Original article

Litterfall, nutrient return, and leaf-litter decomposition in four plantations compared with a natural forest in subtropical China

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Abstract – The amount and pattern of litterfall, its nutrient return, initial chemistry of leaf litter, and dynamics of N, P and K associated with leaf-litter decomposition were studied in 33-year-old plantations of two coniferous trees, Chinese fir (*Cunninghamia lanceolata,* CF) and *Fokienia hodginsii* (FH), and two broadleaved trees, *Ormosia xylocarpa* (OX) and *Castanopsis kawakamii* (CK), and compared with that of an adjacent natural forest of *Castanopsis kawakamii* (NF, ~150 year old) in Sanming, Fujian, China. Mean annual total litterfall over 3 years of observations was 5.47 Mg·ha^{-1} in the CF, 7.29 Mg·ha^{-1} in the FH, 5.69 Mg·ha^{-1} in the OX, 9.54 Mg·ha^{-1} in the CK and 11.01 Mg·ha^{-1} in the NF respectively; of this litterfall, leaf contribution ranged from 58% to 72%. Litterfall in the OX, CK, and NF showed an unimodal distribution pattern, while for the CF and FH, the litterfall pattern was multi-peak. The highest annual Ca and Mg returns were noticed in the FH and in the CK, respectively. The amounts of N, P, and K which potentially returned to the soil were the highest in the NF. The loss of dry matter in leaf litter exhibited a negative exponential pattern during the 750-day decomposition. Using the model $x_t = A + Be^{-kt}$, the annual dry matter decay constants (k) ranged from 1.157 in CF to 4.619 in OX. Initial lignin concentration and lignin/N ratios showed significantly negative correlations with k ($r = -0.916$, $P = 0.011$; $r = -0.473$, $P = 0.041$), whereas initial N concentration showed low positive correlations ($r = 0.225$, $P = 0.038$). Using the model $x_t = A + Be^{-kt}$, the decay constant of N (k_N) ranged from 0.769 in CF to 4.978 in OX; the decay constant of P (k_P) ranged from 1.967 in the OX to 4.664 in the NF; and the decay constant of K (k_K) seemed very similar among these forests (5.250–5.992). The decay constants of nutrients during leaf-litter decomposition can be arranged in the sequence of $k_K > k_P > k_N$, except for leaf litter of OX where $k_K > k_N > k_P$.

litterfall / nutrient return / litter decomposition / reafforestation / natural forest / *Cunninghamia lanceolata* / *Fokienia hodginsii* / *Ormosia xylocarpa* / *Castanopsis kawakamii*

Résumé – Chute de feuilles, retour de nutriments et décomposition des feuilles de la litière dans quatre plantations en comparaison avec une forêt naturelle en Chine subtropicale. La quantité et la dynamique de chute de litière, le retour des nutriments, la composition chimique initiale des feuilles de la litière et la dynamique de N, Pet K associée à la décomposition de la litière ont été étudiés dans 2 plantations de conifères (*Cunninghamia lanceolata*, CF et *Fokienia hodginsii*, FH) âgées de 33 ans et 2 peuplements feuillus (*Ormosia xylocarpa*, OX et *Castanopsis kawakamii*, CK), comparativement à une forêt naturelle adjacente de *Castanopsis kawakamii,* NF, âgée d'environ 150 ans à Sanming, Fujian, Chine. Sur 3 années d'observations, la moyenne annuelle de chute de litière a été de 5,47 Mg·ha^{-1} pour CF, 7,29 Mg·ha^{-1} pour FH, 5,69 Mg·h $^{-1}$ pour OX, 9,54 Mg·hg^{-1} pour CK et 11,01 Mg·ha^{-1} pour NF. Dans ces chutes de litière, la contribution des feuilles variait de 58 à 72 %. La chute de litière présente une distribution unimodale pour OX, CK et NF tandis que pour CF et FH on observe un modèle à plusieurs pics. Le plus important retour annuel de Ca et Mg a été noté respectivement dans FH et CK. Les quantités de N, P et K qui sont potentiellement retournées dans le sol étaient les plus importantes dans NF. La perte de matière sèche dans la litière de feuille présente un modèle exponentiel négatif pendant les 750 jours de décomposition. En utilisant le modèle $x_t = A + Be^{-kt}$, la constante de décomposition de la matière (k) varie de 1,157 dans CF à 4,619 dans OX. La concentration initiale en lignine et le rapport lignine/N présente une corrélation négative significative avec k ($r = 0,916$, $P = 0,001$; $r = 0,473$, $P = 0,041$) alors que la concentration initiale de N montre une faible corrélation positive ($r = 0,225$, $P = 0,038$). En utilisant le modèle $x_t = A + Be^{-kt}$ la constante de décomposition de N (k_N) varie de 0,769 pour CF à 4,978 pour OX ; la constante de décomposition de P (k_P) varie de 1,967 pour OX à 4,664 pour NF et la constante de décomposition de K (k_K) apparaît très similaire pour ces forêts (5,250 à 5,992). Les constantes de décomposition de la litière peuvent être classées de la manière suivante : $k_K > k_P > k_N$ à l'exception de la litière de OX où $k_K > k_N > k_P$.

