the response of litter decomposition and its nutrient release to elevated N deposition in reforested ecosystems in the study region.

Keywords Anthropogenic disturbances · C to nutrient ratio · Litter decomposition · N/P ratio · Nutrient immobilization · Tropics

Introduction

The addition of exogenous nitrogen (N) to the soil-litter subsystem has been reported to considerably alter the rate of litter decomposition. Prescott (1996) reported a direct relationship between decomposition rates and the amount of extractable N in the forest floor, while Vestgarden (2001) reported external N addition had a positive effect on needle litter decomposition. Other studies have shown that external N addition has either no effect (Vitousek 1998; Prescott et al. 1999) or a depressing (Magill and Aber 1998; Ågren et al. 2001; Micks et al. 2004) effect on litter decomposition rate. A positive response in the initial decomposition phase and a negative response in later stages have also been found (Berg and Matzner 1997; Berg et al. 1998). It has been proposed that the addition of N to the soil-litter of N-limited ecosystems should increase microbial activity but that any increase in available N should not affect microbial activity in an N-saturated ecosystem (Berg 1986; Berg and Matzner 1997; Berg et al. 1998). However, most studies of the effects of N addition on litter decomposition have been performed in temperate forest ecosystems, and little information is available about responses to atmospheric N deposition in tropical forests (Vitousek 1998; McGroddy et al. 2004; Micks et al. 2004), especially in the forests of China (Mo et al. 2006).

In Asia, the use and emissions of reactive N increased from 14 TgN $year^{-1}$ in 1961 to 68 TgN $year^{-1}$ in 2000 and is expected to reach 105 TgN $year^{-1}$ in 2030

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(Zheng et al. 2002). At the present time, this leads to high atmospheric N deposition (30–73 kg ha^{-1} $year^{-1}$) in some forests of southern China (Mo et al. 2005). In addition, most of the land originally covered with primary forests in China has been degraded by human activities during the past several hundred years (Wang et al. 1982). In extreme cases, the land has become completely non-vegetated (He and Yu 1984). Chinese deforestation is estimated to have been on the order of 0.61 million ha per year during the 1990s, and the remnant mature native forest area now is less than 9% of the total territory (Liu et al. 2000). Attempts to reverse this process of land degradation have been initiated in the subtropical and tropical region of China, and over the past few decades, large areas have been reforested with a native pine species (*Pinus massoniana*) to prevent further degradation of the landscape. The cutting of the trees is now prohibited, but harvesting of understory and litter is allowed to meet local fuel needs. These rehabilitated forests (reforested but no harvesting) and disturbed forests cover more than half of the total forest area in subtropical and tropical China (Mo et al. 2004). However, the effects of these significant land-use changes on the ecosystems are poorly known (Mo et al. 2003, 2004), and no information is available on the response of litter decomposition and its nutrient release in human-disturbed and -rehabilitated forest ecosystems to increased N deposition.

Atmospheric pollutants (especially N deposition) and human disturbance are two major anthropogenic factors that alter soil nutrient cycling and availability, with profound effects on ecosystem (Baxter et al. 2002). The effects of elevated N deposition and human disturbance are likely to cause significant changes in litter decomposition, a key process affecting soil fertility, nutrient cycling and primary productivity of ecosystems. It is therefore critical to be able to predict and ultimately address the effects of both increasing N deposition and human disturbance on litter decomposition of forests in China, especially in southern tropical China where the industrial and agricultural sectors have shown rapid growth in recent years (Mo et al. 2005).

In an earlier publication (Mo et al. 2006) we reported that, due to previous land-use history, both rehabilitated and disturbed forests in tropical China are still N-limited and that N addition positively affected the mass loss rate of decomposing litter during a 18-month experimental period. In this paper, we focus on the effects of simulated N deposition on changes in C, N and P of decomposing pine (*P. massoniana*) needles in these two forest types during a 24-month experimental period. The objective was to examine the effects of N addition on decomposition and compare this effect between these two forest sites with a different land-use history. Our expectation was that the response of decomposing litter would be more sensitive to N deposition rate in the disturbed forest than in the rehabilitated forest due to the relatively low nutrient status in the former resulting from constant human disturbance.

