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Nutrient dynamics of foliar litter in reciprocal decomposition in tropical and subtropical forests

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Abstract In order to explore the release of nutrients and the effects of global warming on the decomposition rate of forest litter, an experiment is designed to reciprocally decompose forest foliar litter in two sites across climatic zones: Mt. Jianfengling in Hainan Province in the tropics and Mt. Dinghushan in Guangdong Province in the subtropics. The two sites have similar altitudes, soil types, annual mean rainfall and seasonality of dry and wet. The main difference between these two sites is the annual mean temperature with the difference of 3.7°C. Foliar litters of 10 native dominant tree species have been collected respectively from the two sites and divided into single-species litter and mixed litter. They are decomposed reciprocally in the two sites. The results indicate that litter decomposes in the tropical site 1.36–3.06 times more rapidly than in the subtropical site. Apparent Q_{10} , calculated on the basis of the temperature difference between the two sites, ranges from 3.7 to 7.5. The return amount of N, P and C will increase by 32.42, 1.033 and 741.1 kg/hm², respectively in Mt. Dinghushan in the first year's litter decomposition under the prevailing temperature condition. Only in Mt. Dinghushan is the correlation between decomposition rate constant and initial

litter quality high and significant in the ratio of lignin to N, lignin, the ratio of lignin to P, HLQ and C. This is not the case at Mt. Jianfengling.

Keywords tropics, subtropics, forest litter, reciprocal decomposition, nutrient dynamics

1 Introduction

Litter decomposition rate is controlled by both intrinsic factors, such as the chemical and physical properties of litter, and extrinsic factors, i.e. environmental conditions that include biotic factors such as the species, abundance and activity of the microbiomes, and soil fauna; and abiotic factors such as climate, soil and atmospheric compositions (Peng and Liu, 2002).

Studies by Jenney et al. (1949), Mikola (1960), Shanks and Olson (1961), Meentemeyer and Berg (1986), Vitousek et al. (1994) have shown that litter decomposition rates increased with rising temperatures. Jenney et al. (1949) and Mikola (1960) approached the effects of temperature on litter decomposition along the temperature gradient induced by latitudinal gradient, while Heaney and Proctor (1989) and Vitousek et al. (1994) along the temperature gradient induced by altitudinal gradient. In the Pacific island Mauna Loa, Vitousek et al. (1994) found that the decomposition rate decreased exponentially with altitude increase and temperature decrease.

Swift et al. (1979) called the chemical properties of litter as “substrate quality,” which was defined as the relative decomposability of litter. It depended on the mix of liable (N, P and so on) vs. recalcitrant organic components (lignin, cellulose, hemicellulose and polyphenolics, etc.) making up the tissue, on tissue nutrient content, and on structure. The indexes usually used for substrate quality were concentrations of N, P, lignin and cellulose and ratios of C to N, lignin to N and C to P, etc, in which C:N and lignin:N were the best indicators of litter decomposition rate (Hill, 1926;

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Jensen, 1929; Witkamp, 1966; Taylor et al., 1989). Hell et al. (1997) suggested that C:N was the general indicator of substrate quality. In some cases, lignin concentration of litter was a good indicator for prediction of mass loss (Meentemeyer and Berg, 1986; Melillo et al., 1982; Cromack, 1973; Dyer et al., 1990), some studies showed that the N (Flanagan and Van Cleve, 1983) and P concentrations and the C:P ratio were also indicators of litter decomposition (Heal and French, 1974; Coulson and Butterfield, 1978; Schlesinger and Hasey, 1981).

This study was conducted through reciprocal decomposition of transplanting litters in Jianfengling Tropical Forest Ecosystem Research Station in tropics and Dinghushan Forest Ecosystem Research Station in subtropics, which is located in the southern part of NSTEC (The north-south transect in eastern China, the 15th international standard transect). In the reciprocal decomposition experiment with large-scale across climatic zones, we tried to explore: 1) differences of decomposition rates and dynamics of chemical composition in decomposing leaf litters of same species between the two climatic zones; 2) impacts of the initial substrate quality of leaf litter on decomposition rate and nutrient release; 3) the difference of mixed litter and single species litter in nutrient release.

2 Materials and methods

The space-for-time substitution approach was employed in the reciprocal litter decomposition experiment between Jianfengling Tropical Forest Ecosystem Research Station in the tropics and Dinghushan Forest Ecosystem Research Station in the subtropics, which is located in southern part of NSTEC.

2.1 Sites description

Mt. Jianfengling (18°23'–18°50'N, 108°36'–109°05'E) is located between Ledong and Dongfang counties in south-western Hainan Island. Site J (tropical site) was selected in the tropical evergreen forest in Mt. Jianfengling with the altitude of 340–360 m, the mean annual temperature of 22.9°C and the mean annual rainfall of 1,749 mm. There exist apparent dry and wet seasons with the 80%–90% rainfall concentrating in the wet season from May to October and the rest during the dry season from November to March (Jiang et al., 1991). Mt. Dinghushan (23°09'–23°11'N, 112°30'–112°34'E) is located in Zhaoqing City, Guangdong Province. Site D (subtropical site) was selected in subtropical monsoon evergreen broad-leaved forest in Mt. Dinghushan at the altitude of 290–310 m, mean annual temperature of 19.2°C and mean annual rainfall of 1,927 mm. The wet season is from April to September with more than 70% rainfall and the dry season from November to January (Peng, 1996). The two sites have similar mean annual rainfall, dry and wet seasons, soil type, altitude and slope direction except for a temperature difference of 3.7°C.