chute de litière / décomposition de la litière / reforestation / forêt naturelle / *Cunninghamia lanceolata* / *Fokienia hodginsii* / *Ormosia xylocarpa* / *Castanopsis kawakamii* / *Castanopsis kawakamii*
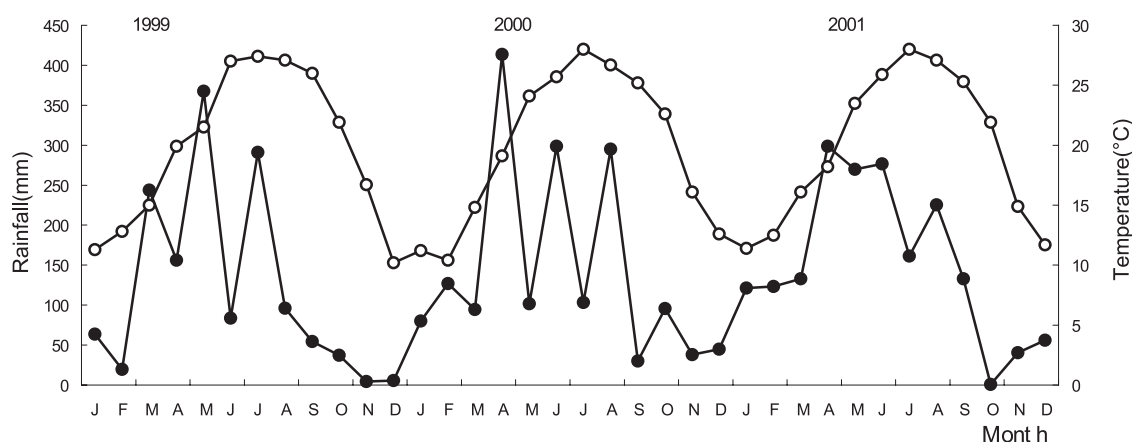
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Figure 1. Temperature and rainfall patterns for the study area. —●— Monthly rainfall; —○— Monthly mean temperature.

1. INTRODUCTION

Large-scale plantation forests have been established in the world to meet the demands for timber, fuel material, and other forest products as a result of the increased pressure on natural resources caused by the increasing human population. However, yield decline and land deterioration (such as loss of surface soils, depletion of soil nutrients, soil compaction) may occur when natural forests are converted to plantations of trees [12, 18, 29, 34]. In South China where high rainfall, steep slopes, and low antierodibility of soils are characteristic, many native broadleaved forests have been cleared and replanted with monoculture plantations (mainly economical conifers) following clear-cutting, slash burning, and soil preparation. As a consequence, soil degradation (e.g., depletion of soil nutrient pools, low in nutrient availability and biochemical activity, inhibition of soil microorganisms, deterioration of soil structure and erodibility) in such disturbed ecosystem has become serious, and yield decline has been found on sites with repeating monoculture of coniferous plantations [46–49]. How to manage tree plantations for maintaining the site productivity has received considerable attention.

Forest litter acts as an input-output system of nutrients and the rates at which forest litter falls and, subsequently, decays contribute to the regulation of nutrient cycling, as well as to soil fertility and primary productivity in forest ecosystems [2, 5, 15, 20, 23, 26, 27, 32]. Thus, it is critical to understand the nutrient dynamics of litter in these forest ecosystems [2, 41, 45]. Despite many studies carried out on litterfall and decomposition dynamics, largely on temperate forests [2, 7, 16, 17, 20, 32, 41], few attempts have been made to comparatively measure litter and nutrient cycling in natural and planted forests under similar climatic and edaphic conditions in subtropical China. The objective of this study, covering a 3 year period, were to: (i) examine the production of forest litter and its patterns in four plantation forests of *Cunninghamia lanceolata* (Chinese fir, CF), *Fokienia hodginsii* (FH), *Ormosia xylocarpa* (OX), and *Castanopsis kawakamii* (CK), and an adjacent natural forest of *Castanopsis kawakamii* (NF); (ii) quantify nutrient return through litterfall

in the five forests; and (iii) determine the rate of dry-matter loss and of nutrient release from decomposing leaf litter in the five forests.

2. MATERIALS AND METHODS

2.1. Site description

The study was carried out from January 1999 to December 2001 in the Xiaohu work-area of the Xinkou Experimental Forestry Centre of Fujian Agricultural and Forestry University, Sanming, Fujian, China (26° 11' 30'' N, 117° 26' 00'' E). It borders the Daiyun Mountain on the southeast, and the Wuyi Mountain on the northwest. The region has a middle sub-tropical monsoonal climate, with a mean annual temperature of 19.1 °C and a relative humidity of 81%. The mean annual precipitation is 1 749 mm, mainly occuring from March to August (Fig. 1). Mean annual potential evapotranspiration is 1 585 mm. The growing season is relatively long with an annual frost-free period of around 330 days. The parent material of the soil is sandy shale and soils are classified as red soils (humic Planosols in FAO system). Thickness of the soil exceeds 1.0 m. In 1999, five 20 m × 20 m plots were randomly established at the midslope position in each of CF, FH, OX, CK, and NF.

