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*Full Length Research Paper*

# Effects of soil mesofauna and microclimate on nitrogen dynamics in leaf litter decomposition along an elevation gradient

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**The nutrient dynamics in decomposing litter has proved to play a crucial role in regulating the nutrient status of ecosystems and vegetation productivity. Little is known, however, about the effect mechanism of decomposer and its environment on the nitrogen (N) mineralisation of litter along an elevation gradient in such sites. We investigated the effects of soil mesofauna using litter bags on N dynamics in decomposing *Castanopsis carlesii* litter along an elevation gradient across four types of ecosystems in southeastern China: evergreen broadleaf forest (EVB), coniferous forest (COF), dwarf forest (DWF) and alpine meadow (ALM). The mean contribution of soil mesofauna to N concentration was 12.6% at EVB, 10.6% at COF, 5.4% at DWF, and 3.1% at ALM. The N concentration of litter with mesofauna was significantly related to *H'* (Shannon-Wiener) and GN (group number) across the four sites. The effects of soil mesofauna on N concentration of litter were significantly linked to some special faunal groups, including Oribatida, Mesostigmata and Collembola. The N concentration in litter bags were positively related with mean annual air temperature, soil temperature and litter moisture along the elevation gradient. We concluded that the rapid accumulation of N in lower elevation sites during the first few months can result in the retention of mobile N in soils and the effects of soil mesofauna on N dynamics may be intimately associated with microclimate (warm and humid) and faunal diversity along the elevation gradient.**

**Key words:** Nitrogen concentration, mesofauna, faunal diversity, elevation gradient, Wuyi National Nature Reserve, China.

## INTRODUCTION

The process of litter decomposition plays a vital role in regulating ecosystem carbon storage and nutrient cycling (Wardle, 2002; Santiago, 2007). The nutrient dynamics of litter related to the decomposition rates directly determine the nutrient status of an ecosystem, thereby exerting crucial control on vegetation productivity (Moretto and Diste, 2003; Knorr et al., 2005; Van Der Heijden et al., 2008). Decomposition and nutrient dynamics are known to be regulated by the decomposer activities (Heneghan et al., 1999; Wang et al., 2003; Strickland et al., 2009), which depend on physical and chemical environmental factors such as temperature, humidity and litter biochemical quality (Vitousek et al., 1994; Lee and Bukaveckas, 2002; Ross et al., 2002; Trinder et al., 2008). It is shown that, the biochemical quality of litter especially nitrogen (N) concentrations as a demand for decomposers, is believed to be related to the rate of litter decomposition (Enríquez et al., 1993; Vivanco and Austin, 2008). The slow litter decay with poor N quality may be a result of decomposer activities that are limited due to a lack of nutrients. Soil biology can cause N immobilization from outside when N concentration in the substrate is low, so the N content in the litter tends to increase, to meet microbial demand (Wang and Huang, 2001; Baker et al., 2001).

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Studies on the N cycling across ecosystem types revealed that, increase in the environmental temperature and moisture generally results in greater rates of microbial activity (Strickland et al., 2009), thereby increasing the rate of decomposition and N mineralization from plant litter. Vitousek et al. (1994) suggested that, decomposition rates decrease exponentially as temperature falls along elevation gradients. The climatic variability in warm humid zones means that the interactions between decomposer and its environment may be the strongest determinants of decomposition dynamics and N mineralization (Lavelle et al., 1993; Turetsky et al., 2008). Forest soils at warm humid zones also support a highly diverse microbial community (Lodge et al., 1996; Lan et al., 2010) and the microbial production also contributes to the retention of N. However, because of this potential for high N immobilization by microbes, microbes may compete with plants for nutrients in N-limiting conditions (Zak et al., 1990).

The contribution of soil mesofauna community to N dynamics can be expected because soil mesofauna can stimulate or inhibit microbial production by grazing some microbes (Lussenhop, 1992). It was found that, in general models of belowground food web and ecosystem process, the faunal effect on decomposition was often determined by the interaction of soil animals and microbial populations (Zheng et al., 1997; Scheu and Falca, 2000; Scheu and Folger, 2004). Whether microbial production increases or decreases in response to grazing appearances depends on the grazing intensity of soil fauna (Hanlon and Anderson, 1979). A faunal influence on microbial N accumulation would therefore, result in greater or lower N concentration for a given mass of litter remaining, depending on the abundance of grazers in the system.

However, the interaction mechanism of soil mesofauna and microbes for litter decomposition and nutrient mineralization are poorly understood (Sulkava and Huhta, 1998). Some mesofauna (Collembola and Oribatida) are proved to prefer ectomycorrhizal over saprotrophic fungi (Shaw, 1992; Hiol et al., 1994; Ruess et al., 2000). Furthermore, many mesofauna can modify the physical environments of plant litter decomposers. Each of these trophic interactions influence nutrient mineralization, but the diversity significance of mesofauna is not well known. In this paper, carbon (C) and N dynamics in decomposing *Castanopsis carlesii* litter confined in litterbags along an elevation gradient in the Wuyi Mountains was examined. Our objectives were to examine: (1) The N dynamics in decomposing litter along the elevation gradients; (2) the relationships between the composition and diversity of the soil mesofauna and their contribution to litter N concentration along the elevation gradient; (3) the interaction effects of soil mesofauna and its microclimate (warm and humid) in regulating N concentration of litter across the four sites.