2.2 Experimental methods

The method of space-for-time substitution was used to simulate the temperature rise, namely the difference of mean annual temperature 3–4°C between subtropical site (site D) and tropical site (site J) across climate zones substituted for the process of likely 3–4°C of temperature rise in Dinghushan under global warming scenario. Litterbag technique was used to quantify litter decomposition. Leaf litters of dominant tree species (species were listed and grouped under six types) were collected from sites J and D, respectively, in the 2001 dry season, August and September, by picking the senescent leaves and newly deciduous leaves on the ground. The air-dried leaf litters were put into the nylon mesh bags 15 cm×15 cm in size and 1.0 mm mesh size. Each bag was filled with 15 g leaf litter of a single species or 20 g of mixed-leaf litter.

Tropical litters (the leaf litter collected from site J) were divided into following three groups: J₁: *Vatica mangachapoi*, the predominant species (with highest dominance) in tropical evergreen forest in Mt. Jianfengling; J₂: *Schima superba*; J₃: Mixed-leaf litter of 10 dominant species of tropical seasonal evergreen rain forest that were mixed at equal weights, including *V. mangachapoi*, *S. superba*, *Alseodaphne hainanensis*, *Sindora glabra*, *Litchi chinensis* var. *euspontanea*, *Lithocarpus fenzelianus*, *Canarium album*, *Madhuca hainanensis*, *Castanopsis carlesti* var. *hainanica* and *Gironniera subaequalis*.

Subtropical litter (the leaf litter collected from site D) was also divided into following three groups:

D₄: *C. chinensis*, the predominant species (with highest dominance) in monsoon evergreen broad-leaved forest of Mt. Dinghushan; D₅: *S. superba*; D₆: mixed-leaf litter of 10 dominant species of subtropical monsoon evergreen broad-leaved forest, which were mixed with same weight, including *C. chinensis*, *S. superba*, *Cryptocarya chinensis*, *Cryptocarya concinna*, *Aporosa yunnanensis*, *Syzygium rehderianum*, *Acmena acuminatissima*, *G. subaequalis*, *Ficus nervosa* and *Lindera chunii*.

In September 2001 the litterbags were randomly placed on the forest floor to decompose both in sites J and in D. The litterbags were retrieved every 3 months, i.e. in December March, June and September. Each litter type had seven repetitions. The remaining mass of litter was determined by oven drying at 70°C for calculating the mass loss and decomposition rate. Seven replicates of litter samples were combined into three replicates for chemical analyses. Total carbon was determined after oxidation by K₂Cr₂O₇-H₂SO₄, total N by semimicro Kjeldahl, P by colorimetry following (Agro-Chemistry Committee of China Soil Society, 1983), lignin and holocellulose by the Van Soest procedure (1963). Ash content was measured and all the results were calculated based on ash-free dry weight.

2.3 Data analysis and statistical methods

The differences between sites for mass loss and remaining

content of chemical components were tested by Mann–Whitney U Test. A multivariate analysis was performed on the differences of the remaining mass among litter types within a site followed by Tukey's HSD test. The differences of initial chemical component among litter types were analyzed by one-way ANOVA followed by Tukey's test. The correlation between litter decomposition rate and initial chemical component was analyzed by Spearman's rho. The remaining content of chemical component was expressed by the remaining percentage. The formula was remaining percentage = [(the concentration at t time $\times$ the remaining weight at t time)/(initial concentration $\times$ the initial weight)]. The statistical analyses were performed using SPSS version 10.0 for Windows.

3 Results

3.1 Effects of site characteristics

In this study, the litter mass remaining percentages were measured and showed in Table 1 and Fig. 1 by using the first-order exponential equation to fit the decomposition process. $\ln(M_t/M_0)$ is equal to $X - kt$ or the transformation form, $y = ae^{-kt}$. Where M_0 is the initial mass, M_t is the mass at time t , X is the intercept, k is the exponential decomposition constant, y is the $\ln(M_t/M_0)$ and $\ln a$ is the X . The k values for six litter types in two sites were showed in Table 1. There was significant difference between two sites for all

the six litter types. The decomposition was faster in site J than in site D. The apparent Q_{10} calculated by subtropical litter types ranged from 3.7 to 7.5. Where Q_{10} is the temperature coefficient (the proportional increase in decomposition for 10°C increase in temperature).

The changes in chemical components: N, P, C, lignin and holocellulose with time are shown in Fig. 2, the changes in the ratios of the chemical components in Fig. 3 and the content of chemical components in remaining litter in litterbag (expressed as the remaining percentage) are shown in Fig. 4.