Selected forest characteristics and some properties of the surface soil (0–20 cm) of the five sites are described in Table I. NF represents the evergreen, broadleaved *C. kawakamii* forest in mid-subtropical China with high purity (85% of total stand basal area for *C. kawakamii*), old age (~ 150 year), and large area (~ 700 ha) [22, 50]. In addition to *C. kawakamii*, the overstory also contained other tree species, such as *Pinus massoniana*, *Schima superba*, *Lithocarpus glaber*, *Symplocos caudate*, *Machilus velatina*, *Randia cochinchinensis*, and *Symplocos stellaris*. In 1966, part of this NF was clear-cut, slashed and burned. In 1967, the soil was prepared by digging holes and then 1-year-old seedlings of *C. lanceolata* (Chinese fir), *F. hodginsii*, *O. xylocarpa*, and *C. kawakamii* were planted at 3 000 trees per hectare.

2.2. Litter collection

Fifteen 0.5 m × 1.0 m litter traps made of nylon mesh (1 mm mesh size), were arranged in each forest and were raised 25 cm above the

Table I. Stand characteristics and soil properties of the study sites.

Parameters	Forest type[1]				
	CF	FH	OX	CK	NF[2]
Mean tree age[3] (years)	33	33	33	33	~150
Mean tree height (m)	21.9	21.4	18.4	18.9	24.3
Mean tree diameter at breast height (cm)	23.3	21.6	17.2	24.2	42.2
Stand density (stem·ha^{-1})	1117	975	1109	875	255
Stand volume[4] (m^3·ha^{-1})	425.91	379.57	209.01	412.43	398.31
Standing biomass of forest floor[5] (Mg·ha^{-1})	3.15	2.65	7.22	7.44	7.72
Soil (A horizon, 0–20 cm depth)					
Bulk density (g·cm^{-3})	1.20	1.13	1.15	1.10	0.93
Organic C (mg·g^{-1})	16.9	17.7	17.5	17.1	26.4
Total N (mg·g^{-1})	1.12	1.37	1.29	1.12	1.88
Total P (mg·g^{-1})	0.29	0.35	0.30	0.31	0.36
C/N ratio	15.1	12.9	13.6	15.3	14.0
Hydrolyzable N (mg·g^{-1})	0.110	0.118	0.125	0.115	0.136
Available P[6] (µg·g^{-1})	4.7	5.6	6.8	5.9	7.6

[1] CF, Chinese fir (*Cunninghamia lanceolata*) plantation forest; FH, *Fokienia hodginsii* plantation forest; OX, *Ormosia xylocarpa* plantation forest; CK, *Castanopsis kawakamii* plantation forest; NF, natural forest dominated by *C. kawakamii*.
[2] Only *Castanopsis kawakamii* is considered.
[3] Age in 1999 since plantation.
[4] Commercial portion of the stump.
[5] The forest floor was sampled by line transect method every season in 1999.
[6] Soil available P was extracted using 0.05 mol·L^{-1} HCl-0.025 mol·L^{-1} H$_2$SO$_4$, and then their concentration were determined using (NH$_4$)$_6$Mo$_7$O$_{24}$-KSbOC$_4$H$_4$O$_6$-C$_6$H$_8$O$_6$ method.

ground, and the litterfall was collected at 10-day intervals from January 1999 to December 2001. The collected litter at each time was oven-dried at 80 °C to constant weight. At the end of each month, the oven-dried litter was combined by month and trap, and sorted into leaves, small branches (< 2 cm in diameter), flowers, fruits, and miscellaneous material (insect fecal, unidentified plant parts, etc.). Furthermore, collected leaf and small-branch litter in the NF were separated into two classes, viz. *C. kawakamii* and other tree species in tree layer. Thereafter monthly mass of each fraction was determined and sub-samples of litters of each forest were taken by month, trap, and fraction for nutrient (N, P, K, Ca, and Mg) analysis.

2.3. Leaf-litter decomposition

The litterbag technique was used to quantify decomposition of leaf litter of dominant tree species in their respective stands. In April 1999, freshly fallen/senescent leaves from tree species in four plantations and from *C. kawakamii* in the NF were collected on nylon mesh screens for decomposition experiment. Three sub-samples from each leaf-litter species were retained for the determination of initial chemical composition. A known amount of air-dried leaf litter (20 g) of each species was put into a 20 cm × 20 cm, 1.0 mm mesh size nylon bag. For each species, 80 bags were prepared and randomly placed on the forest floor in the respective stands at the end of April 1999. 30, 60, 90, 150, 210, 270, 330, 390, 510, 630, and 750 days after placement of samples, 6 litterbags were recovered at random from each forest site, and transported to the laboratory. The adhering soil, plant detritus and the "ingrowth" roots were excluded, and the bags were then dried at 80 °C to constant weight for the determination of remaining weight. Sub-samples by species and date were reserved for the analysis of N, P, and K concentrations.