## MATERIALS AND METHODS

### Site descriptions

This study was carried out at the Wuyi National Nature Reserve in the northern Fujiang province; a 56,527 ha forested area in the southeast of China (117°27′-117°51′E, 27°33′- 27°54′N). The vegetations in the Wuyi Mountains are distributed with clear vertical zonation along elevational gradients. Four sites with a range of elevation from 300 m to 2158 m above sea level were established to investigate the relationships between soil mesofauna and N dynamics across an altitudinal gradient. The vegetation types of the four sites were evergreen broadleaf forest (EVB), coniferous forest (COF), dwarf forest (DWF) and alpine meadow (ALM), respectively. A brief summary of their characteristics of climate, vegetation and soil are given in Table 1.

### Experimental design and sampling

Recently senesced leaves of *C. carlesii*, dominate plant species in the Wuyi Field Ecological Research Station, were collected in the evergreen broadleaf forest at the Wuyi Mountains and approximately 4 g of air-dried litter was placed in nylon litter bags (10 x 10 cm). The original N content of the litter was 1.47% and the initial C concentration was 50.26% (C: N ratio of 34). Leaf litter samples were oven-dried at 60°C to establish the relationship between air-dry and oven-dry mass.

Within an environmentally homogeneous part of each site, a total of 288 litter bags were placed horizontally on the soil surface in the field: 72 in each of the sites (EVB, COF, DWF and ALM). At each site, 72 litter bags containing leaf litter of *C. carlesii* were placed into each of three random blocks (50 × 60 m). Each block was spaced about 10 m apart.

Within each block, two 4 × 4 m plots were randomly set up. Two treatments were randomly assigned to the two plots within each block: control (1.00 mm mesh size) and mesofauna-excluded (0.01 mm mesh size). 12 litter bags were placed on each plot.

Every two months for one year, 12 litter bags (six from mesofauna-excluded litterbags and six from control ones) were collected at random from each site and six litter bags (two from each block) per treatment per site were taken to the laboratory for analyses. All collected litter bags were subjected to faunal extraction (see further) and then, oven-dried at 60°C and weighed to determine the remaining litter mass. Litter moisture within litter bags at the four sites was surveyed and calculated as the difference between litter wet and dry weights divided by the dry weight and expressed as a percent [(wet weight - dry weight)/dry weight) × 100].

Four sets of HOBO onset microclimatic recorders (U23-002) were used to measure the air temperature at 15 min intervals at each of the four sites. Soil temperature in plots was measured hourly with data loggers (Onset Computer Corporation, Pocasset, MA, USA) placed in the center of each plot 5 cm below the soil surface. Soil moisture was calculated as: soil moisture (%) = 100 (wet weight-dried weight)/dried weight. Soil pH in the site floor was measured in 10:1 slurry of deionized water and 2.0 g of sample. Total C and total N of the soil and litter were analyzed by combustion, using a Carlo Erba C/N analyzer (Carlo Erba, Milan).

### Calculations and statistical analysis

The N concentration contributed by mesofauna (NCCM) was calculated as NCCM = (control litter bags-mesofauna-excluded litter bags) / mesofauna-excluded litter bags. In the laboratory of the Wuyi Field Ecological Research Station, collected litter bags were immediately placed in modified Tullgren extractors to remove the

**Table 1.** Characteristic of vegetation and soil along the elevation gradients.

| Elevation (m) | EVB | COF | DWF | ALM |
|---|---|---|---|---|
| | **500** | **1150** | **1750** | **2100** |
| Dominant tree species | *C. carlesii* | *Pinus tanwanensis* | *Symplocos paniculata*and*Stewartia sinensis* | For example,*Calamagrostis brachytricha, Miscanthus sinensis,*and*Lycopodium clavatu* |
| Mean annual temperature (℃) | 17-19 (He et al. 1994) | Approximately 14.5 (Zheng and Fang, 2004) | 11.2 (He et al., 1994; Zheng and Fang, 2004) | Nearly 9.7 (He et al., 1994; Zheng and Fang, 2004) |
| Annual mean rainfall (mm) | 1700 | 2000 | 2200 | 3100 |
| Height (m) | 14.7 | 11.4 | 4.5 | 0.25 |
| Soil depth (cm) | ≥80 | 35 | ≥70 | 25 |
| Soil temperature (℃) | 16.86$^a$ | 13.99$^b$ | 11.78$^c$ | 9.38$^d$ |
| Soil moisture (%) | 21.94$^a$ | 32.96$^b$ | 44.75$^c$ | 48.47$^d$ |
| Total C (g kg $^{-1}$) | 33.09$^a$ | 36.85$^a$ | 66.44$^b$ | 95.93$^c$ |
| Total N (g kg $^{-1}$) | 4.96$^a$ | 5.10$^b$ | 6.41$^c$ | 8.12$^d$ |
| C:N | 6.59$^a$ | 7.36$^b$ | 10.10$^c$ | 11.35$^d$ |
| pH | 4.88$^a$ | 4.55$^a$ | 4.85$^a$ | 5.03$^b$ |

Same lowercase letters within a column indicate no significant difference between sites. EVB, evergreen broadleaf forest; COF, coniferous forest; DWF, dwarf forest; ALM, alpine meadow.

litter invertebrates (Wallwork, 1976). All extracted faunal samples were preserved in 75% ethanol and then, sorted under a dissecting microscope (Leica MZ 125) into broad taxonomic groups (Oribatid, Mesostigmatid and Prostigmatid mites, Collembola and Hymenoptera). Diversity, abundance and group number were calculated for mesofauna communities in the 60-day interval of 12 months of decomposition in the four sites. Group number (GN) and abundance (A) were expressed as the number of dw litter. Diversity was measured with the Shannon-Wiener Index ($H'$): $H'=-\sum n_i/N \times \ln(n_i/N)$ where $n_i$ are individuals of group $i$ and $N$ totals of the groups in community (Whittaker, 1972).