In N dynamics, there was an apparent difference between the two sites. In site J, N concentration in litter increased with time in the first 9 months. However, the absolute content of N, i.e. N remaining percentage experienced decline, increment and decline periods, which were consistent with the three phases, i.e. leaching, accumulation and final release phases (Berg and Staaf, 1981). The decline of N remaining in the first 3 months was related to the rapid mass loss and strong leaching. In early-stage N leaching was very intensive and no net N immobilization occurred. At the 12th month, N release reached 58.09%–87.33%. In site D, N concentration increased with time in the whole year and net N immobilization occurred (except mixed litters J₃ and D₆). At the 12th month the largest N release was 48.87%, which appeared on J₃, and had not reached 50%. D₅ had net N immobilization with only the accumulation and release phases. In both sites, mixed litters released more N than single-species litters.

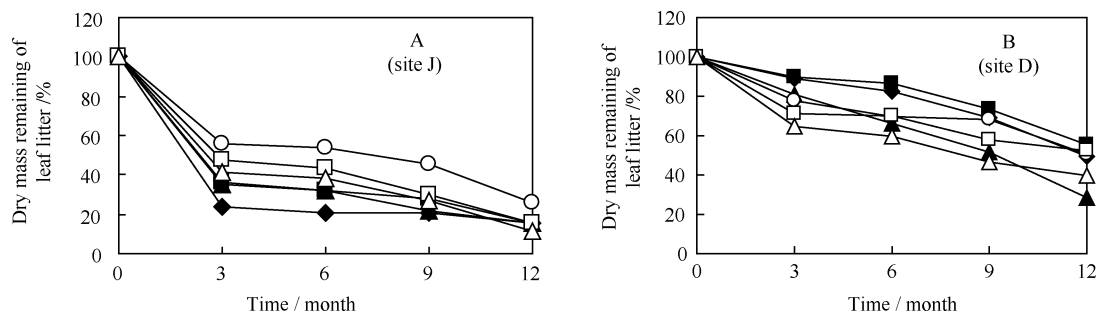


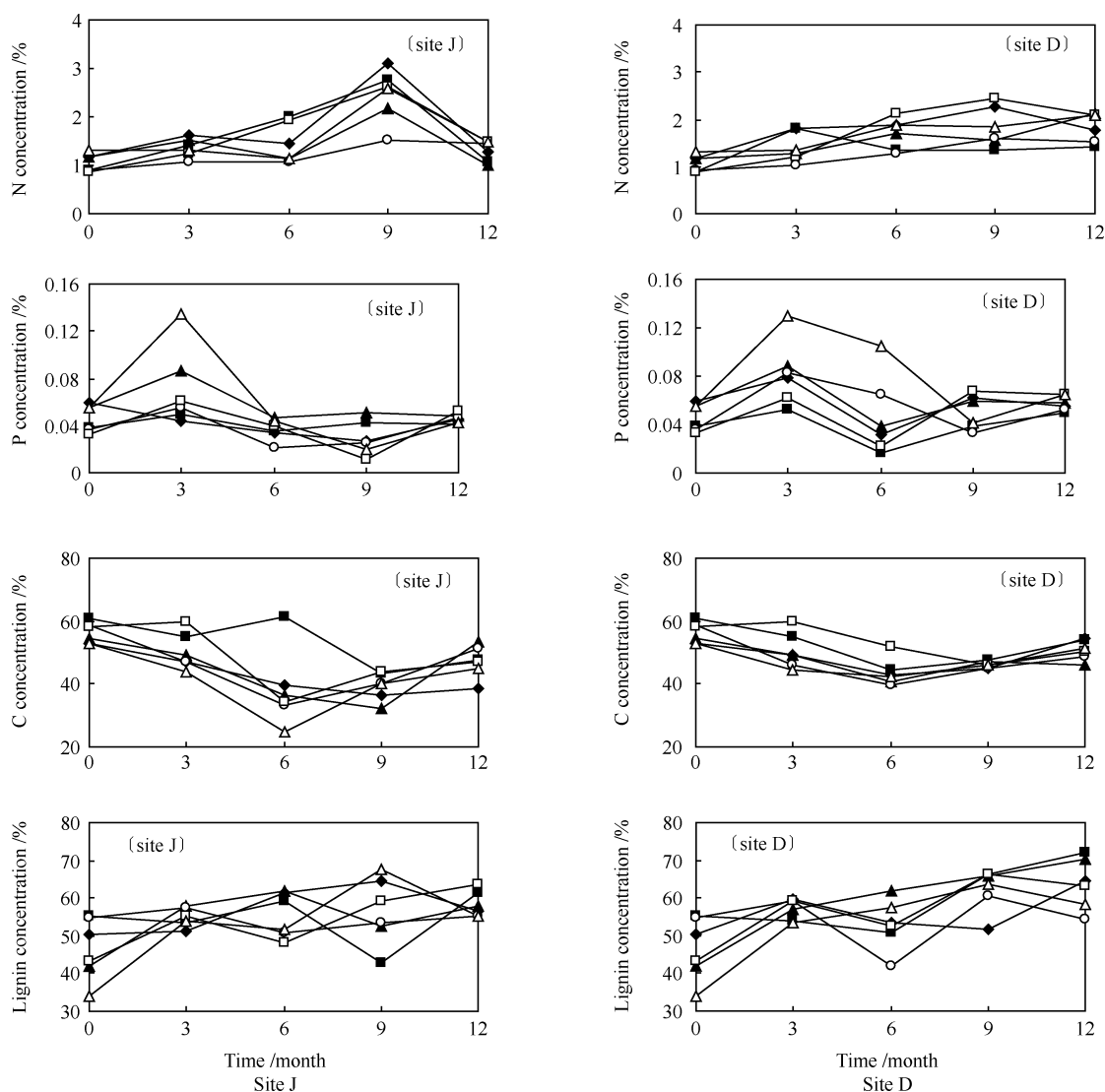
Fig. 1 The percent mass remaining of litter over time for six types in sites J and D

