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Original article

Nutrient dynamics in decomposing needles of *Pinus luchuensis* after typhoon disturbance in a subtropical environment

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Abstract – Decomposition of typhoon-generated and normally fallen needles and their dynamical patterns of nutrient release for ten elements (C, N, P, K, Ca, Mg, S, Fe, Al, and Mn) were investigated over 3 yr using the litterbag technique in a subtropical pine plantation (*Pinus luchuensis* Mayr.) in Okinawa, southwestern Japan. After 3 yr, decomposition rates (k values) were 0.361 and 0.323 yr^{-1}, respectively, for typhoon-generated and normally fallen needles. The typhoon-generated needles decomposed significantly more rapidly than the normally fallen needles did, which was due to the higher N and P concentrations. Nutrient transfer patterns for elements varied greatly. However, significant differences in mass dynamic patterns of elements between typhoon-generated and normally fallen needles were found only in N and P ($P < 0.001$). Nutrient mobilities during the decomposition processes were similar in both typhoon-generated and normally fallen needles and was ordered as follows: K > Ca ≥ Mg ≥ C > S ≥ N ≥ Mn > P ≫ Fe ≥ Al. Rapid decomposition with rapid release of P and N in typhoon-generated needles indicates that typhoon disturbances can drive P and N cycling at a somewhat higher rates, which is more important from the standpoint of forest productivity since P and N are limiting nutrients in the subtropical forests in Okinawa.

litter chemical quality / needle decomposition / nutrient release / pine plantation / *Pinus luchuensis* / typhoon impact

Résumé – Dynamiques des nutriments dans les aiguilles en décomposition de *Pinus luchensis* après les perturbations liées à un typhon dans un environnement subtropical. La décomposition des chutes d'aiguilles normales et occasionnées par un typhon et leur modèle de libération des nutriments ont été étudiés pour 10 éléments (C, N, P, K, Ca, Mg, S, Fe, Al et Mn). L'étude a été faite dans une plantation de pin (*Pinus luchensis* Mayr.) à Okinawa (SO du Japon). Elle a duré 3 ans et a utilisé la technique des bacs à litière. Après 3 ans les taux de décomposition étaient de 0,361 et 0,323 an^{-1} respectivement pour les chutes d'aiguilles liées au typhon et les chutes normales d'aiguilles. Les chutes aiguilles liées au typhon se décomposent significativement plus rapidement que les chutes normales d'aiguilles, ce qui est du à une plus forte concentration en N et P. Les modèles de transfert des éléments varient fortement. Toutefois, des différences significatives dans les modèles de dynamique de masse des éléments entre les deux types de chute d'aiguille ont seulement été mises en évidence pour N et P ($P < 0{,}001$). La mobilité des éléments pendant les processus de décomposition étaient similaires dans les deux types de chute d'aiguilles et s'ordonnait de la façon suivante : K > Ca ≥ Mg ≥ C > S ≥ N ≥ Mn > P ≫ Fe ≥ Al. Une décomposition rapide avec une libération rapide de P et N pour les aiguilles dont la chute a été occasionnée par le typhon indique que la perturbation par le typhon peut conduire le cycle de P et N à un taux quelque peu plus rapide, ce qui est important du point de vue de la productivité de la forêt puisque P et N sont des nutriments limitants dans les forêts subtropicales d'Okinawa.

qualité chimique de la litière / décomposition des aiguilles / libération des nutriments / plantation de pin / *Pinus luchensis* / typhon impact

1. INTRODUCTION

Pine forests are widely distributed from boreal to tropical regions of East Asia. In Japan, the secondary pine forests are composed of Japanese red pine (*Pinus densiflora* Sieb. et Zucc.), Japanese black pine (*P. thunbergii* Parl.), and Luchu pine (*P. luchuensis* Mayr.). *P. densiflora* is distributed on the Osumi Islands, Kyushu, Shikoku, Honshu and the southern part of Hokkaido Island; *P. thunbergii* is distributed on the Tokara Islands and northward except for Hokkaido Island [34]. The distribution of *P. luchuensis* is limited to the Ryukyu Islands, southwestern Japan [14]. Luchu pine was introduced to the Bonin Islands and some national forests in Kyushu, and was also introduced to Taiwan [39]. In Okinawa, Luchu pine is one of the most important tree species for timber production, and covers about 62% of the total forest plantations. The majority of Luchu pine plantations were established during 1950s and 1960s [39].