2.4. Chemical analyses

All oven-dried litter sub-samples were ground and passed through a 1-mm mesh screen before chemical analysis. For the determination of C, the plant samples were digested in K$_2$Cr$_2$O$_7$-H$_2$SO$_4$ solution using an oil-bath heating and then C concentration was determined from titration. For determination of N, P, K, Ca, and Mg, the samples were digested in the solution of H$_2$SO$_4$-HClO$_4$, and then N concentration was determined on the KDN-C azotometer, P concentration was analyzed colorimetrically with blue phospho-molybdate, K by flame photometry, and Ca and Mg concentrations were determined by the atomic absorption method [10]. The initial organic constituents of fresh leaf litter samples including lignin, cellulose, hemicellulose, coarse protein, alcohol, and water soluble compounds were determined by the proximate chemical analysis [43]. All chemical analyses were carried out in triplicate on the same subsample.

2.5. Statistical analyses and calculations

The data on mean annual litterfall amounts, mass losses after 750 days and initial chemical composition of fresh leaf-litter were analysed using a one-way ANOVA. The multiple comparisons were determined with the least significant difference (LSD) test at a significance level of 0.05 [33]. Statistical analysis of data expressed as percentages was performed after square-root arcsine transformation.

The monthly, potential nutrient input to the forest floor through each litter fraction was computed by multiplying monthly values of each fraction mass with its corresponding nutrient concentrations. Annual, potential nutrient input was the sum of monthly nutrient inputs based on 12 monthly estimations.

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Table II. Quantity (kg·ha^{-1}·yr^{-1}) and proportion in the total (%, in parentheses) of litterfall in the five forests.

Forest type	Leaf	Leaves from other trees[1]	Subtotal of leaves	Small branches	Branches from other trees[1]	Subtotal of branches	Flowers	Fruits	Miscellaneous	Total
CF	3 188 ± 424 (58)		3 188 ± 424a (58)	1 367 ± 62 (25)		1 367 ± 62a (25)	79 ± 2.2a (1.5)	253 ± 16a (4.6)	582 ± 137ab (10.7)	5 468 ± 431a (100)
FH	4 778 ± 497 (66)		4 778 ± 497b (66)	1 374 ± 127 (19)		1 374 ± 127ab (19)	258 ± 26b (3.5)	289 ± 53a (4.0)	592 ± 121ac (8.1)	7 291 ± 767b (100)
OX	3 775 ± 215 (66)		3 775 ± 215a (66)	1 228 ± 51 (22)		1 228 ± 51b (22)	8.5 ± 1.8c (0.15)	25 ± 11b (0.45)	650 ± 72a (11.44)	5 687.50 ± 229.54a (100)
CK	6 865 ± 159 (72)		6 865 ± 159c (72)	2 132 ± 357 (22)		2 132 ± 357c (22)	13 ± 9cd (0.14)	142 ± 154a (1.5)	386 ± 42b (4.0)	9 538 ± 532c (100)
NF	5 400 ± 274 (49)	1 171 ± 249 (11)	6 571 ± 562cd (60)	2 298 ± 393 (21)	241 ± 39 (2.2)	2 539 ± 146cd (23)	204 ± 126be (1.8)	662 ± 337c (6.0)	1 032 ± 138d (9.4)	11 008 ± 529d (100)

Values are means ± s.d. of 15 traps at each forest over 3 years. Means followed by different letters on the same column indicate significant differences at $P < 0.05$. [1] Other tree species in the NF indicate those species in the tree layer, except *C. kawakamii*. Other symbols as in Table I.

The model for the loss of dry mass and nutrients during the studied decomposition period is represented by the following equation [30]:

$$x_t = A + Be^{-kt}$$

$$x_0 = A + B$$

where x_t is the weight remaining at time t, x_0 is the initial weight, and the constants A, B, and k are the recalcitrant fraction, the labile fraction, and the decay constant, respectively. Correlation coefficients (r) between k and the initial chemical properties of leaf litter were also calculated.

3. RESULTS

3.1. Litterfall

There were significant differences in the litter production among study forests ($P < 0.05$), except between the CF and the OX (Tab. II). Average annual litterfall (1999–2001) ranged from 5.47 Mg·ha^{-1}·yr^{-1} for the CF to 11.01 Mg·ha^{-1}·yr^{-1} for the NF and decreased in the order: NF > CK > FH > OX > CF. Leaf litter comprised 58 to 72% of the total annual litterfall in the five forests. Non-leaf litterfall included twigs, reproductive parts, and miscellaneous materials and the sum of these components ranged from 28 to 42% of the total litterfall.