Table 1 Regression equations and decomposition rate constants for six types of leaf litter collected from sites J and D and decomposed in both sites

Litter type	Decomposition rate k /(g·g ⁻¹ ·year ⁻¹)		Equation	R^2		
	Site D	Site J		Site D	Site J	Site J
J ₁	0.657	1.606	$y = 105.782e^{-0.657t}$	$y = 60.359e^{-1.606t}$	0.919	0.709
J ₂	0.548	1.679	$y = 105.069e^{-0.548t}$	$y = 76.249e^{-1.679t}$	0.902	0.897
J ₃	1.205	1.643	$y = 109.079e^{-1.205t}$	$y = 75.395e^{-1.643t}$	0.930	0.887
D ₄	0.548	1.168	$y = 96.437e^{-0.548t}$	$y = 91.743e^{-1.168t}$	0.929	0.908
D ₅	0.621	1.716	$y = 92.502e^{-0.621t}$	$y = 91.975e^{-1.716t}$	0.917	0.947
D ₆	0.876	1.935	$y = 91.231e^{-0.876t}$	$y = 89.637e^{-1.935t}$	0.948	0.921

J₁: *V. mangachapoi*, J₂: *Sc. superba* collected from site J, J₃: mixed litter of 10 species collected from site J;

D₄: *Cr. chinensis*, D₅: *Sc. superba* collected from site D, D₆: mixed litter of 10 species collected from site D



◆: J₁ (*V. mangachapoi*), ■: J₂ (*Sc. superba*), ▲: J₃ (mixed litter of 10 species collected from site J),
○: D₄ (*Cr. chinensis*), □: D₅ (*Sc. superba*), △: D₆ (mixed litter of 10 species collected from site D).

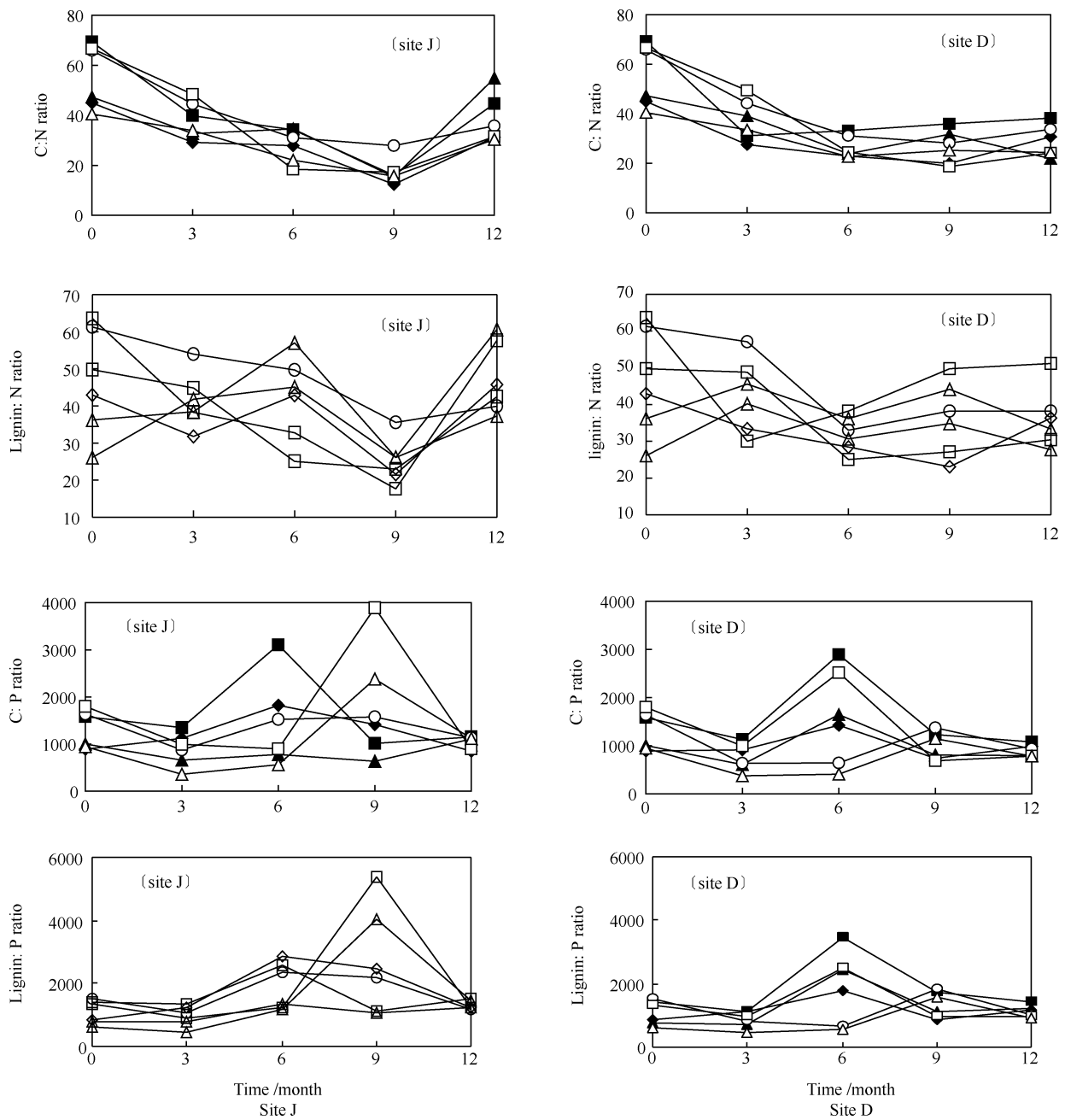
Fig. 2 Concentrations of chemical composition in foliar litters