In the forest ecosystems, litterfall represents a major biological pathway for nutrient transfer from vegetation to soils. However, nutrient availability for plant growth is mainly determined by decomposition rate [29]. Decomposition processes are, therefore, an important part of the nutrient cycling. A thorough understanding of this process is essential in understanding the structure and functioning of terrestrial ecosystems. For this reason, a large number of studies have investigated the decomposition of plant litter from a wide range of species and the biotic and abiotic factors regulating this process [1, 9, 15]. On the other hand, typhoon disturbances have a significant impact on the annual litter production [27, 36, 38].

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Typhoons occur frequently in Okinawa. During 1996–2000, typhoon occurred 15 times (maximum wind velocity over 15 m s^{-1}). Fine litterfall generated by typhoons ranged from 1.21 to 4.32 Mg ha^{-1} yr^{-1} in subtropical evergreen forest [38] and from 2.21 to 5.12 Mg ha^{-1} yr^{-1} in pine plantations [36]. Litter resulting from typhoon is usually composed of lot of green leaves and twigs. Green leaves are rich in nutrients and soluble organic C fractions, and is, therefore, qualitatively very different from the normally fallen litter materials [11, 16, 37]. The addition of a high amount of green leaves may also affect the decomposition and nutrient dynamics on the forest floor. Litter decomposition and nutrient release are controlled by a combination of factors including litter quality, the physico-chemical environment, and the nature and activity of decomposer organisms [3, 33]. Although the decomposition process has frequently been studied in forest ecosystems, data on the decomposition process in Luchu pine plantation, particularly on the differences between typhoon-generated needles and normally fallen ones, are few. The objective of the present study is to determine the pattern of nutrient release in decomposing pine needles resulting by typhoon disturbance in comparison with the normally fallen needles, to improve our understanding of the impact of typhoon disturbances on nutrient cycling processes in a pine plantation in the subtropical environment. The nomenclature employed in this article follows that of Hatushima and Amano [14].

2. MATERIALS AND METHODS

2.1. Study site

The study site is located in the Yona Experimental Forest at the University of the Ryukyus, northern part of Okinawa Island. The latitude and longitude of the site are 26° 45′ 30″ N and 128° 5′ E, respectively. The area is characterized by a subtropical climate and abundant rainfall throughout the year. Annual mean temperature is about 21.8 °C. Annual mean rainfall is 2680 mm over last 30 years (Experimental Forest, University of the Ryukyus). Mean annual relative humidity reaches 82%. Typhoons frequently occur between June and October. Monsoons, from the south or southwest, bring a rainy season between spring and early summer, and from the north or northwest create a relatively dry season in winter.

The experimental plot situated in hilly terrain on a midslope (22°) facing N 30° W at an altitude of 130 m a.s.l. This *Pinus luchuensis* plantation was established in 1951. The detailed description of the sampling stand was given by Xu and Hirata [36]. The annual mean fine litterfall in the sampling stand was 12 Mg ha^{-1} from 1996 to 1998 [36]. The soil at study site has a clay loam texture, and has developed from tertiary sandstone, with acid characteristics. Soil pH(H_2O) is 4.8. Concentrations of total organic C and total N in the surface soil horizon are 105 and 5 g kg^{-1}, respectively. Available P (Bray II method) is 29 mg kg^{-1}. Exchangeable cations (extracted by 1 N NH_4Cl) are: K^+ 0.66, Ca^{2+} 2.13, Mg^{2+} 1.24 cmol (+) kg^{-1}, respectively.