Methods

Site description

This study was conducted in the Dinghushan Biosphere Reserve (DHSBR), which lies in the middle part of Guangdong Province in southern China (112°10′E, 23°10′N) and occupies an area of approximately 1200 ha. We established two research sites in this reserve: a mixed pine and broadleaf forest (named the rehabilitated forest) and a pine forest (named disturbed forest). The rehabilitated forest, at about 200 m a.s.l. occupies approximately 50% of the total area of the reserve, and the disturbed forest, at about 50–200 m a.s.l. occupies approximately 20% of the total area of the reserve (Zhang et al. 2000; Mo et al. 2003). These two forest sites are approximately 4 km from each other. Both the rehabilitated and disturbed forests originated from a 1930s clear-cut followed by the establishment of pine plantations. The original sites of both forests were badly eroded and degraded (Wang et al. 1982; Mo et al. 1995, 2003). However, the disturbed forest was subject to continuous human disturbances (generally the harvesting of understory and litter) between 1930 and 1998 so that the tree layer remained dominated by *P. massoniana* (Mo et al. 1995, 2003; Brown et al. 1995). Since 1998 there has been no or very little harvesting. Conversely, colonization from natural dispersal of regional broadleaf species has changed the plant composition in the rehabilitated forest (Mo et al. 2003).

The survey conducted in June 2003 (before the start of the N addition experiment) showed that the major species in the canopy layer of the rehabilitated forest were *P. massoniana*, *Schima superba* and *Castanopsis chinensis*. The disturbed forest was dominated by *P. massoniana*. Stem density, tree height and diameter at breast height (DBH) in the two forests are given in Table 1 (Fang et al. 2006). In the rehabilitated forest, *P. massoniana* contributed 31% of the total leaf litter (Zhang et al. 2000), while in the disturbed forest, about 91% of total leaf litter was contributed by *P. massoniana*. The mean annual litter production was 8.5 and 3.3 Mg ha^{-1} $year^{-1}$ for the rehabilitated and disturbed forests, respectively (Zhang et al. 2000), while standing floor litter measured in June 2003 was 23.7 ± 4.8 and 20.0 ± 0.4 Mg ha^{-1} (mean ± standard error, $n = 3$) for the disturbed and rehabilitated forests, respectively (Fang et al. 2006).

The reserve has a monsoon climate and is located in a subtropical moist forest life zone, (but still located in the tropical belt; see Holdridge 1967). The mean annual rainfall of 1927 mm has a distinct seasonal pattern, with 75% of it falling from March to August and only 6% from December to February (Huang and Fan 1982). Nitrogen deposition was 36–38 kg ha^{-1} $year^{-1}$ in the 1990s (Huang et al. 1994; Zhou and Yan 2001). Annual average relative humidity is 80%. Mean annual temperature is 21.0°C, with an average temperature of the

Table 1 Indices[a] of the forest structure in a disturbed and a rehabilitated forest in tropical China

Species	Stem density (tree ha^{-1})	Mean height (m)	Mean DHB[b] (cm)	Basal area (m^2 ha^{-1})	Relative basal area (%)
Disturbed forest					
Pinus massoniana	456	6.9	17.5	13.3	95.1
Other trees	311	4.3	4.4	0.7	4.9
Total	767			14.0	100
Rehabilitated forest					
Pinus massoniana	133	10.2	22	5.6	41.0
Schima superba	1,567	5.2	6.4	7.4	53.6
Other trees	233	4.2	5.1	0.8	5.4
Total	1,933			13.8	100

[a] Data are from Fang et al. (2006)

[b] DBH, Diameter at breast height

coldest (January) and warmest (July) month of 12.6 and 28.0°C, respectively. Daily precipitation and temperature of at the DHSBR from August 2003 to August 2004 largely followed this long-term seasonal pattern (Fang et al. 2006).

The soils in the two study sites are oxisols with variable depths: in the rehabilitated forest, the depth ranges from 30 to 60 cm, and in the disturbed forest, the depth is generally less than 30 cm to bedrock (Brown et al. 1995; Mo et al. 2003). Soil properties were measured using the samples collected in July 2004 (Mo et al. 2006). The results were similar to those reported for these forests by Mo et al. (2003) and showed that soil pH, total C, total N, C/N ratio, available P and bulk density in the disturbed forest was 3.93 ± 0.08, 22.7 ± 3.1 mg g^{-1}, 1.3 ± 0.1 mg g^{-1}, 17.0 ± 1.4, 3.6 ± 0.2 mg kg^{-1} and 1.16 ± 0.05 g cm^{-3}, respectively, and in rehabilitated forest, 3.91 ± 0.03, 17.3 ± 1.2 mg g^{-1}, 1.2 ± 0.1 mg g^{-1}, 14.4 ± 1.0, 4.2 ± 0.3 mg kg^{-1} and 1.22 ± 0.01 g cm^{-3}, respectively (Mo et al. 2006).