The N concentration on each sampling date at each site was examined with repeated measures analysis of variance. Preplanned contrasts of N concentration in the control and mesofauna-excluded litterbags were performed with repeated measures analysis of variance. The difference in the percentage of litter N content in the litter was contrasted, using measured analysis of variance. Pearson's correlation coefficients were used to express the relationships of the N concentration with the litter mesofauna abundance, Shannon index and group number. Statistical analyses were performed using the SPSS Program (SPSS, 2004). Differences at the p < 0.05 level were reported as significant.

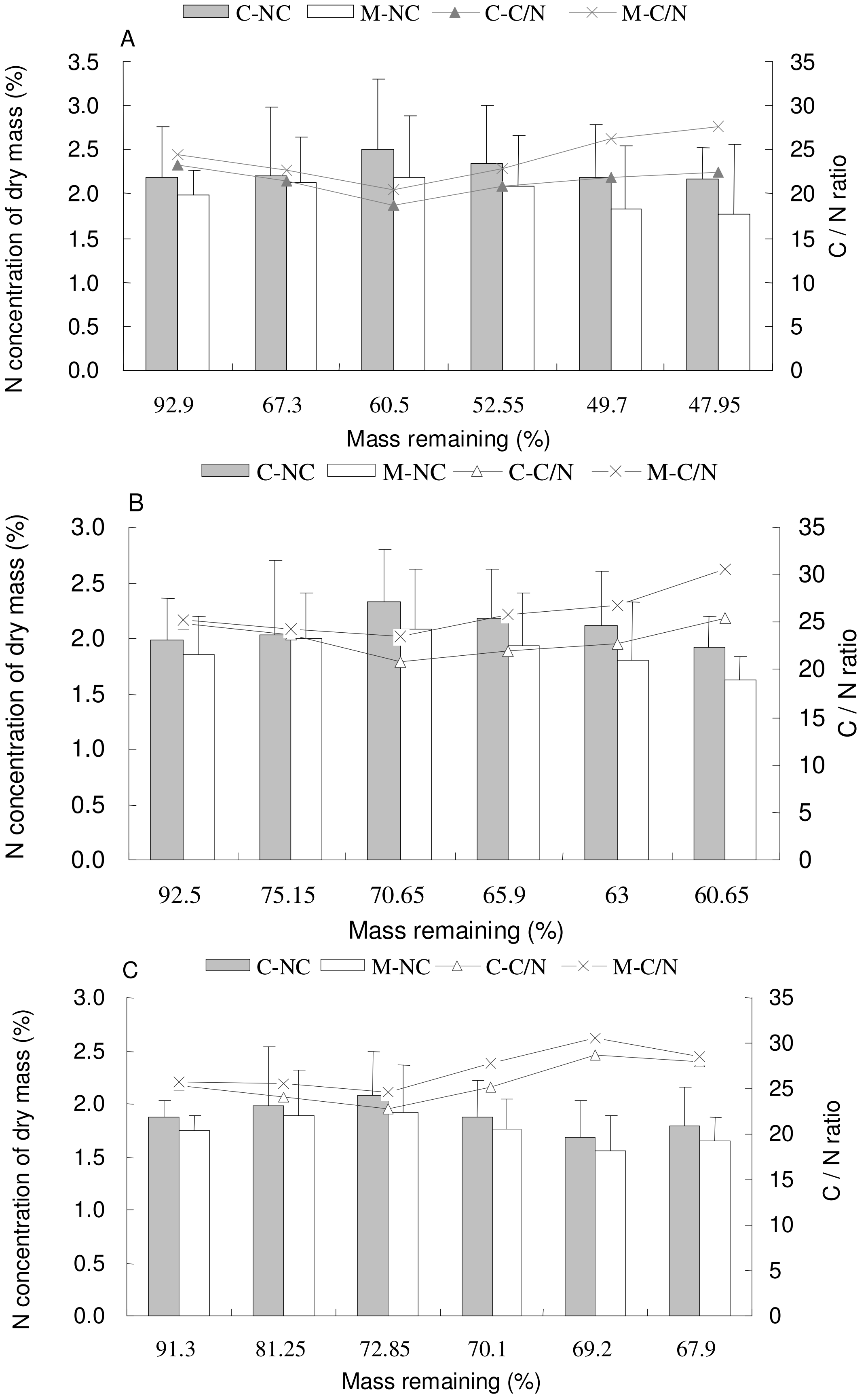
## RESULTS

### N dynamics across the elevation gradient

The N concentration of litter and C/N ratio in the litter bags, as decomposition proceeded, decreased signifycantly along an elevation gradient ($p < 0.05$; Figure 1). The N concentration of litter (mean value of six sampling) in the control and mesofauna-excluded litter bags were 2.26 ± 0.64 and 1.99 ± 0.57%, respectively, in EVB was 2.08 ± 0.44, was 1.88 ± 0.48% in COF, 1.87 ± 0.34 and 1.75 ± 0.28% in DWF and was 1.79 ± 0.45 and 1.71 ± 0.47% in ALM. The N concentration increased up to a mass loss of 30 to 40% at EVB, COF and DWF, where it increased at a slow rate (Figure 1a, b, c). The N concentration at ALM went up to a mass loss of 20 to 30% from which point it decreased and then, increased to a maximum in the end (a mass loss of nearly 30 to 40%) (Figure 1d). The C: N