2.2. Litterbag experiment

Needle decomposition studies were carried out using the litterbag technique [7]. Litter bags (20 cm × 15 cm) were made of 1-mm polyester mesh. Decomposition rate was measured for two needle types, i.e. typhoon-generated and normally fallen needles. The two types of needles were collected with litter traps at the same plot during the peak fall in July 1997 (normal) and after a strong typhoon occurred in August 1997 (typhoon-generated), respectively. The needles collected were oven dried at 70 °C, then sealed in polythene bags and preserved below 15 °C in the laboratory. Before the experiment, four subsamples from the respective samples were taken to determine moisture and initial chemical concentrations (Tab. I). The equivalent of 10 g of dry litter was sealed in each bag. Ninety-six litterbags per needle type were randomly placed in six blocks on the soil surface at the study site. The experiment, lasting 3 yr, started on 5 July 1998. Collections were made every month in the first 6-month period, and then in 3-month intervals. Six replicate litterbags were sampled at each time, one in each block. The bagged litter samples collected were cleaned of soil and other extraneous materials, and oven-dried within 24 h at 70 °C to a constant weight, and then milled for chemical analysis.

2.3. Chemical analysis

All samples in the present study were analyzed for C, N, P, K, Ca, Mg, S, Al, Fe, and Mn. The concentrations of total organic carbon and total nitrogen were determined by dry combustion with a C-N analyzer (Yanaco, MT-500, Kyoto, Japan). The subsamples of 1.0 g of the ground samples were digested with HNO_3-$HClO_4$ reagent , and analyzed for the concentrations of P, K, Ca, Mg, S, Al, Fe, and Mn, by inductively coupled plasma spectrometer (Shimadzu, ICPS-2000, Kyoto, Japan).

2.4. Statistical analysis

There were six replicates of each needle type and all litterbags were randomly selected for collection. All data were analyzed by Statistica [31]. The decomposition rate (k) was calculated from the percentage of dry mass remaining (ash free) using an exponential decay model [23]:

$$W_t/W_0 = e^{-kt}$$

where W_t/W_0 is the fraction of initial mass remaining at time t, and t is the elapsed time (yr) and k is the decomposition constant (yr^{-1}). As suggested by Olson [23], the time required for 50% mass loss and nutrient release was calculated as $T_{1/2} = 0.693/k$. Paired-sample t-test analysis was used to determine differences in mass loss, decomposition constant and substrate chemistry between needle types. In all analyses, $P < 0.05$ was the criterion for significant differences.

3. RESULTS

3.1. Initial nutrient concentrations

As expected, there is a marked difference in the initial nutrient concentrations between the typhoon-generated and normally fallen needles (Tab. I). Concentrations of N, P, K, and Mg were significantly higher in the typhoon-generated needles than in the normally fallen ones. Aluminium and Mn concentrations were greater in the normally fallen needles, while there were no significant differences in total C, S, Ca and Fe concentrations between the two needle types.

Table I. Initial chemical composition (mg g^{-1} D.W.) with S.E. in the parentheses (n = 4) in the typhoon-generated and normally fallen needles of *Pinus luchuensis Mayr. in* subtropics. Values with the different letters in a column are significant different (t-test; P < 0.05).

Needle type	C	N	P	K	Ca	Mg	Al	Fe	Mn	S	C:N	C:P
Normal fall	517	6.53a	0.143a	1.79a	5.31	1.57a	0.256a	0.133a	0.323a	0.489	79a	3615a
	(6.53)	(0.19)	(0.010)	(0.12)	(0.37)	(0.11)	(0.010)	(0.011)	(0.017)	(0.012)	(7.3)	(92)
Typhoon-generated	513	8.86b	0.237b	3.38b	4.96	1.89b	0.186b	0.113b	0.281b	0.515	58b	2165b
	(7.21)	(0.21)	(0.012)	(0.18)	(0.45)	(0.11)	(0.009)	(0.010)	(0.015)	(0.015)	(6.6)	(59)