Total litterfall followed an unimodal distribution pattern for the OX, CK, and NF, with a distinct peak in March or April every year. The CF showed a multi-modal pattern and these litterfall peaks occurred between April or May, August, and November, respectively. Two major peaks of litterfall in the FH were observed in May and December (Fig. 2).

3.2. Potential nutrient return through litterfall

Returns of N, P, and K through total litterfall in the NF and the CK were significantly higher than for the two coniferous forests ($p < 0.05$) (Tab. III). The NF returned two to three times the amount of N, P, and K associated with the CF. The K return in OX was very similar to that in FH. Mean annual potential return of Ca ranged from 32 kg·ha^{-1}·yr^{-1} in the CK to 62 kg·ha^{-1}·yr^{-1} in the FH. Total potential return of Mg to the soil through forest litterfall ranged from 6 to 14 kg·ha^{-1}·yr^{-1}.

Comparison of annual, potential nutrient return between different litter fractions indicated that for all the forests the leaf fraction had the highest amount of potential return of N, P, K, Ca, and Mg (Tab. III). The OX had the highest potential returns of N and P through leaf litter. The leaf fraction of the CK returned potentially higher amounts of K and Mg than those of all other forests. Potential return of Ca through leaves ranged from 58% of the total in the NF to 75% of the total in the FH.

3.3. Initial chemistry of leaf litter

Initial leaf litter N concentrations did not differ significantly between the five forests ($P > 0.05$), from 6.8 mg·g^{-1} (Chinese fir) to 11.1 mg·g^{-1} (*O. xylocarpa*). P concentration was relatively low, varying between 0.28 to 0.81 mg·g^{-1} (Tab. IV). Analysis of variance detected significant differences ($P < 0.05$) between forests for P and C concentrations in leaf litter (Tab. IV); P concentrations of leaf litter of Chinese fir and *O. xylocarpa* were significantly lower than that of *F. hodginsii*. Leaf litter of broadleaved trees (*O. xylocarpa* and *C. kawakamii*) had significantly lower C concentrations compared with needle litters of the two conifers (Chinese fir and *F. hodginsii*).

Some significant differences ($P < 0.05$) between forests were observed for all components, except lignin and alcohol-soluble compounds (Tab. IV). Maximum concentrations of lignin and alcohol-soluble compounds were observed in leaves of Chinese fir (33%) and *C. kawakamii* in the CK (18%), respectively.

3.4. Leaf-litter decomposition

The regressions describing decay rates over time were significant for all forests ($P < 0.05$, R^2 values range from 0.80 to 0.99). Decomposition was characterized by an initial faster rate of disappearance. For instance, leaves of *C. kawakamii* in the NF and CK, and *O. xylocarpa* lost 91%, 86% and 88% of their initial weight in the first 150-day period, respectively, compared with 9.4%, 14% and 9.9% of those in the later 600-day period. In broadleaved forests (the OX, CK, and NF), all the leaves lost their mass completely within the period ranging from 510 to 750 days; this was not the case for needles of Chinese
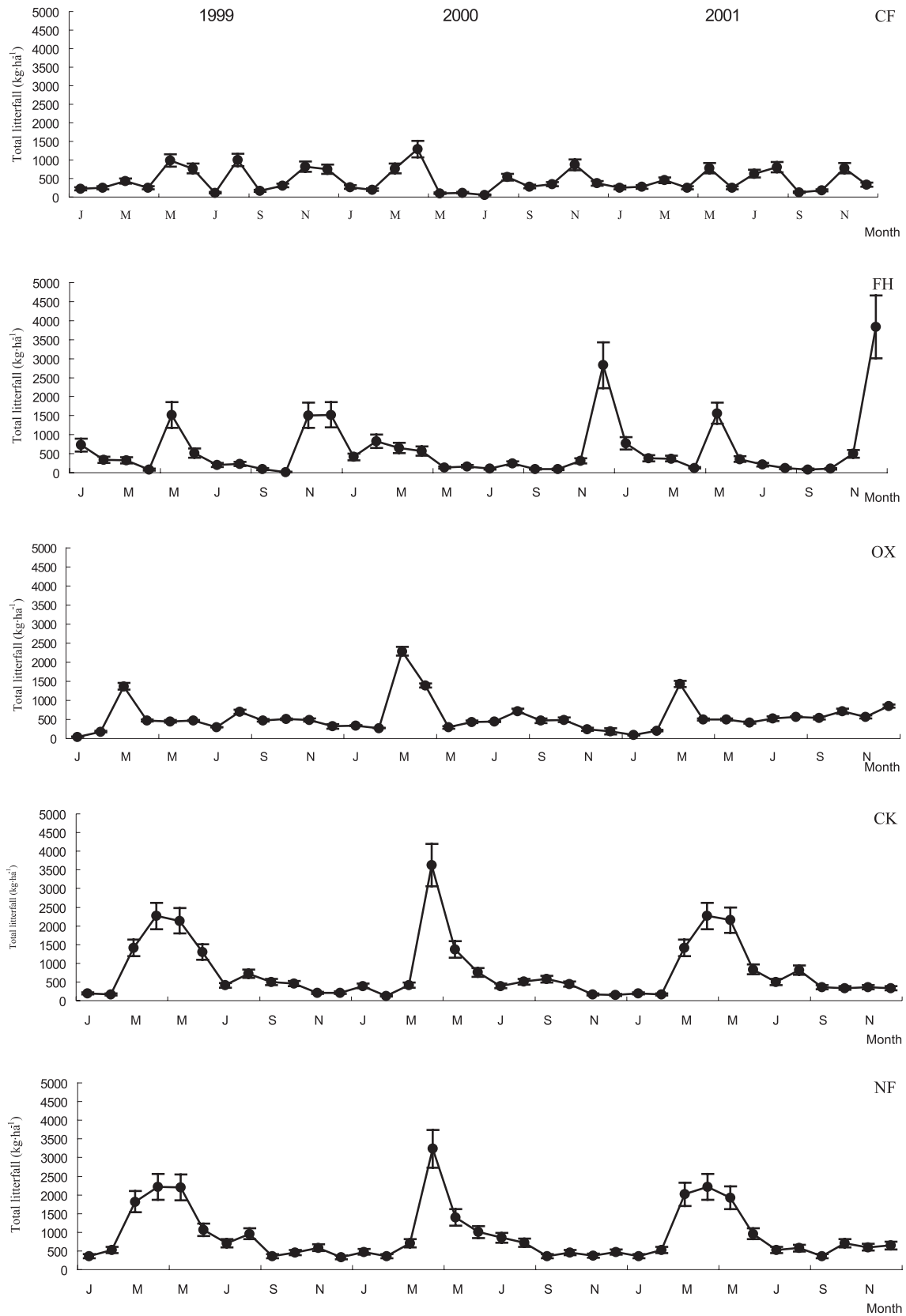
Figure 2. Monthly variations in total litterfall in the five forests. Bars indicate ± s.d., *n* = 15.