ratio of the litter decreased until it reached a mass loss of 30 to 40% but then increased slightly from approximately 30 to nearly 50% (Figure 1). Strong initial N immobilization across the four sites resulted in a rise in the concentration of N in the litterbags for the first two months of the experiment (Figure 2). It was the greatest at EVB, where the amount of N increased to 148.7% of the original amount in the litterbags with animals. The maximum of N immobilization in the control litterbags at EVB, COF and DWF was found at 180 days, while that at ALM was at 360 days (Figure 2).

### Effects of soil mesofauna and its diversity on the N mineralisation of litter

Litter N content compared with initial N was significantly influenced by mesofauna at EVB, COF and DWF, while fauna had little influence on litter N content at ALM (Figure 2). Litter N content at EVB was strongly affected by the presence of mesofauna (Figure 2a). After six


C-NC
M-NC
C-C/N
M-C/N
A
N concentration of dry mass (%)
C / N ratio
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
35
30
25
20
15
10
5
0
92.9
67.3
60.5
52.55
49.7
47.95
Mass remaining (%)
C-NC
M-NC
C-C/N
M-C/N
B
N concentration of dry mass (%)
C / N ratio
3.0
2.5
2.0
1.5
1.0
0.5
0.0
35
30
25
20
15
10
5
0
92.5
75.15
70.65
65.9
63
60.65
Mass remaining (%)
C
C-NC
M-NC
C-C/N
M-C/N
N concentration of dry mass (%)
C / N ratio
3.0
2.5
2.0
1.5
1.0
0.5
0.0
35
30
25
20
15
10
5
0
91.3
81.25
72.85
70.1
69.2
67.9
Mass remaining (%)

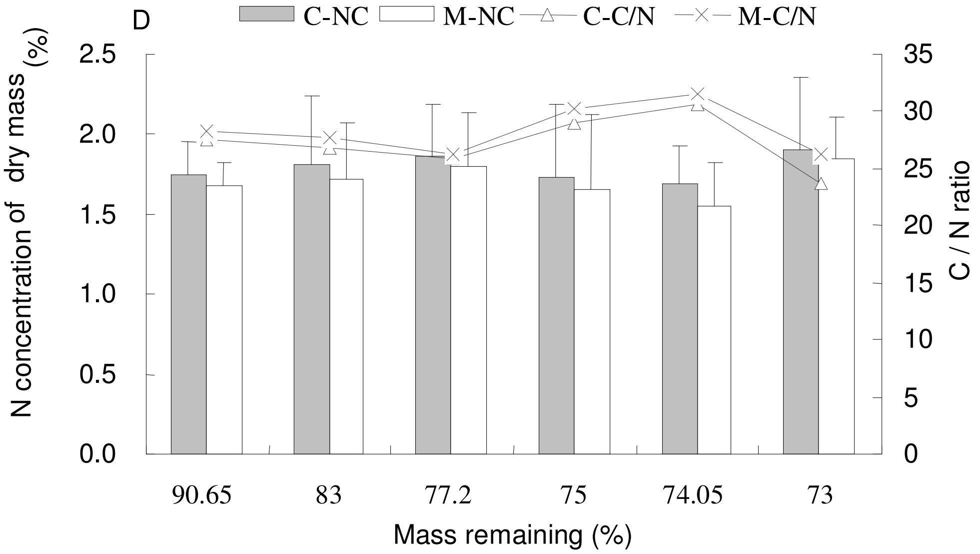
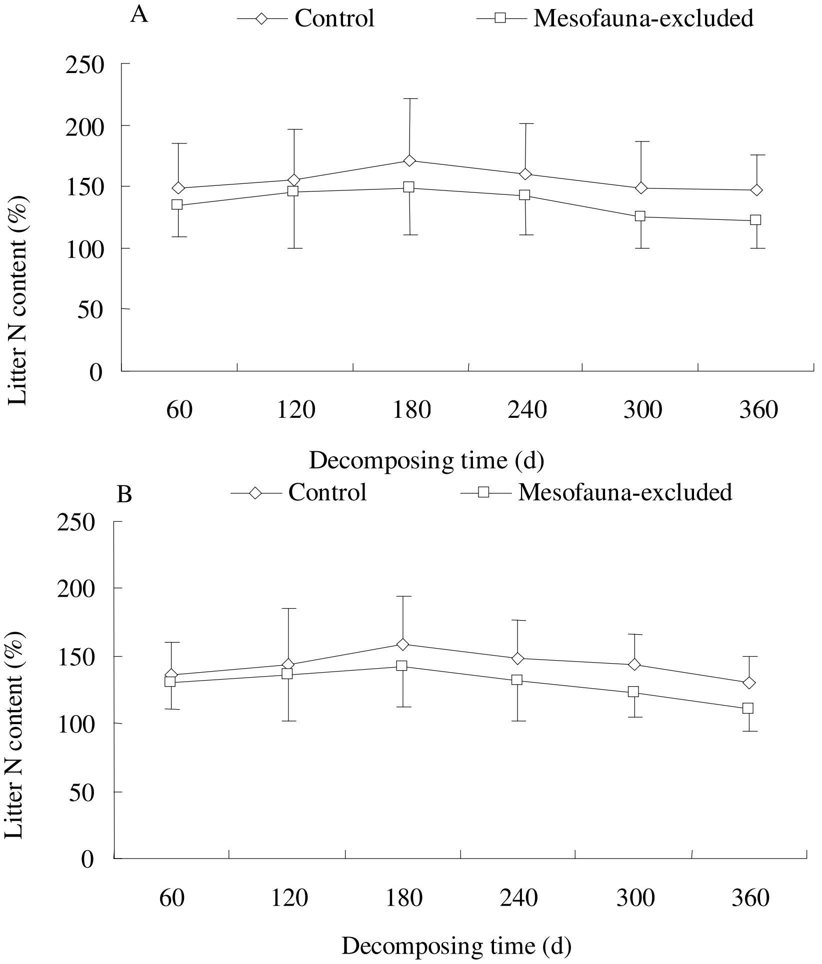