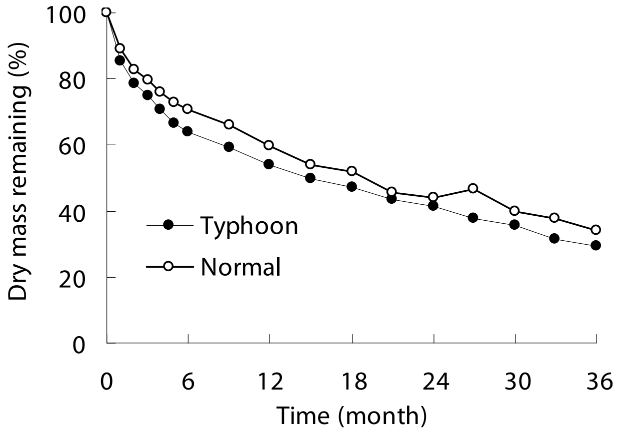

Figure 1. Percentage of dry mass remaining for the typhoon-generated and normally fallen needles of *P. luchuensis* during a 3-yr decomposition process in subtropics.

Table II. Mean percent loss in dry mass, decomposition constant (k; yr^{-1}), and half-life time ($T_{1/2}$) for the typhoon-generated and normally fallen needles of *Pinus luchuensis* in the subtropics. Standard errors are in the parentheses (n = 6). Values with the different letters in a column are significantly different between needle types at P < 0.05.

	1 yr decomposition		3 yr decomposition		
Needle type	Loss (%)	k	Loss (%)	k	$T_{1/2}$
Normal fall	46.2a	0.564a	70.8a	0.361a	1.92a
	(2.14)	(0.036)	(2.23)	(0.009)	(0.05)
Typhoon-generated	40.4b	0.47b	66.0b	0.323b	2.15b
	(2.37)	(0.031)	(2.66)	(0.016)	(0.11)

3.2. Weight loss and decomposition rate

The average dry mass loss from the litterbag is shown in Figure 1. During the first 6 months of incubation, the dry mass loss in typhoon-generated needles reached 41%, while the normal ones 34%. Although there were not high differences, the average values resulted significantly different. Dry mass remaining over 3 yr decomposition differed significantly between the two needle types (F = 4.494; df = 1, 16; P < 0.0001).

Dry mass loss and decomposition constants (k values) after 3 yr are given in Table II. Significant differences between needle types were found (P < 0.01). The half-life time for the typhoon-generated needles was 1.92 yr, which is significantly lower than that for the normally fallen needles (2.15 yr; t = 4.177; df = 6; P = 0.009). This indicates a significant effect of needles type on decomposition rate.

3.3. Nutrient dynamics

Patterns of nutrient transfer indicate how rapidly elements are lost from decomposing needles. Nutrient transfer patterns for elements varied greatly, from a net accumulation to a rapid loss (Fig. 2). Significant differences in element mass dynamics between typhoon-generated and normally fallen needles were found only for N and P (P < 0.001).

3.3.1. Nitrogen and phosphorus

Concentrations of N and P increased with mass loss in both typhoon-generated and normally fallen needles. However, N immobilization was not found over the 3-yr decomposition. N release was significantly greater from typhoon-generated needles than from the normally fallen ones (Fig. 2A). P immobilization was pronounced in this study. The normally fallen needles showed a net immobilization of P over 3 yr, while typhoon-generated needles showed a net immobilization in the first 2 yr and rapid release afterwards (Fig. 2B).

3.3.2. Carbon and sulphur

Carbon concentration kept almost constant during the decomposition except for the third year with a slight decrease, while S concentration increased in the first 2 yr and then decreased in both typhoon-generated and normally fallen needles. The pattern of C mass dynamics was similar to the dry mass with a progressive decrease (Fig. 2A). However, S mass dynamics showed a net immobilization in the first 1.5 yr and a rapid release afterwards (Fig. 2B).

3.3.3. Potassium, magnesium and calcium

The result showed that K and Mg were subject to extensive leaching from decomposing needles in the initial phase. The mass dynamical patterns of K and Mg demonstrated a rapid decrease in the first 3–6 months and after then a slight decrease for the two needle types measured (Figs. 2C and 2D).