The increment of phosphorus concentration was shorter than that of N concentration. It increased until the third month, and then declined. In site J, phosphorus remaining percentages declined with time without P net immobilization. All litter types had no P net immobilization, and P remaining percentages were lower than 35% at the end of the year. In site D, P net immobilization occurred, and P remaining percentages increased initially and peaked at the third month, before declining, in which D₄ and D₆ were released P after the sixth month. At the 12th month, P release was in the range of 66.38%–91.48% in site J, but the largest P release was 69.79% in site D, and even D₅ was in P net immobilization. In both sites, mixed litters released more P than most single-species litters (except J₁ in site J).

All C concentrations in litters experienced early decrement and late increment in both sites. They reached the bottom at the sixth month and then increased. C remaining

percentages declined with time. In site J, C concentrations decreased rapidly in the first 3 months, and then declined slowly. At the 12th month, C release was in the range of 77.09%–90.46%. In site D, C remaining percentages declined more or less evenly and nearly linearly. At the 12th month, C release was in the range of 49.02%–75.98%. The curves of C remaining percentage were very much similar to their corresponding mass remaining ones in respective site.

The general trend of lignin concentrations was increasing with time in both sites. The curves of lignin remaining percentage were very different between the two sites. Lignin remaining percentages declined rapidly in the first 3 months and slowly afterwards in site J, but they tended to decrease quite slowly throughout the year in site D. At the 12th month, the lignin remaining percentage was in a narrow range of 55.26%–61.25% in site J, while in a relatively wider range of 54.21%–72.21% in site D.



◆: J₁ (*V. mangachapoi*), ■: J₂ (*Sc. superba*), ▲: J₃ (mixed litter of 10 species collected from site J),
○: D₄ (*Cr. chinensis*), □: D₅ (*Sc. superba*), △: D₆ (mixed litter of 10 species collected from site D).

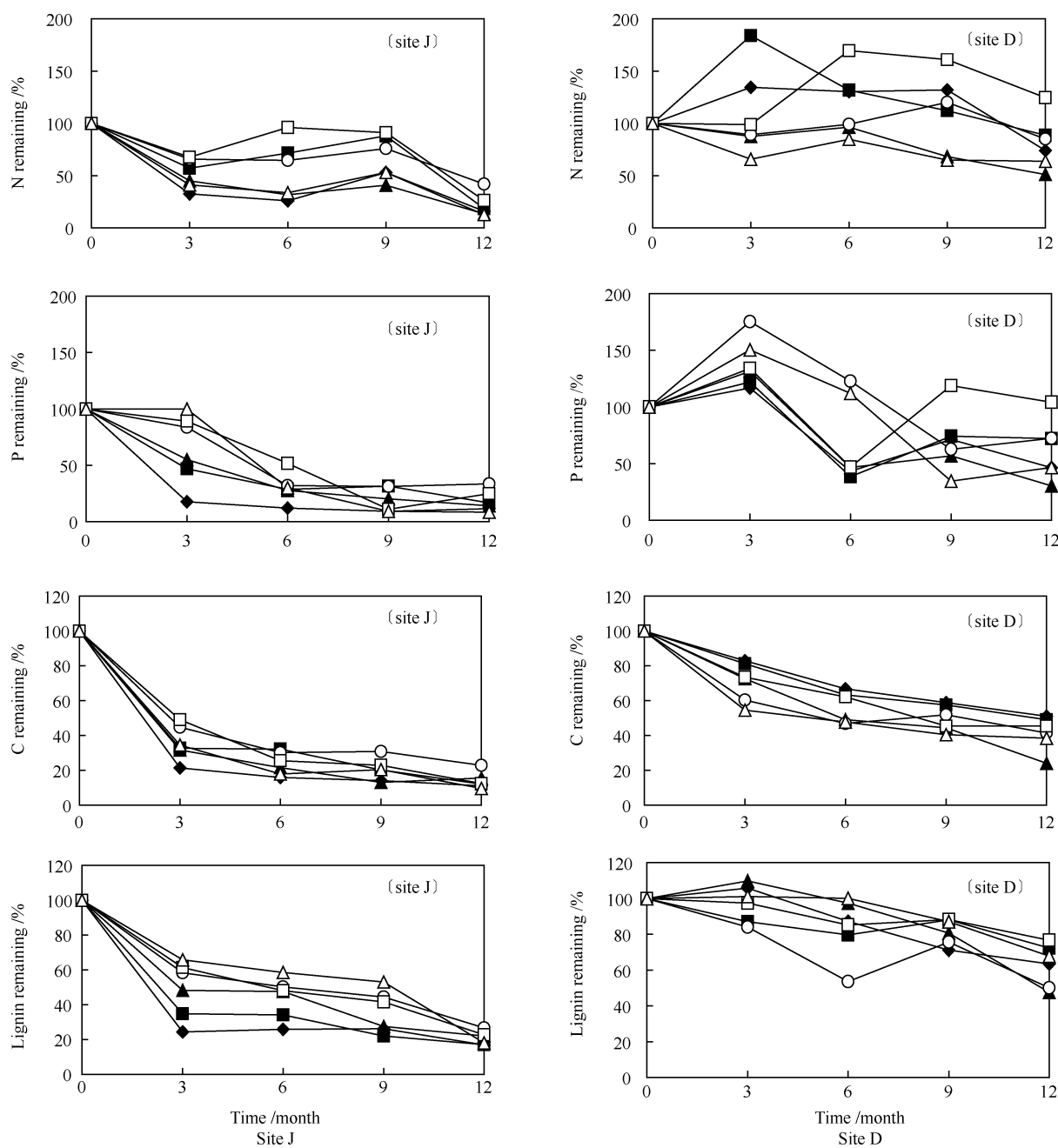
Fig. 3 Ratios of chemical composition in foliar litters