Table III. Annual, potential nutrient return kg·ha^{-1}·yr^{-1} through litterfall in the five forests.

Forest type	Litter fraction	N	P	K	Ca	Mg
CF	Leaf	22 ± 1.2	1.3 ± 0.07	8.8 ± 0.89	33 ± 2.2	5.6 ± 0.33
	Small branch	6.4 ± 0.45	0.48 ± 0.03	2.6 ± 0.21	9.1 ± 0.62	1.7 ± 0.12
	Flower	0.84 ± 0.05	0.05 ± 0.00	0.15 ± 0.02	0.68 ± 0.05	0.13 ± 0.02
	Fruit	1.8 ± 0.15	0.14 ± 0.02	1.3 ± 0.12	0.92 ± 0.11	0.35 ± 0.04
	Miscellaneous material	5.7 ± 0.51	0.43 ± 0.06	1.7 ± 0.14	7.0 ± 0.53	1.3 ± 0.12
	Subtotal	37	2.4	14	50	9.1
FH	Leaf	30 ± 1.9	1.7 ± 0.02	17 ± 0.67	46 ± 1.5	4.7 ± 0.22
	Small branch	7.0 ± 2.6	0.28 ± 0.09	1.3 ± 0.13	7.9 ± 2.3	0.60 ± 0.12
	Flower	2.4 ± 0.08	0.16 ± 0.00	0.71 ± 0.11	1.1 ± 0.36	0.27 ± 0.01
	Fruit	1.8 ± 0.25	0.25 ± 0.04	1.8 ± 0.05	2.4 ± 0.14	0.40 ± 0.08
	Miscellaneous material	4.6 ± 0.70	0.24 ± 0.02	1.5 ± 0.31	3.9 ± 0.08	0.62 ± 0.06
	Subtotal	46	2.6	22	62	6.6
OX	Leaf	54 ± 9.6	4.9 ± 1.6	16 ± 3.1	21 ± 3.1	4.3 ± 0.71
	Small branch	7.5 ± 0.62	0.24 ± 0.03	1.6 ± 0.19	8.9 ± 0.68	0.98 ± 0.07
	Flower	0.10 ± 0.03	0.01 ± 0.00	0.01 ± 0.00	0.03 ± 0.01	0.01 ± 0.00
	Fruit	0.31 ± 0.11	0.02 ± 0.006	0.16 ± 0.06	0.10 ± 0.04	0.02 ± 0.009
	Miscellaneous material	6.1 ± 0.34	0.43 ± 0.04	4.6 ± 0.34	3.7 ± 0.25	1.0 ± 0.07
	Subtotal	68	5.6	22	33	6.4
CK	Leaf	52 ± 5.0	3.9 ± 0.35	41 ± 4.2	21 ± 2.3	11 ± 0.99
	Small branch	13 ± 1.0	0.96 ± 0.08	4.1 ± 0.32	8.5 ± 0.53	2.5 ± 0.20
	Flower	0.15 ± 0.04	0.03 ± 0.00	0.05 ± 0.02	0.05 ± 0.01	0.03 ± 0.01
	Fruit	0.78 ± 0.11	0.07 ± 0.00	0.99 ± 0.16	0.48 ± 0.08	0.31 ± 0.05
	Miscellaneous material	4.6 ± 0.48	0.52 ± 0.06	2.3 ± 0.22	1.7 ± 0.16	0.58 ± 0.06
	Subtotal	70	5.5	49	32	14
NF	Leaf	39 ± 4.0	3.1 ± 0.27	32 ± 3.0	17 ± 1.6	6.0 ± 0.58
	Leaf of other tree species	8.2 ± 0.43	0.78 ± 0.02	3.6 ± 0.17	4.9 ± 0.21	1.1 ± 0.06
	Small branch	13 ± 0.83	0.92 ± 0.05	4.3 ± 0.28	9.0 ± 0.47	1.5 ± 0.11
	Branch of other tree species	1.4 ± 0.13	0.11 ± 0.03	0.54 ± 0.05	1.0 ± 0.08	0.19 ± 0.02
	Flower	2.9 ± 0.69	0.35 ± 0.11	0.82 ± 0.21	0.74 ± 0.14	0.30 ± 0.07
	Fruit	3.5 ± 0.32	0.34 ± 0.04	4.5 ± 0.50	1.3 ± 0.13	0.59 ± 0.07
	Miscellaneous material	10 ± 0.70	1.1 ± 0.10	5.3 ± 0.34	3.9 ± 0.18	0.93 ± 0.06
	Subtotal	78	6.6	51	38	11