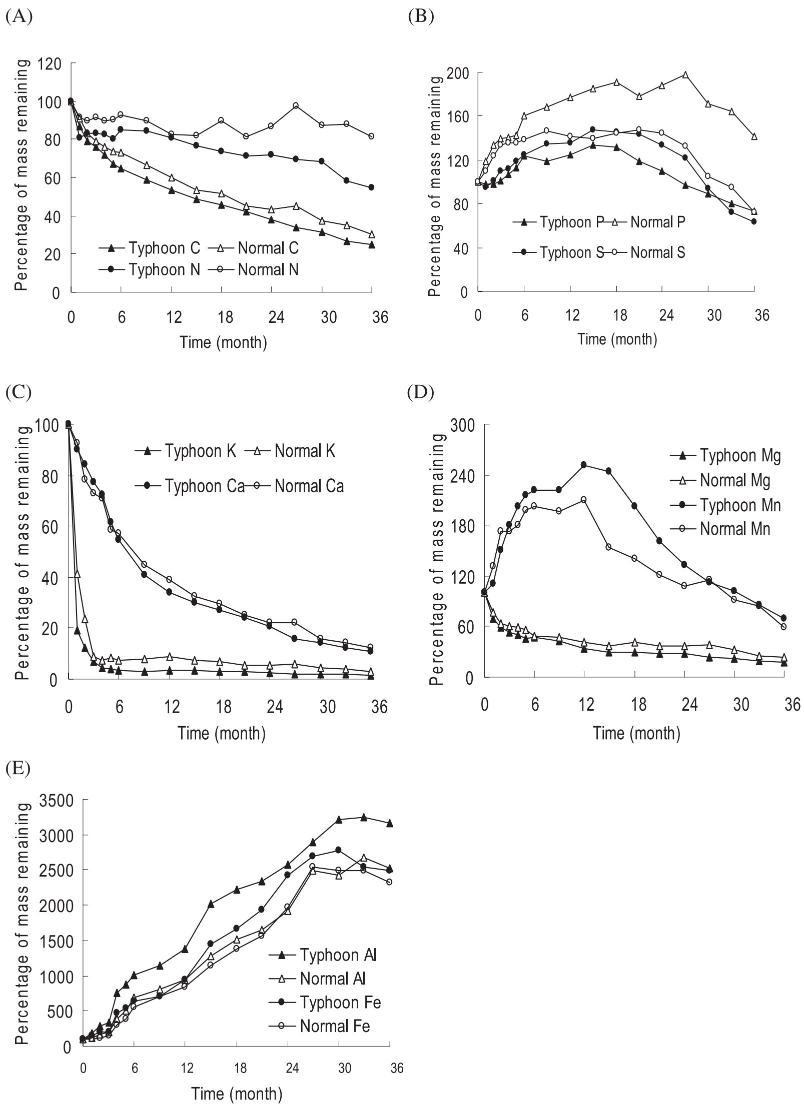

Figure 2. Percentage of mass remaining for different nutrient elements in the typhoon-generated and normally fallen needles of *P. luchuensis* during a 3-yr decomposition process in subtropics.

Ca concentration increased slightly in the first 3-month period, and after then declined progressively. The release of Ca mass was somewhat rapid in both typhoon-generated and normally fallen needles in this study (Fig. 2C).

3.3.4. Manganese, aluminium and iron

Concentrations of Al and Fe increased significantly over 3-yr study period for both needle types. Significant accumulations of Al and Fe were found in decomposing pine needles (Fig. 2E). Mn concentration increased steadily in the first year of decomposition and decreased slightly after then. Significant net accumulation of Mn was observed in first 2 yr (Fig. 2D). The maximum net immobilization of Mn reached 232 and 210% of the initial mass, respectively, in the typhoon-generated and normally fallen needles.

3.4. C:N and C:P ratio changes over time

Variations in C:N and C:P ratios of the two needle types during the 3-yr decomposition were shown in Figure 3. Although the two needle types showed the similar pattern, the time course was significantly different in C:N and C:P ratios (Fig. 3). C:N ratio decreased progressively over time, while C:P ratio decreased rapidly in the first year and lowly afterwards in decomposition processes.

4. DISCUSSION

4.1. Dry mass loss and decomposition rate

The decomposition rate of the typhoon-generated needles was significantly higher than that of the normally fallen ones.