Experimental treatments

Nitrogen addition experiments were initiated within each of the two forest types in 2003 (Mo et al. 2006). Three N addition treatments (in three replicates) were established in both forest types: control (no added N), low-N (5 g N m^{-2} $year^{-1}$) and medium-N (10 g N m^{-2} $year^{-1}$). The low-N treatment (86–88 kg ha^{-1} $year^{-1}$) corresponded to a value higher than the current atmospheric N deposition (30–73 kg ha^{-1} $year^{-1}$) but lower than the projected N deposition (45–113 kg ha^{-1} $year^{-1}$) in 2030 in southern China (Zheng et al. 2002). Eighteen plots of 20 × 10 m were established – nine in the rehabilitated and nine in the disturbed forest – surrounded by a 10-m wide buffer strip. All plots and treatments were laid out randomly. A NH_4NO_3 solution was sprayed monthly by hand onto the floor of these plots as 12 equal applications over the whole year, beginning in July 2003 and continuing until the end of the experiment. The fertilizer was weighed, mixed with 20 l of water and applied to the plots using a backpack sprayer below the canopy. Two passes were made across each plot to ensure an even distribution of fertilizer. The control plots received 20 l water with no N added.

Field sampling

Decomposition was determined by placing fresh needle litter in mesh bags in the plots. Pine needles were collected using litter traps and nylon mesh placed on the forest floor under the pine trees in the study sites during May and June 2003, the season of peak litterfall (Zhang et al. 2000). The selected trees were also shaken as needed. All of the needles were air-dried to a constant weight. The needles of each forest type were mixed to obtain a uniform mixture before filling the mesh bags. Six sub-samples (about 10.00 g per sub-sample) from each forest were analyzed for the initial oven-dry weight (conversion rate from air-dried to 105°C) and initial C, N and P concentrations. A total of 216 litter bags (approximately 25 × 25 cm) were prepared from mesh (0.5 mm at the bottom and 2 mm at the top) polyvinyl screen at the beginning of the study (June 2003). The number and contents of the bags were as follows: 108 bags for each forest, with each bag filled with about 10.00 g air-dried mass of needles originating from its own forest type (i.e. needles from the rehabilitated forest for bags destined for that forest and likewise for the disturbed forest). At the end of June 2003, these litter bags were evenly distributed among each plot and incubated on the litter layer.

Two litter bags (a total of 18 bags for each forest) were collected from each plot (a total of 18 plots: nine in rehabilitated and nine in disturbed forests) at about 3, 6, 9, 12, 18 and 24 months after the start of the study (July 2003), yielding a sample size of six for each treatment. The bags were returned to the lab for separation and analysis.

Laboratory procedures

In the laboratory, ingrown roots, if any, were removed from the bags, and the needles were brushed free of foreign materials and oven-dried in paper bags to a constant weight at 40°C. After drying, each bag was weighed individually (Sundarapandian and Swamy 1999).

The C concentration of the needle litter was determined by a total organic carbon analyzer (Shimadzu TOC – VCPH); N concentration was determined by the semimicro-Kjeldahl digestion method (Bremner and

Mulvaney 1982) followed by the detection of ammonium with a Wescan ammonia analyzer. Total P concentration was analyzed colorimetrically (Anderson and Ingram 1989). Subsamples of litter materials were dried to 105°C, and all results were recorded at that temperature.

Data analyses

The model for decomposition that we used is represented by the following equation (Olson 1963):

$$\frac{X}{X_{\mathrm{o}}} = \mathrm{e}^{-kt},$$

where X/X_{o} is fraction mass remaining at time t, X the mass remaining at time t, X_{o} the original mass, “e” the base of natural logarithm, k the decomposition constant (year^{-1}) and t the time. The exponential model was fit to the data using least squares regression of the natural logarithm of mean fraction mass remaining (Kuperman 1999). Nutrient content at each time point was calculated by multiplying the nutrient concentration by the mass remaining (McGroddy et al. 2004).

A repeated measure ANOVA with Tukey’s HSD test was performed to examine the overall effect of N addition on the concentrations of N, C and P, on the ratios of C/N, C/P and N/P and on the fraction of initial mass, C, N and P content of decomposing needles (values of X/X_{o}). A one-way ANOVA test was performed to examine the difference in initial chemical quality of pine needles between rehabilitated and disturbed forests. Differences between forests in control plots in terms of the final mass remaining were compared using one-way ANOVAs. The relationship between the fraction of initial mass remaining and ratios of C/N, C/P and N/P at each time point was calculated using Pearson’s correlation analysis (McGroddy et al. 2004). All analyses were conducted using SPSS ver. 10.0 (SPPS, Chicago, Ill.) for windows. Statistical significant differences were set with P values < 0.05 unless otherwise stated.

Results

Initial chemical quality

At the beginning of the experiment, there was a significantly higher concentration of N and P in the pine needles of the rehabilitated forest than in those of the disturbed forest ($P < 005$), but there was no significant difference in C concentration and C/N ratio (Table 2). However, there was a significantly lower ratio of C/P and N/P in the pine needles of the rehabilitated forest than in those of the disturbed forest ($P < 0.05$).