Values are means ± s.d. of 15 traps at each forest over 3 years. Other symbols as in Table I.

fir and *F. hodginsii*. The percentage of leaf litter mass remaining during the first year ranged between 1.8% (NF) and 39% (CF). Decay-rate coefficients (k) for decomposing leaf litter samples ranged between 1.157 (Chinese fir) to 4.619 (*O. xylocarpa*). Comparatively lower k values was observed in the CF compared to the other 4 forests (Tab. V and Fig. 3).

3.5. Nutrient dynamics of decomposing leaf litter

Varying degree of increase of N concentrations was observed in leaf litter (Fig. 4). At the end of one year, N concentration in needles of Chinese fir was still 135% of the initial N concentration. In case of *F. hodginsii* the increase in N concentrations
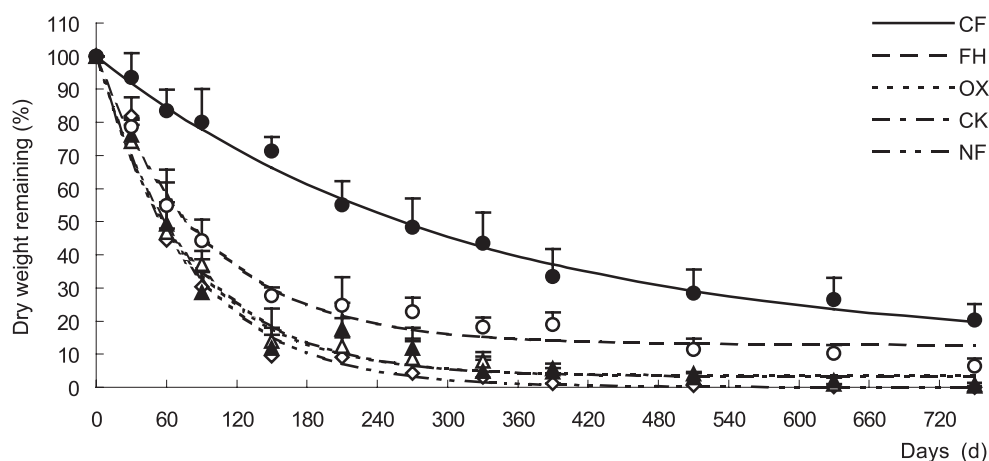
Figure 3. Percentage of dry mass remaining in the various leaf litters over a 750 day period. Bars indicate + s.d., $n = 6$. Lines represent the fitted curves by the model $X_t = A + Be^{-kt}$. ● Needle litter of Chinese fir in the CF; ○ Needle litter of *F. hodginsii* in the FH; ▲ Leaf litter of *O. xylocarpa* in the OX; △ Leaf litter of *C. kawakamii* in the CK; ◇ Leaf litter of *C. kawakamii* in the NF.

Table IV. Initial chemical composition of leaf litter from the five forests.