**Figure 1.** N concentrations (+ SD) in the control (C-NC) and mesofauna-excluded litter bags (M-NC), and C/N in control (C-C/N) and mesofauna-excluded litterbags (M- C/N) in relation to mass remaining in the leaf litter of *C. carlesii* at. (A), Evergreen broadleaf forest (EVB); (B), coniferous forest (COF); (C), dwarf forest (DWF); (D), alpine meadow (ALM).



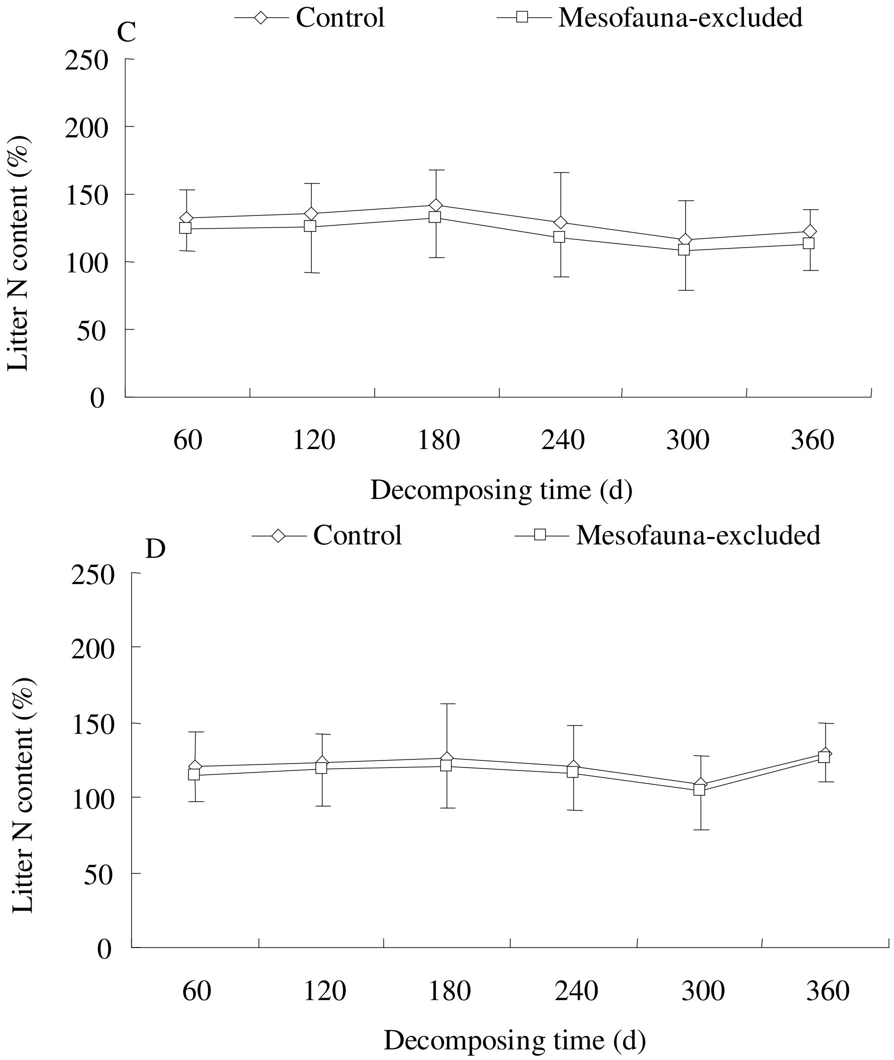


**Figure 2.** Change in litter N content (%) (+ SD) compared with initial N during the decomposition process. (A), Evergreen broadleaf forest (EVB); (B), coniferous forest (COF); (C), dwarf forest (DWF); (D), alpine meadow (ALM).

months, 70% of N in the litter bags compared with the initial N had been fixed when the contribution of the mesofauna was 14% (Figure 2a; Figure 3). After 180 days in the field, the litter N content in the litter bags from the control sites was 60% at COF and 40% at DWF and the mesofauna contribution to the N concentration of litter was 11% at COF and 8% at DWF, respectively (Figures 2b, c and 3). Litter N content compared with the initial N at ALM, however, increased slowly to maximum (only 30%) in the end, while the mesofauna contribution to the N concentration of litter was less than 3% (Figures 2d and 3). The mean contribution of soil mesofauna to the N concentration of litter was 12.6% at EVB, 10.6% at COF, 5.4% at DWF and 3.1% at ALM (Figure 3).