The patterns of C:N ratios between sites were also somewhat different. In site J, the ratios decreased until the ninth month in the range of 12.4–27.9 (five of the six litter types are lower than 20), and then increased. This was due to the decrement of the N concentration after the ninth month. In site D, the ratios decreased until the sixth month and then remained relatively constant in the range of 20.0–33.8. This was because N immobilization was maintained.

It is net immobilization when the remaining percentage

of nutrient element is larger than 100%, and net release when less than 100%. Generally, the releases of N and P were slower than mass loss. Over a decomposition period of one year, the releases of N, P and C in site J was greater than that in site D. And in site D, net immobilization of N and P in D₅ kept at the end of the year.

Previous studies showed that the litter biomass of monsoon evergreen forest in Mt. Dinghushan was 9.056×10^3 kg/(hm²·year) from 1983 to 1990, and 8.25×10^3 kg/(hm²·year) from 1993 to 1997; leaf litter accounted for



◆: J₁ (*V. mangachapoi*), ■: J₂ (*Sc. superba*), ▲: J₃ (mixed litter of 10 species collected from site J),
○: D₄ (*Cr. chinensis*), □: D₅ (*Sc. superba*), △: D₆ (mixed litter of 10 species collected from site D).

Fig. 4 Remaining percentages of chemical composition in foliar litters

52.7% and 60%, respectively (Weng et al., 1993; Zhang et al., 2000). The average leaf litter was estimated at 4.85×10^3 kg/(hm²·year) based on extrapolation from the above data. Subtropical mixed litter (D₆) were used to calculate the returns of nutrients and C. It was estimated that if the temperature in Mt. Dinghushan rose from 3.7°C under global warming to the present temperature in Mt. Jiangfengling,

the return of N, P and C from leaf litter would increase to 32.42, 1.033 and 741.1 kg/hm², respectively in the first year's decomposition (see Table 5). Part of the return of C would be emitted as CO₂ into the atmosphere and contribute to the increase in concentration of greenhouse gas, positively contributing to temperature warming.

Table 2 Parameters of the initial substrate quality of litters

Litter type		N/(mg·g ⁻¹)	P/(mg·g ⁻¹)	C/(mg·g ⁻¹)	Lignin/%	Holocellulose/%	C:N	Lignin:N	C:P	Lignin:P
J ₁	Mean	11.84ab	0.597a	528.3b	50.32ab	31.86a	44.96b	42.98ab	890.7b	852.1bc
	SD	1.40	0.052	11.1	8.17	1.64	4.58	9.42	92.7	189.8
J ₂	Mean	8.84 b	0.386b	609.8a	55.36a	22.06c	69.31a	63.61a	1584.6a	1427.6a
	SD	0.84	0.024	7.5	9.40	0.72	5.84	16.15	115.9	159.2
J ₃	Mean	11.75ab	0.546a	546.2b	42.10ab	29.96ab	47.26b	36.18ab	1004.2b	776.4c
	SD	1.87	0.043	2.6	2.63	4.28	7.48	3.45	74.8	102.2
D ₄	Mean	9.03b	0.365b	590.0a	54.73a	29.28ab	65.90a	61.29a	1637.1a	1527.8a
	SD	0.98	0.051	14.9	9.25	1.34	8.16	13.22	245.9	378.1
D ₅	Mean	8.75b	0.326b	582.5a	43.31ab	20.95c	66.68a	49.75ab	1801.3a	1336.1ab
	SD	0.57	0.039	10.3	5.35	1.49	3.19	8.21	204.0	179.6
D ₆	Mean	13.07a	0.558a	528.0b	34.08b	25.71bc	40.45b	26.10b	946.8b	611.0c
	SD	0.76	0.005	11.8	2.94	0.49	1.56	2.33	18.2	48.6