Changes in mass

The amount of mass remaining in the decomposing needles (Fig. 1a, b) over the 18-month period followed the expected patterns, with about 50% of the initial mass remaining at the end of the experiment.

Changes of mass in decomposing needles in control plots reflect the natural process without N additions. During the whole experimental period (24 months), the amount of mass remaining in decomposing needles decreased exponentially with time; in both forests, this trend was characterized by an initial faster rate of decomposition, followed by a subsequent slower rate for both forests (Fig. 1a, b). The regression equations describing the decomposition rates over time were significant ($P < 0.01$) in both forests. The coefficients of determination (r^2) were 0.81 and 0.95 for the disturbed and rehabilitated forest, respectively.

The decomposition constant (k) was higher in the rehabilitated forest (0.30) than in disturbed forest (0.24). At the end of the experiment, the remaining mass was significantly lower in the rehabilitated forest (51% of initial value) than in disturbed forest (57% of initial value) ($P < 0.01$, Fig. 1a, b).

Both levels of N addition significantly increased the decomposition rate relative to the control level in the rehabilitated forest ($P = 0.004$). The response of mass remaining to N addition in the disturbed forest followed a trend similar to that in the rehabilitated forest, however, only medium N addition was found to have significant effects on the decomposition rate over the entire decomposition period (Fig. 1a, b).

Changes in content of C, N and P

The amount of remaining C content in decomposing needles in the control plots followed the patterns observed for needle mass of the corresponding forests (Fig. 1c, d). Exponential models were also found to best describe the changes in C content in decomposing needles in both forests ($P < 0.05$), predicting a rapid initial C loss, followed by a subsequent slower rate of loss. The

Table 2 Initial chemistry[a] of pine (*Pinus massoniana*) needles in a disturbed and a rehabilitated forest of tropical China

Forest type	n	N (mg g^{-1})	C (mg g^{-1})	P (mg g^{-1})	C/N	C/P	N/P
Rehabilitated	6	13.08 (0.04) a	523.8 (18) a	0.81 (0.02) a	40.1 (1.7) a	646.7 (21) a	16.4 (0.9) a
Disturbed	6	12.49 (0.05) b	492.8 (13) a	0.66 (0.02) b	39.5 (1.9) a	746.7 (33) b	19.0 (1.0) b

[a] Values are means with 1 SD in parentheses; columns sharing different letters are significantly different at $P < 0.05$