The abundance, Shannon index and group number were surveyed at the four sites and the effects of mesofauna diversity on the N concentrations were examined in the litter bags from the control plots (Figure 4). The N concentration in the *C. carlesii* leaf litter from the control plots was found to be significantly correlated with the abundance of Mesostigmata mites in one year of decomposition at the four sites (Table 2). However, it was only in the coniferous forest that N concentrations significantly related to the total of all mites, while total mesofauna only related to that in the Alpine Meadow. The abundance of Oribatids significantly contributed to the N concentration only in the forest sites (EVB, COF and DWF). The dynamics of the N concentration was significantly related to an abundance of Collembolans in the evergreen broadleaf forest and dwarf forests. Furthermore, the abundance of Prostigmata and Astigmata mites were not significantly correlated with the N concentration in the litterbags from the control plots.

There were distinctively difference in the total abundance

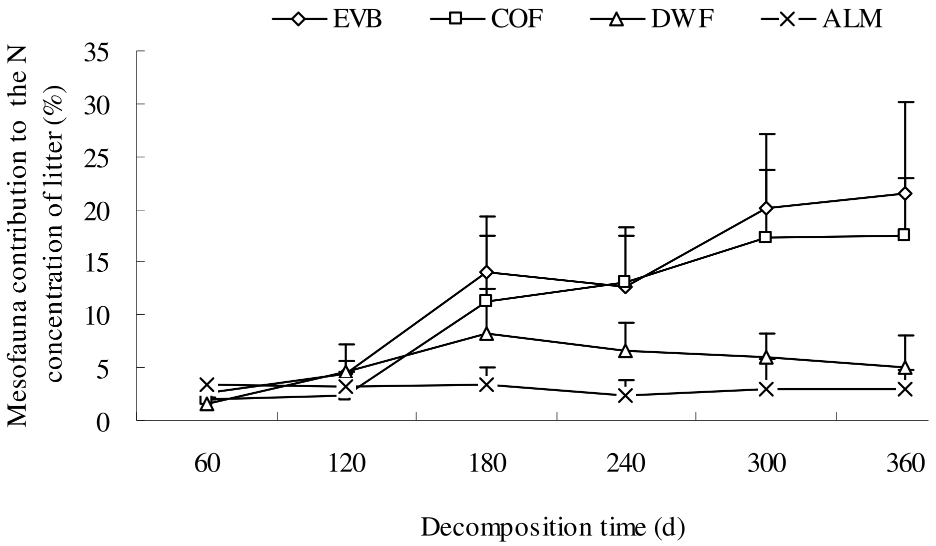


**Figure 3.** Contribution of soil mesofauna (+ SD) to the N concentration of litter at the four sites.

**Table 2.** Correlations between N concentrations of litter and the abundance of litter mesofauna in the control treatment litter bags (1 mm) at the four sites. Values are Pearson's correlation coefficients (n = 6); *P < 0.05, **P < 0.001.

| Parameter | EVB | COF | DWF | ALM |
|---|---|---|---|---|
| Acari | 0.447 | 0.871* | 0.559 | 0.638 |
| Oribatids | 0.784* | 0.822* | 0.805* | 0.575 |
| Prostigmata | 0.635 | 0.702 | 0.148 | 0.472 |
| Mesostigmata | 0.856* | 0.778* | 0.840* | 0.884* |
| Astigmata | 0.353 | 0.225 | 0.447 | 0.156 |
| Collembola | 0.884** | 0.624 | 0.863* | 0.546 |
| Others | 0.851* | 0.527 | -0.375 | 0.832* |
| Total | 0.668 | 0.104 | 0.653 | 0.812* |

of mesofauna with elevation (F=46.647, p < 0.002) but not was significantly related to the N concentrations along the elevation gradients. The Shannon index (F=5.455, p = 0.043) and group number (F=5.830, p = 0.046) both decreased with elevation and the N concentrations in the litter bags with mesofauna were significantly related to *H'* ($r^2$=0.867, p = 0.032) and GN ($r^2$=0.853, p=0.038) across the four sites (Figure 4).

## Microclimate effects on N dynamics across the elevation gradient

The mean N concentration along the elevation gradient was found to be positively associated with mean annual air temperature and soil temperature (Figure 5, p < 0.05).

There was no difference in the litter moisture between the control litterbags and mesofuana-excluded litter bags at the four sites (P > 0.05). Litter moisture which was decreased along the elevation gradient, had a significant influence on the change of N concentration across the four sites (Figure 5, P < 0.05). The litter moisture and soil temperature at EVB with the highest group number, abundance and Shannon index of soil mesofauna, were higher than those at the other three sites, suggesting that the microclimate (moisture and temperature ) affected N dynamics via its effect on the composition and diversity of soil mesofauna (Figures 4 and 5) .