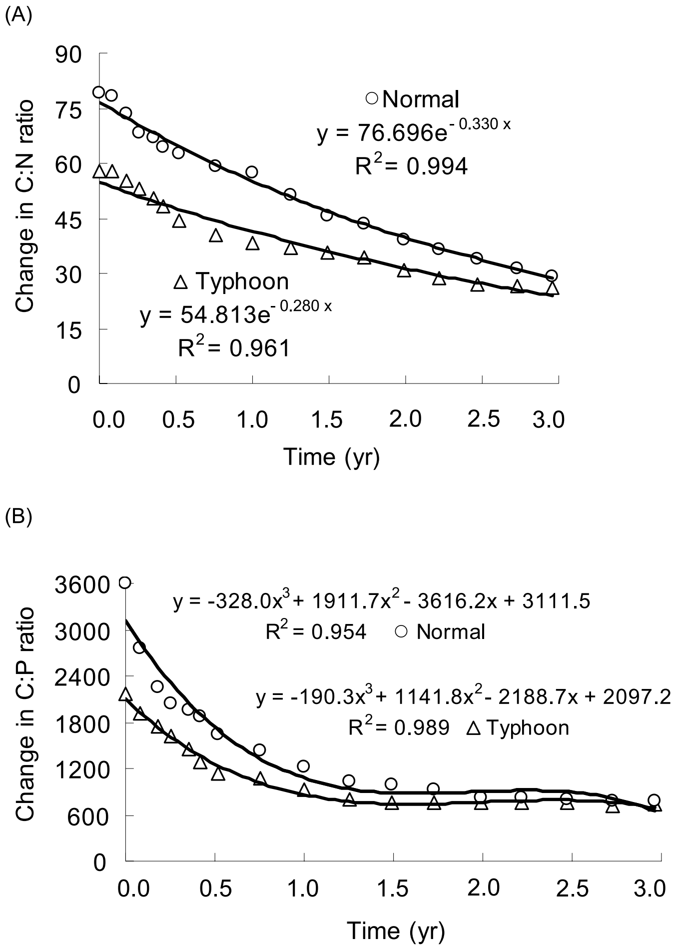

Figure 3. Variation in (A) C:N and (B) C:P ratios of the typhoon-generated and normally fallen needles of *P. luchuensis* during a 3-yr decomposition process in subtropics.

This result was similar to the findings by Whigham et al. [35] and Xu et al. [37] in studies conducted on Hurricane- and typhoon-generated litter in tropical and subtropical rain forests. Rapid decomposition of the typhoon-generated needles should have contributed to its special features of both anatomical structure and initial substrate [11, 28, 35]. The typhoon-generated needles, particularly the green ones, were usually premature, which should be not as hard as the normally fallen needles in anatomical structure. Moreover, these needles showed higher concentrations of nutrients especially N and P, and had higher labile and lower recalcitrant C fractions [11]. These special features for the typhoon-generated litter tend to increase the decomposition rate.

After 3 yr decomposition, the decomposition constants (k) were 0.361 and 0.323 yr^{-1}, respectively, for typhoon-generated and normally fallen needles (Tab. II). The constants (k) were similar to those reported (0.26–0.42 yr^{-1}) previously in some pine forests [8, 13, 24, 30], but were higher than those (0.13–0.19 yr^{-1}) reported for pine forests in Mediterranean climate [19, 22].

4.2. Initial litter quality and nutrient dynamics

Different nutrients in decomposing litter have different patterns of release and retention over time. Microbial immobilization is a major mechanism [25, 33]. The status of a nutrient, whether it is limiting or non-limiting to microbial activity, determines its release dynamics. The limiting nutrients to microbial activity would thus be retained resulting in immobilization, whereas those in excess would be released during decomposition [4]. In addition, nutrient release and turnover are further influenced by the nature of chemical bonds which attach the elements to humic substances [26, 32].