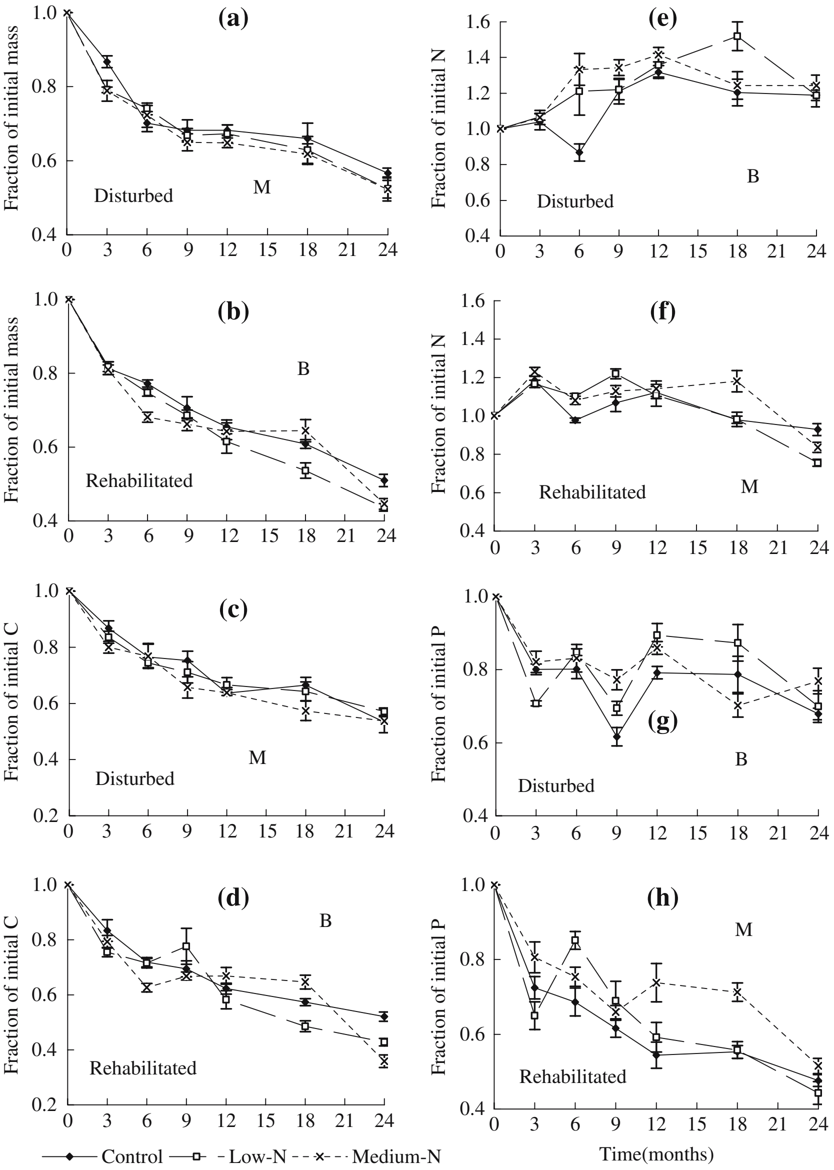

Fig. 1 Changes in mass and in contents of C, N and P in decomposing pine (*Pinus massoniana*) needles in a rehabilitated (**b**, **d**, **f**, **h**) and a disturbed (**a**, **c**, **e**, **g**) forest in tropical China. *B* indicates a significant difference between the control and low/medium-N addition plots at $P < 0.05$ ($n = 6$), *M* indicates a significant different between the control and medium-N addition plots at $P < 0.05$ ($n = 6$), *N* indicates no significant N addition effect at $P < 0.05$ ($n = 6$)

coefficients of determination (r^2) were 0.90 and 0.92 for the disturbed and rehabilitated forest, respectively. However, the decomposition constant (k) was slightly higher in the rehabilitated forest (0.30) than in the disturbed forest (0.28). At the end of the experiment (after 24 months), there was no significant difference in the remaining C content between the disturbed forest (53% of initial value) and the rehabilitated forest (52% initial value) (Fig. 1c, d).

The changes in N content in decomposing litter showed a four-phase pattern in both forests (Fig. 1e, f): net gain (net immobilization) from 0 to 3 months, leaching from 3 to 6 months, net gain from 6 to 12 months and leaching from 12 to 24 months. At the end of the experiment, the N content was significantly higher in the disturbed forest (118% of initial value) than in the rehabilitated forest (93% of initial value) ($P < 0.01$).

The P content in decomposing needles decreased sharply in the first 3 months for both forests; this was followed by a four-phase pattern in the disturbed forest and a slow decrease over with time in the rehabilitated forest (Fig. 1g, h). At the end of the experiment, the P content was also significantly higher in the disturbed forest (68% of initial value) than in the rehabilitated forest (48% of initial value) ($P < 0.01$).

Significant positive effects of N addition at both levels were found on C release in the rehabilitated forest over the entire decomposition period ($P = 0.014$), but these significant effects were found only between medium-N addition plots and control plots in the disturbed forest (Fig. 1c, d). However, the effects of N addition on the release of N and P from decomposing needles were dramatically different from those of mass loss and C release (Fig. 1e, h). N contents in decomposing needles were significantly higher in low/medium-N plots than in control plots over the entire decomposition period in the disturbed forest ($P = 0.007$; Fig. 1e, f), but a significant difference was found only between the control and medium-N in the rehabilitated forest ($P < 0.05$). The response of P content to N addition followed patterns similar to those for N content in both forests (Fig. 1g, h).

Changes in the concentration of C, N and P

In control plots, the changes in C concentration in decomposing needles were relatively constant in both forests (Fig. 2a, b). At the end of the experiment, the C concentration of the decomposing needles was 93 and 102% of the initial values for the disturbed and rehabilitated forest, respectively. However, the concentrations of N in decomposing needles increased with time in both forests (Fig. 2c, d). At the end of the experiment, N concentration was 210 and 182% of the initial values for the disturbed and rehabilitated forest, respectively. The changes in P concentration followed a pattern similar to that for N concentration in the disturbed forest, while it showed a pattern similar to that for C concentration in the rehabilitated forest (Fig. 2e, f). After 24 months, the final P concentration was 120 and 93% of the initial values for the disturbed and rehabilitated forest, respectively.