Note: Means with the same letter were not significantly different by columns ($P < 0.05$)

Table 3 Correlation coefficients between the parameters of initial litter quality and decomposition rate constants ($n = 6$)

Site		N	P	C	Lignin	Holocellulose	C:N	C:P	Lignin:N	Lignin:P	HLQ
Site J	Spearman's rho	0.029	-0.029	-0.314	-0.543	-0.657	-0.086	0.029	-0.371	-0.543	0.143
	Sig. (two-tailed)	0.957	0.957	0.544	0.266	0.156	0.872	0.957	0.468	0.266	0.787
Site D	Spearman's rho	0.657	0.543	-0.829*	-0.886**	0.486	-0.771	-0.543	-0.943**	-0.886*	0.886*
	Sig. (two-tailed)	0.156	0.266	0.042	0.019	0.329	0.072	0.266	0.005	0.019	0.019

** Correlation is significant at the 0.05 level (two-tailed), * Correlation is significant at the 0.01 level (2-tailed).

HLQ: lignocellulose quotients = holocellulose/(lignin + holocellulose)

3.2 Effects of litter types

The indices of litter initial quality were the concentrations of N, P and C, and the ratios of C:N, lignin:N, C:P, lignin:P. The quantity of the indices and their differences were presented in Table 2.

Based on the quality parameters (Table 2), the litters could be approximately divided into two groups, i.e. J₁, J₃ and D₆ in one group with relatively higher concentration of N and P and relatively lower concentration of C and ratios of C:N and lignin:N, while J₂, D₄ and D₅ in another group with relatively lower concentration of N and P and relatively higher concentration of C and ratios of C:N and lignin:N. The predominant single species in each site (J₁ and D₄) was different significantly in P, C, C:N, C:P and lignin:P. But there were no significant differences in quality indices between J₂ and D₅ (two types of *Sc. superba* litter collected from different sites) and between J₃ and D₆ (two types of mixed litter collected from different sites).

The comparison of mass loss rates of the six types within site showed that there were more comparative pairs with significant difference in site D than in site J. This might suggest that litter species effect in a tropical site did not play the leading role. The categorized group of initial litter quality did not completely correspond to the litter decomposition rates. It had better corresponding relation in categorizing by single-species litter and mixed litters.

In site J, the Spearman's rho correlation coefficients of initial quality and decomposition constant k were both lower and insignificant. In site D, the coefficients were higher and significant in C ($r = -0.829$, $p = 0.042$), lignin ($r = -0.866$, $p = 0.019$), lignin:N ($r = -0.943$, $p = 0.005$), lignin:P ($r = -0.886$, $p = 0.019$) and HLQ ($r = 0.886$, $p =$

0.019). The highest correlation was between k and lignin:N, while HLQ (lignocellulose quotients = lignin/(lignin+ holocellulose)) could also be the predictor of decomposition (Table 7).

4 Discussion

4.1 Effects of sites

The study on the decomposition of leaf litter of dominant species *Metrosideros polymorpha* in the Pacific island, Mauna Loa by Vitousek et al. (1994) indicated that decomposition rate exponentially decreased with the higher altitude and lower temperature. Anderson and Swift (1983) reviewed that the higher the temperature, the more rapidly the litter decomposed in tropical lowland forest and montane forest in the world. In NSTEC, the decomposition rates decreased with increasing latitude. For instance, the k values were in the range of 0.209–0.351 (Wang et al., 2001) and 0.49–0.99 (Hu et al., 1986) in northern China in the warm temperate zone, 1.16–3.54 in Xiqing, Fujian Province in the middle subtropical zone (Lin et al., 2001), 0.288–1.398 in Dinghushan (Zhang et al., 2000) and 0.422–1.108 in Heshan (Zhou et al., 1995) in the southern subtropical zone and 0.422–1.578, 1 in Jianfengling in the tropical zone (Jiang et al., 1991). In this study, the k values in site J were higher than, and those in site D were closed to values found in previous studies on Heshan and Dinghushan. It was difficult to directly compare litter decomposition rates in different sites due to non-uniform conditions and methods used in the experiments. It would be difficult to directly compare the decomposition rates among different study

sites, if the differences of factors other than temperature had not been minimized in the experiment design, since the decomposition of forest litter was affected by many factors. In this study, the difficulty was partially overcome by using space-for-time substitution and reciprocal decomposition experiment.

The results of this study showed that for the same litter (regardless whether single-species litters or mixed litters), the decomposition rates were significantly different between two sites, i.e. the higher in the tropical site than in the subtropical one. The site effect could be mainly attributed to temperature effect. The response intensity of litter decomposition to temperature effect could be reflected by apparent Q_{10} . In this study, the Q_{10} was in the range of 3.7–7.5. It nearly coincided with the range of 4.0–6.2 for leaf litter by Vitousek et al. (1994) in Hawaii, and higher than Heaney and Proctor's (1989) result ($Q_{10}=1.78$).