Results from the present study showed that the concentrations of most elements (N, P, S, Mn, Al, and Fe) increased as the litter decomposed. In contrast to these nutrients, K, Ca, and Mg concentrations clearly decreased. However, the change in absolute amount of an element during decomposition (net immobilization or the net release) is a function of both mass loss and change in the relative concentrations of the element in the residual litter. In the present study, the patterns of mass dynamics varied significantly amongst elements in decomposition processes. N, C, Mg, Ca, and K showed a decrease phase (net release), while Al and Fe showed an increase phase (net immobilization), and P, S, and Mn demonstrated an increase-decrease phase (initially net immobilization and then net release) over the 3-yr decomposition. In general, nutrient release from litter in the early stage (first 1 to 3 months) is usually caused by leaching. In the following stages, by comparing curves of litter decomposition and nutrient dynamics, it is possible to observe the release of nutrients due to leaching and to microbial decomposition, respectively. According to Gosz et al. [12], if a nutrient is lost at a rate equal to or lower than dry mass loss, it is likely released by decomposition of organic matter; any nutrient loss at a rate higher than dry mass loss would result from leaching. The rapid release of K and Mg in the early phase observed in the present study could be attributed to the physical removal by leaching. The release of the other elements might be controlled by biological and chemical processes [20].

The significant increases in N and P concentrations in typhoon-generated and normally fallen needles indicated that they were limiting to decomposer organisms. The significant positive correlations between mass loss and accumulated N (R^2 = 0.799 and 0.470 for typhoon and normally fallen needles) and P (R^2 = 0.567 for normally fallen needles) confirm this. In the present study, P was retained more strongly than N indicating that it was probably the most limiting element to the decomposer community. The immobilization and very slow release of N and P [20, 24, 37] in decomposing litter are more important from the standpoint of forest productivity, since they are the most commonly limiting nutrients [2]. Jorgensen et al. [17] reported for other pine forests that N was the most slowly release macronutrient with only about 27% of it released over 8 yrs. In the present study, only about 19% of N was released and no net P release occurred from normally fallen needles after 3 yrs. In typhoon-generated needles, however, about 46% of N and 27% of P were released. Other studies, such as that of Piatek and Allen [24], N release was similar to our result. They also reported sustained P immobilization throughout 26 months, which may be due to lower initial P concentration (0.2 g P kg^{-1}; similar to this study).

Slow release of Ca was observed during decomposition, which was similar to the dry mass loss because Ca is a structural component and thus protected from physical leaching [10, 12]. Like many previous studies [e.g. 12, 20, 26, 37], Al and Fe were highly immobilized in decomposition processes. The accumulation of Al and Fe during decomposition process may be ascribed to an abiotic formation of highly stable complexes with humic substances [26] or to a biotic accumulation in decomposer microorganisms [5, 32], suggesting that the dynamics of Al and Fe release could be controlled by both biological and chemical processes despite of the addition from exogenous sources also for these elements.

Release of S and Mn during litter decomposition showed similar pattern. However, Mn was immobilized more rapidly in the initial phase and released faster in the late phase than S did in the present study. This release pattern particularly for Mn is different from some previous studies [12, 13, 20], which showed a net release of Mn in decomposition processes. It is probably due to microbial immobilization and/or addition of Mn from exogenous sources [21].

After 3 yr decomposition, nutrient mobility (similar in both typhoon-generated and normally fallen needles) was as follows: $K > Ca \geq Mg \geq C > S \geq N \geq Mn > P \gg Fe \geq Al$. High mobility of P and Mn has been noted previously [6, 13, 18, 40]. The rate of release was higher for the macro-elements (C, N, K, Ca, Mg, S) than for the micro-elements (Mn, Fe, Al) with the exception of P which behaved as the microelements.

Typhoon disturbances can return large amounts of plant material into the forest floor [36, 38]. Those litterfall, particularly the green ones had higher nutrient concentrations than the normal litter for those nutrients that are translocated during senescence. On the other hand, the results from the present study showed that needle litter resulting from typhoon disturbances decomposed more rapidly than did the normally fallen needles, with a rapid release of P and N. This leads to increases in the P and N availability in soil after typhoons. Therefore, typhoon disturbances redirect nutrient elements (especially N and P that are usually bound up in wood) into a more mobile form, cycling them at somewhat higher rates. To a certain extent, the rapid cycling of N and P driven by typhoons appears to be an important mechanism to maintain forest productivity in this subtropical environment.

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