## DISCUSSION

### N concentrations in the litter bags across an elevation gradient

The N concentration of litter or C to N ratio has been shown to be a useful predictor of N mineralization from plant litter (Aber and Melillo, 1980; Högberg et al., 2007). This study illustrated that, N concentrations in decomposing litter are as a function of litter mass remaining. The changes in the N contents closely followed the mass loss dynamics of the decomposing litter. The N concentration of the litter increased with litter decomposition, as has been commonly observed in other research studies (Titus and Malcolm, 1999; Hyvönen and Olsson, 2000; Pandey et al., 2007), but the extent and emergence period of the maximum value of N concentration was different at the four sites in our study. N concentration of litter at EVB which was the highest among the four sites, increased quickly to maximum at six months when 70% of N in the litter bags compared with the initial N had

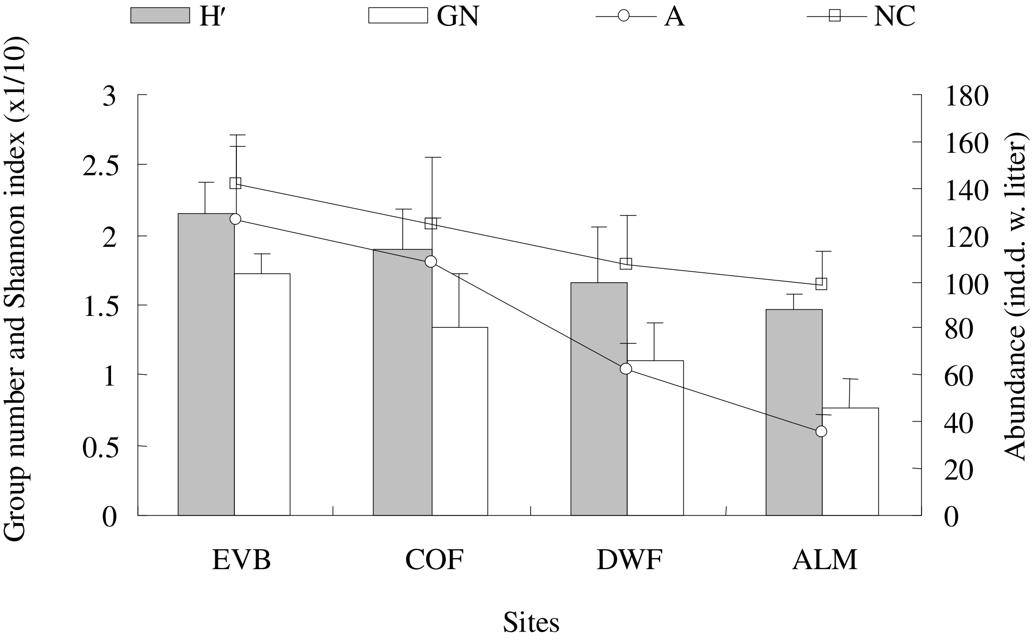


**Figure 4.** Effects of the Shannon index (*H′*), the group number (GN) and abundance (A) on the N concentration (NC) in *C. carlesii* leaf litter in the control litterbags at the four sites. Values are means + SD of the three replicates of each.

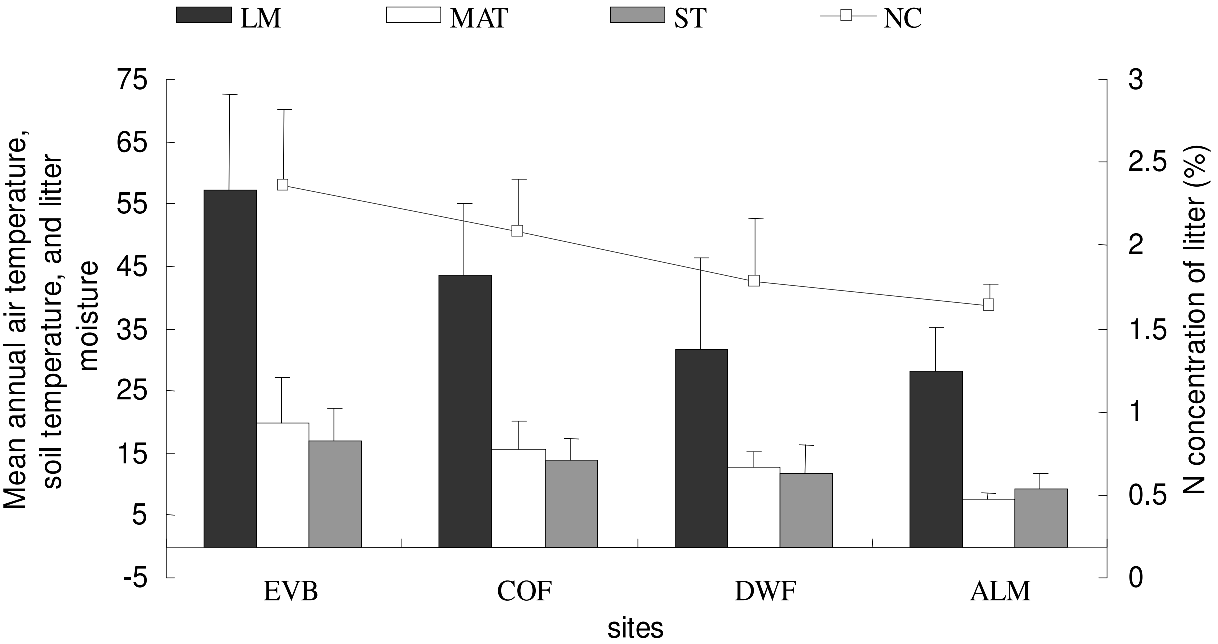


**Figure 5.** Effects of soil temperature (ST, °C), mean annual air temperature (MAT, °C) and litter moisture (LM) on the N concentration (NC) along the elevation gradient. Values are means + SD of the three replicates of each.

been fixed. The rapid N accumulation in lower elevation sites during the first few months could have resulted in the retention of mobile N in soils. N retained in the soil can be significant at a time when leaf flush creates a demand for nutrients (Heneghan et al., 1999).