The concentrations of N, P, C, lignin and holocellulose, the releases of nutrient and C and the ratios of chemical components in litters were apparently different between the two sites. The releases of N, P and C were earlier in site J than in site D, and the releases of N and P were earlier in site J than in site D. Net immobilizations of N and P were occurred in site D, but not in site J. The mixed litter from the subtropical site decomposed under the temperature in tropical site (3.7°C higher), the release rates of N, P and C increased 51.14%, 38.02% and 28.95%, respectively, and the return of N, P and C from leaf litter increased 32.42, 1.033 and 741.1 kg/hm², respectively, in the first year's decomposition. The reasonable inference is that global warming will speed up litter decomposition and releases of C and nutrients in subtropical forests in China.

4.2 Effects of species

In both sites, mostly mixed litter decomposed more rapidly than single-species litter (except insignificant difference between J₂ and J₃ in site J). It might be due to the fact that mixed litter increased the heterogeneity of resources and changed the abundance of decomposers (Blair et al., 1990). Chapman et al. (1988) found that there were larger quantities of soil fauna in mixed forest of spruce and pine than in the forests with the respective single-species tree.

Nutrient releases were different among litter types, especially between single-species litter and mixed litter. In site D, net N immobilization occurred in all single-species litters but not in mixed litters J₃ and D₆. In both sites, one year's N releases of mixed litters J₃ and D₆ were larger than the four single-species litters. The increment of P concentrations in the early period (the first 3 months) was large in mixed litters than in single-species litters. The releases of C were not different greatly between mixed litters and single-species litters.

Leaf litters could be categorized according to the initial N concentration (higher or lower N concentration), mixed or single-species, and sources (i.e. collected from site J or

site D). Within a site, the difference in dynamics of N and P between mixed litters and single-species litters, the difference in dynamics of N between litters with higher or lower initial N concentration and the differences in the dynamics of P, lignin and holocellulose between litter sources were remarkable. The dynamics of C was not sensitive to litter types. Summarily categorizing by mixed and single-species litter had larger differences, although each categorizing type showed some differences in certain aspects, but there was no clear-cut regulation.

The result of this study shows that the correlation between litter quality and decomposition rate was lower in the tropical than in the subtropical site. Decomposition rate was controlled more strongly by litter quality in subtropical climatic condition than in tropics. The control of initial litter quality to litter decomposition rate was weaker in the site with higher temperature. Therefore, climate factors had stronger effect on litter decomposition rate than initial litter quality in the scale of across climatic zones. The variation in climatic factors had stronger impact on the litter decomposition rate in sites across climatic zones (Meentemeyer, 1978). In constant climatic condition (for instance within site), the influences of substrate quality, soil animals and microorganisms on decomposition rate were prominent (Blair, 1990).

There were many reports about the increment of N concentration and absolute quantity in litter decomposition process (Berg and Staaf, 1981; Melillo et al., 1982; Blair et al., 1990). The likely reason was the extrinsic resources of nitrogen being combined into the biomass and by-products of microorganisms (Blair et al., 1992). In the litter decomposition process, heterotrophs needed N apparently, since the C:N ratios of bacteria, actinomycetes and fungi were 5, 6 and 10, respectively. It meant litter was commonly in short of nitrogen. Therefore, microorganisms immobilize most of the N in the litter and the extrinsic N in the ambient micro-environment, hence increasing N concentration in litter. When the C:N ratio was higher than 25 in the remaining litter, N immobilization happened (Brady and Weil, 1996). Killham and Foster (1994) suggested that litter N hastened release when C:N ratio < 30. Some investigators (Parnas, 1975; Lousier and Parkinson, 1978) suggested the crucial value of C:N ratio for N immobilization was higher than 30; when the C:N ratio was at or less than 30, mineralization happened. In the present study, C:N ratios declined to 12.35–27.88 at the lowest level after 9 months and then increased in site J, and those declined to 20.00–33.79 after 6 months and remained in the range in site D. Thus, the crucial values of C:N ratio were even lower. It reflected that assimilation of microorganisms in the tropics was more intensive than in the subtropics, and more extrinsic resources of N were needed.

Normally, the initial holocellulose concentration in leaf litter was higher than lignin in the temperate and tropics (Berg et al., 1984; Cuevas and Medina, 1988; Aber et al., 1990). But others reported that lignin concentration was higher than holocellulose, for instance, lignin concentration

was 52%–54% in terra firme in the Amazon (Mesquita et al, 1998), 47% in *Ceanothus megacarpus* in south California and higher than holocellulose (Schlesinger and Hasey, 1981), 35%–51% in conifers and beeches in Sweden (Berg et al., 1996; Berg and Ekbohm, 1993), and 5%–10% higher holocellulose than Low Bana forest in Santa Colors in Venezuela (Cuevas and Medina, 1988). In the present study, the initial lignin concentrations were 34.08%–55.36%, higher than those of holocellulose, i.e. 20.95%–31.86%.

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