There was no significant N addition effect on the C concentration in decomposing needles for either forest

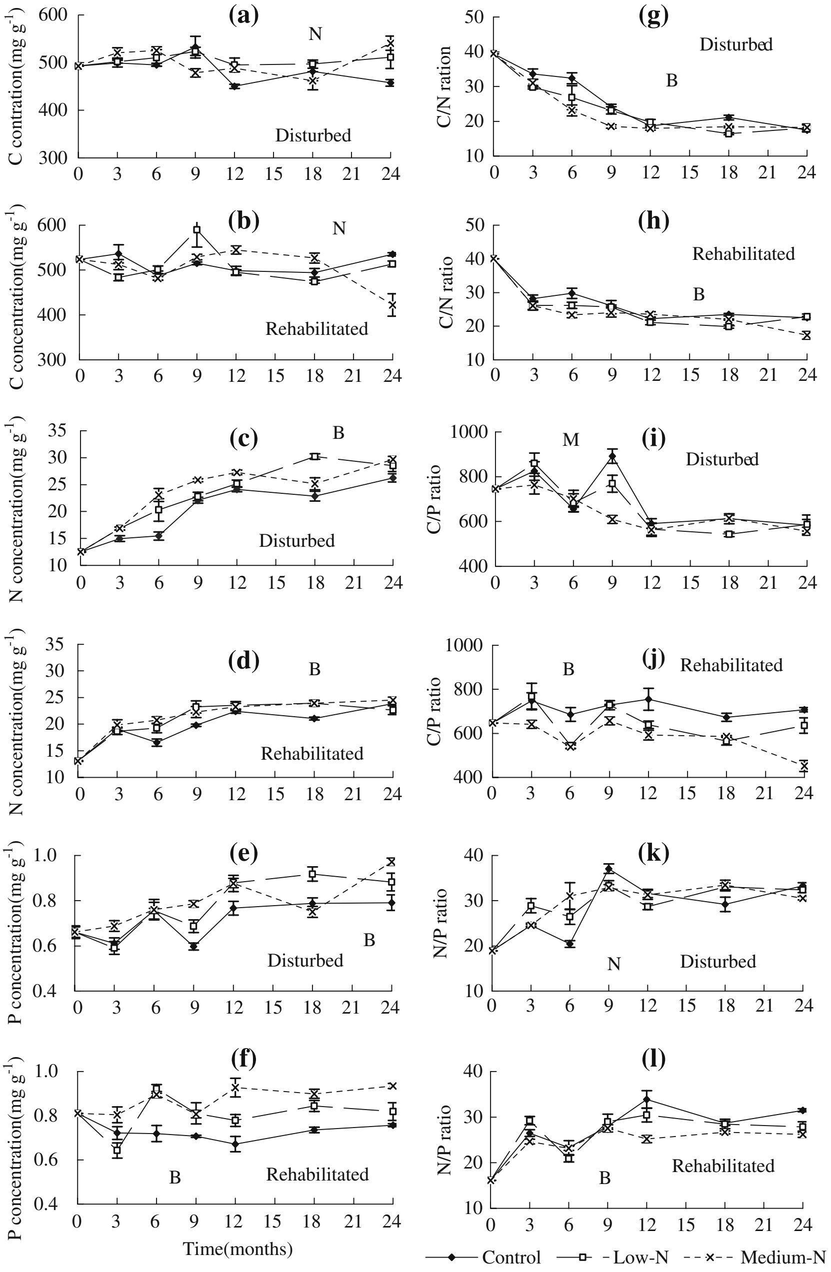

Fig. 2 Changes in the concentration of C, N and P and changes in the ratio of C/N, C/P and N/P in decomposing pine (*P. massoniana*) needles in a rehabilitated (**b**, **d**, **f**, **h**, **j**, **l**) and a disturbed (**a**, **c**, **e**, **g**, **I**, **k**) forest in tropical China. *B* indicates significant different between the control and low/medium-N addition plots at $P < 0.05$ ($n = 6$), *M* indicates significant different between the control and medium-N addition plots at $P < 0.05$ ($n = 6$), N indicates no significant N addition effect at $P < 0.05$ ($n = 6$)

(Fig. 2a, b). However, there were significant positive effects of both levels of N addition on the concentration of N and P in the decomposing needles in both forests ($P < 0.01$; Fig. 2c, f).

Changes in ratio of C/N, CP and N/P

In the control plots, the C/N ratio of the decomposing needles declined with time during decomposition for both forests (Fig. 2g, h). After 24 months, the final C/N ratio was 44 and 56% of the initial values for the disturbed and rehabilitated forest, respectively. However, the N/P ratio in decomposing needles increased with time during the first 9 or 12 months, remaining relatively constant thereafter for both forests (Fig. 2k, l). The final N/P ratio was 176 and 195% of the initial values for the disturbed and rehabilitated forest, respectively. The change in the C/P ratio in the decomposing needles showed a similar pattern, with changes occurring during the first 9 or 12 months and the C/P ratio remaining relatively constant thereafter for both forests (Fig. 2I, j). The final C/P ratio was 78 and 109% of the initial values for the disturbed and rehabilitated forests, respectively.