Decomposer immobilization, initial C: N ratios and the N availability in soils may be responsible for the N accumulation in litter. N concentrations tended to increase in the decomposing leaf litter, which was considered to be related to external biological immobilization (Gessner, 2000; Liu et al., 2000; Aerts, 2006). Biological immobilization was an important process that controlled the nutrient dynamics of litter during decomposition (Gessner, 2000; Parton et al., 2007). In our study, there were significant difference between the N concentration of litter in the control and the mesofauna-excluded litter bags, indicating that mesofauna immobilization can also be expected. As a result, the nutrient concentrations and even the contents in the litter tended to increase. Also, it was found that this process was regulated by the initial C: N ratio of the litter and the N availability in the various environments (Köchy and Wilson, 1997). In this study, because of initially higher C: N ratio, the decomposer took available N from the surroundings to maintain its activities, indicating that the initial C: N ratio was an important index in indicating the intensity of N accumulation or release. The mesofaunas were likely to immobilize N in the litter with low N % during decomposition (Baker et al., 2001).

In the study, the total mass loss and N concentration decreased along the elevation gradient, while all the sites had N immobilization in the decomposition process. The Wuyi Mountains are located in the humid and warm subtropics of southeast China with a strong climatic variation along the elevation gradients. The climatic variability in warm and humid zones means that the interactions between decomposer and its environment may be the strongest determinants of decomposition dynamics and N mineralization (Lavelle et al., 1993; Ross et al., 2002). In this study, soil temperature and annual air temperature decreased and soil C: N increased along an elevation gradient. An increase in soil temperature, annual air temperature and decrease of soil C/N ratio generally results in greater rates of decomposer activity, thus, increasing the rates of mass loss and N mineralization of the plant litter (van Cleve et al., 1990; Sharifi et al., 2007).

## Effects of mesofauna and microclimate on immobilization of N in the sites

Abundance and diversity of soil mesofauna are known to play a vital role in the nutrient mineralization processes through the direct effect of their own metabolism (Verhoef and Brussaard, 1990; De Ruiter et al., 1993) and the indirect modifications of the structure and activity of the microbial community (Coleman and Cole, 1983; Anderson, 1987; Wolters, 1991). The especially complicated makeup of faunal decomposers stimulated the decomposition and nutrient mineralization process through their effect on microorganisms (Mikola et al., 2002; Adeduntan, 2009).

This study has illustrated that the N accumulation in the litterbags can be accelerated by soil mesofauna. Soil mesofauna had a significant influence on the dynamics of litter N content at EVB, COF and DWF, but no statistic difference at ALM. The mean contribution of soil mesofauna to litter N content ranked EVB, COF, DWF and ALM. The presence of high-diversity mesofauna in the sites can cause a greater initial immobilization of nitrogen, while some faunal activities may enhance nutrient mobilization (Tian et al., 1992; Verhoef, 1996; Adeduntan, 2009). In our study, the Shannon index and group number were found to be decreased along the elevation gradient, which resulted in the highest N concentration in the evergreen broadleaf forest. The effect of soil mesofauna at ALM was only marginally significant where there was the lowest faunal diversity. Hence, distinctive abundance and diversity of soil mesofauna among sites resulted in the different effect of soil mesofauna on N dynamics.

Different faunal groups can exhibit different effects on soil processes. Fungivores, for example, Oribatida and Collembola, which are highly abundant and usually dominate soil communities, feed on both mycorrhizal and saprotrophic fungi to accelerate nutrient transfers between plant litter, mineral soil and plant roots (Tiunov and Scheu, 2005). Selective grazing affects fungal biomass and activity, regulating the fungal succession and nutrient transfer in decomposing litter (Parkinson et al., 1979; Lussenhop, 1992). In the experiment, it was found that the abundance of Mesostigmata mites significantly correlated with the N concentration in *C. carlesii* leaf litter at the four sites, while the abundance of Oribatids significantly contributed to N concentration in the forest sites (EVB, COF and DWF). However, it was only at COF that N concentrations was significantly related to the total Acari as well as the abundance of Collembolans at EVB and DWF. The results indicated that, some special groups of soil mesofauna had a significant contribution to N concentrations but the effect varied across the environmental gradients.

Decomposer effect on nutrient dynamics was often considered to depend on the environmental factors of decomposition (Vitousek et al., 1994; Lee and Bukaveckas, 2002; Ross et al., 2002). In the study, N concentration along the elevation gradient was found to be positively associated with mean annual air temperature, soil temperature and litter moisture, indicating that the microclimate had significant effects on N dynamics of litter. The litter moisture and soil temperature at low elevation sites with the highest diversity of mesofauna were higher than in the high one, suggesting that the microclimate (moisture and temperature) may have favored the activity of soil fauna, thus, affected the N mineralization of litter.

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