N addition at both levels significantly decreased the C/N, C/P and N/P ratios in decomposing needles over the entire decomposition period in both forests, with the exception of the C/P ratio in the low-N addition plot and the N/P ratio for both levels of N addition, in the disturbed forest ($P < 0.05$, Fig. 2g, l).

The initial mass remaining of decomposing needles was significantly correlated with changes in the C/N ratio of the decomposing needles for all treatments and forests ($P < 0.001$; figure not shown). Similarly, the initial mass remaining of decomposing needles was significantly correlated with changes in the C/P and N/P ratios in decomposing needles for all treatments in the disturbed forest, but it was not significantly correlated in the rehabilitated forest ($P < 0.001$; figure not shown).

Discussion

We reported previously that the decomposition coefficients (*k*) of pine needles in control plots of disturbed and rehabilitated forests were 0.27 and 0.31, respectively, for an 18-month experimental period (Mo et al. 2006). The results from the present study reveal that with a 6-month extension to the study time (= 24 months), the decomposition rates (0.24 and 0.30 for disturbed and rehabilitated forests, respectively) were slightly lower. Because litter decomposition rates were significantly enhanced by the N additions, the low soil N availability was assumed in the first investigation to be the cause for the low litter decomposition rates in both the disturbed and rehabilitated forests (Mo et al. 2006); the results from this study support this assumption.

In the early stages of decomposition, the soil microbial biomass is capable of taking up and assimilating soluble, low-molecular-weight nitrogenous organic compounds for growth (Molina et al. 1983). It therefore is a well-accepted concept that decomposing litter will gain (net immobilization) N from a soil solution during the early stage of decomposition if microbial decomposition by microbes is limited by N availability (Staaf and Berg 1981; Magill and Aber 1998; Kuperman 1999). Our results indicated that needles in control plots of both forests gained (net immobilization) nitrogen during decomposition process, especially during the first year period (Fig. 1e, f). These are partially consistent with the results found in our previous litter decomposition experiment in disturbed forest (Mo et al. 1995) in which pine needles immobilized nitrogen during the first 200–250 days of decomposition. The results above suggest that pine needles contained insufficient nitrogen to support microbial use of the C in both disturbed and rehabilitated forests. Furthermore, N additions significantly increased net N immobilization of decomposing pine needles in both forests relative to the control plots (Fig. 1e, f), which is also evidence of N limitation for litter decomposition in our study forests (Conn and Day 1996; Ostertag and Hobbie 1999).

The increased rates of litter decomposition at elevated atmospheric N inputs have been attributed to improved litter quality (Koopmans et al. 1998). The C/N ratio of decomposing litter has long been considered to be a sound predictor of decomposition rate (Berg et al. 1998; Xuluc-Tolosa et al. 2003). Kuperman (1999) attributed these positive effects to the increasingly available exogenous N pools that would lower the substrate C/N ratios available to decomposers during litter decomposition. This hypothesis was supported by the highly significant relationship between the C/N ratio and percentage mass remaining that was found in his study. Aerts et al. (1995) found the same trend – that the C/N ratio of leaf litter was reduced and decomposition rates increased with an enhanced N supply. Our results also support the hypothesis above. Nitrogen additions had no significant effect on C concentration, but they did significantly increase N concentration in decomposing pine needles for both forests (Fig. 2a–d). As a result, C/N ratios were significantly reduced by the N additions (Fig. 2g, h), and these changes corresponded to the response of mass loss rate to N addition in both forests (Fig. 1a, b). Furthermore, the initial mass remaining of decomposing pine needles was significantly correlated with changes in the C/N ratio of decomposing pine needles for all treatments and forests in our study ($P < 0.001$; figure not shown).

Our results also indicate that the enhanced decomposition by N additions was still slower than the values cited from available literature by Mo et al. (2006) for pine and other types of forests in temperate, subtropical and tropical regions. At the end of the experiment (after 24 months), the remaining mass in the disturbed forest was about 5% lower in the medium-N addition plots than that in control plots, but it was similar between the low-N addition and control plots. In the rehabilitated forest, however, the remaining mass was 6–7% lower in the low/medium-N addition plots than that in control plots (Fig. 1a, b). These results indicate that factors other than N availability still limit decomposition and suggest that the site conditions in both forests are still poor for litter decomposition. As reported above, the original sites of both rehabilitated and disturbed forests were badly eroded and degraded (Brown et al. 1995; Mo et al. 1995, 2006). The disturbed forest had been continuously subjected to man-made pressures since it was planted in 1930 up until late 1990s, primarily in the form of harvesting of the understory and litter (about two to three times a year; Brown et al. 1995; Mo et al. 1995). This harvesting practice not only removes the nutrients therein, but it also removes organic matter and, thus, substrate for microbial activity, resulting in higher N leaching losses. As a result, the site productivity was low (Brown et al. 1995; Mo et al. 1995, 2003, 2004).

Similarly, the rehabilitated forest, originating from a planted pine forest that was naturally invaded and colonized by broadleaf species, has not fully recovered its site condition during the past several decades (Mo et al. 2003, 2004). For example, compared with an adjacent non-disturbed mature forest, both disturbed and rehabilitated forests are considerably lower in the abundance of soil fauna (Xu et al. 2005), in the quantity of soil microbial biomass (Yi et al. 2002), in soil water storage capacity (Zhang and Zhou 1989) and in soil available P (Mo et al. 2006). These same factors are also very important for litter decomposition. Hence, N availability is not the single factor limiting decomposition in both the disturbed and rehabilitated forests.

An interesting finding was that both levels of N addition significantly increased the decomposition rate in the rehabilitated forest ($P = 0.004$), while only the medium-N addition had such a significant effect in the disturbed forest (Fig. 1a, b). This suggests that the positive effect of N addition on mass loss rate was more sensitive to the N addition rate in the rehabilitated forest than in the disturbed forest. As mentioned above, in addition to N availability, other factors were also limiting decomposition in both forests. Thus, the possible explanation for the more sensitive response in the rehabilitated forest could be this forest has a higher nutrient status (Table 2).

The difference in nutrient status is most likely one of the reasons why decomposition rates were faster in the rehabilitated forest than in the disturbed forest. For example, the soil available P was higher in the rehabilitated forest (4.21 mg kg^{-1}) than in the disturbed forest (3.59 mg kg^{-1}). Similarly, the initial P concentration of pine needles was significantly higher in the rehabilitated forest (0.81 mg g^{-1}) than in the disturbed forest (0.66 mg g^{-1}) ($P < 0.01$, Table 2). These higher values corresponded significantly to the higher decomposition rate of pine needles in the rehabilitated forest compared with that in the disturbed forest (Fig. 1a, b). It is generally accepted that litter decomposition is faster in nutrient-rich sites than in nutrient-poor sites and that litter with a high initial nutrient concentration decomposes relatively faster.

The N and P contents of decomposing pine needles were significantly higher in low/medium-N plots than in control plots over the entire study period in the disturbed forest ($P < 0.01$; Fig. 1e, h), but such a significant difference was only found between the control and medium-N plots in the rehabilitated forest ($P < 0.05$). This indicates that the negative effects of N addition on the release of N and P from decomposing pine needles were more sensitive to the N addition rate in the disturbed forest than in the rehabilitated forest. The reasons for this increased sensitivity in the disturbed forest can also be explained by the difference in nutrient status between the two forest types (Table 2). Pine needles in the disturbed forest had a significantly lower initial N concentration, indicating that N was more limiting in the disturbed forest than in the rehabilitated forest.

The more sensitive response of P contents in the disturbed forest could be attributed to the fact that pine needles in the disturbed forest had a significantly lower initial P concentration and a higher initial C/P ratio (Table 2); consequently, the content of P in the needles of the rehabilitated forest may be sufficient for microbial activity or P could be a limiting factor for microbial activity in the disturbed forest. This hypothesis is supported by the results from our study. Decomposing pine needles in the control plots gained (net immobilization) P during the decomposition process in the disturbed forest but not in the rehabilitated forest (Fig. 1g, h), suggesting that the needles in the disturbed forest contained insufficient P to support microbial use of the C (Staaf and Berg 1981; Magill and Aber 1998; Kuperman 1999). Furthermore, the concentrations of P in decomposing pine needles increased with time in the disturbed forest, but not in rehabilitated forests (Fig. 2e, f). The increase in nutrient concentrations in decomposing litter generally indicates which nutrients are limiting the activity of decomposer organisms (Anderson et al. 1983; McGroddy et al. 2004; Sayer 2006). In addition, the mass loss of the decomposing needles was significantly correlated with changes in the C/P and N/P ratios in decomposing needles for all treatments in the disturbed forest, but there were no respective significant correlations in the rehabilitated forest ($P < 0.001$; figure not shown).

Conclusion

In summary, N addition increased (positive effect) mass loss rate and C release rate, but suppressed (negative effect) the release rate of N and P from decomposing needles in both the disturbed and rehabilitated forests. The enhanced needle decomposition rate by N addition was significantly related to the reduction in the C/N ratio in decomposing needles. However, N availability was not the sole factor limiting needle decomposition in both the disturbed and rehabilitated forests. The positive effect was more sensitive to N addition rate in the rehabilitated forest than in the disturbed forest, but the reverse was true for the negative effect. These results suggest that nutrient status could be one of the important factors in controlling the response of litter decomposition and its nutrient release to elevated N deposition in the reforested ecosystems in the study region.

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