Composition (mg·g^{-1} D.M.)	CF	FH	OX	CK	NF
Lignin	333 ± 26a	324 ± 23a	310 ± 23a	301 ± 25a	295 ± 26a
Cellulose	159 ± 28a	150 ± 10a	109 ± 9.5b	165 ± 32a	165 ± 24a
Hemicellulose	118 ± 30ac	124 ± 7.3a	122 ± 5.6a	96 ± 10bc	95 ± 6.2bc
Alcohol soluble compounds	140 ± 8.6a	137 ± 7.1a	135 ± 8.1a	176 ± 36a	136 ± 9.5a
Water soluble compounds	113 ± 14a	118 ± 8.2a	164 ± 13b	153 ± 15bc	174 ± 16bd
Coarse protein	37 ± 10a	61 ± 8.8b	72 ± 11b	38 ± 9.5a	37 ± 11a
C	493 ± 9.5a	493 ± 7.3a	458 ± 13b	444 ± 9.7bc	460 ± 14bd
N	6.8 ± 1.6a	10.6 ± 2.5a	11.1 ± 3.0a	7.6 ± 1.6a	7.5 ± 1.4a
P	0.37 ± 0.03a	0.81 ± 0.09b	0.28 ± 0.02c	0.62 ± 0.07bd	0.63 ± 0.08be
C/N ratio	72	46	41	58	61
C/P ratio	1333	608	1634	716	730
Lignin/N ratio	49	30	28	40	39

Values are means ± s.d., $n = 3$. Different letters on the same rows indicate significant differences ($P < 0.05$). D.M.: dry matter. Other symbols as in Table I.

Table V. The parameters of the decomposition models: $X_t = A + Be^{-kt}$.

Tree species	Dry matter				Nutrient contents					
	A	B	k	R^2	k_N	R^2	k_P	R^2	k_K	R^2
Chinese fir	0.119	0.881	1.157	0.9930	0.769	0.97751	4.216	0.80911	5.761	0.97354
F. hodginsii	0.128	0.872	3.922	0.9844	2.991	0.97207	4.300	0.99176	5.771	0.99126
O. xylocarpa	0.035	0.965	4.619	0.9821	4.978	0.99183	1.967	0.95523	5.992	0.99585
C. kawakamii in the CK	0.032	0.968	4.462	0.9930	3.643	0.99089	4.364	0.9933	5.250	0.99649
C. kawakamii in the NF	0.000	1.000	4.518	0.9826	4.129	0.98265	4.664	0.98519	5.279	0.98554

All regressions were significant at the 0.05 level. Other symbols are the same as in Table I.

occurred only up to early 60 days and thereafter there was a sharp decline. P concentrations in leaves of *C. kawakamii* in the CK and NF decreased during decay, while they increased initially and then decreased in leaves of CF, FH, and OX (Fig. 4). Generally, K concentrations declined during decomposition for all tree species (Fig. 4), because of its strong solubility.
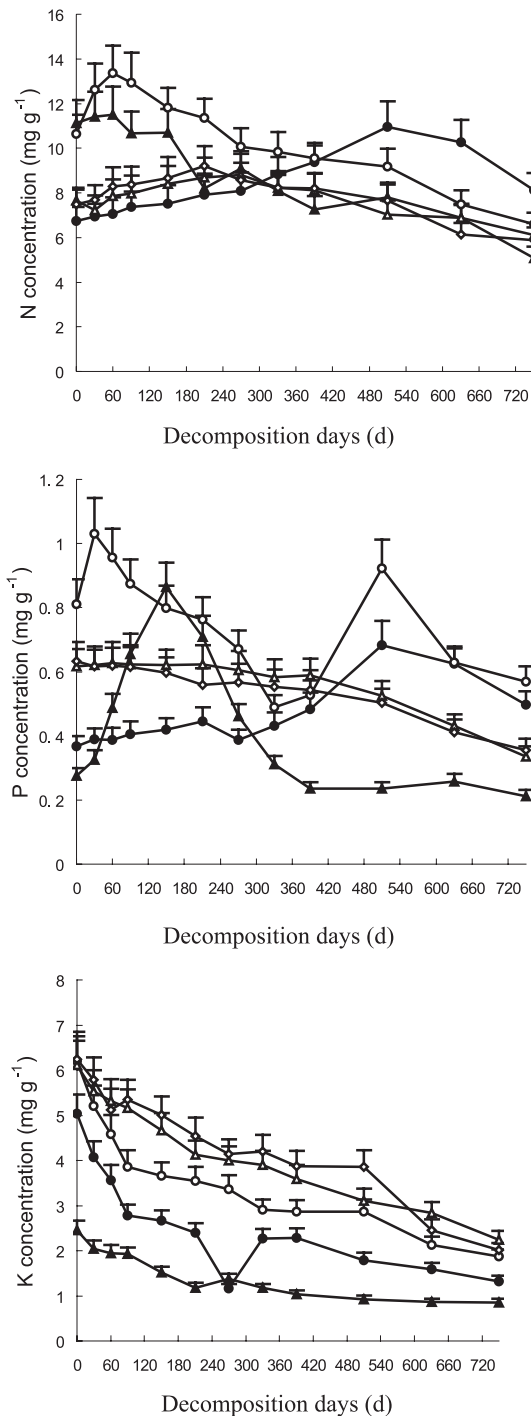
Figure 4. Changes of concentrations of N, P, and K in the various leaf litters over a 750 day period. Same symbols as in Figure 3. Bars indicate + s.d., $n = 6$.
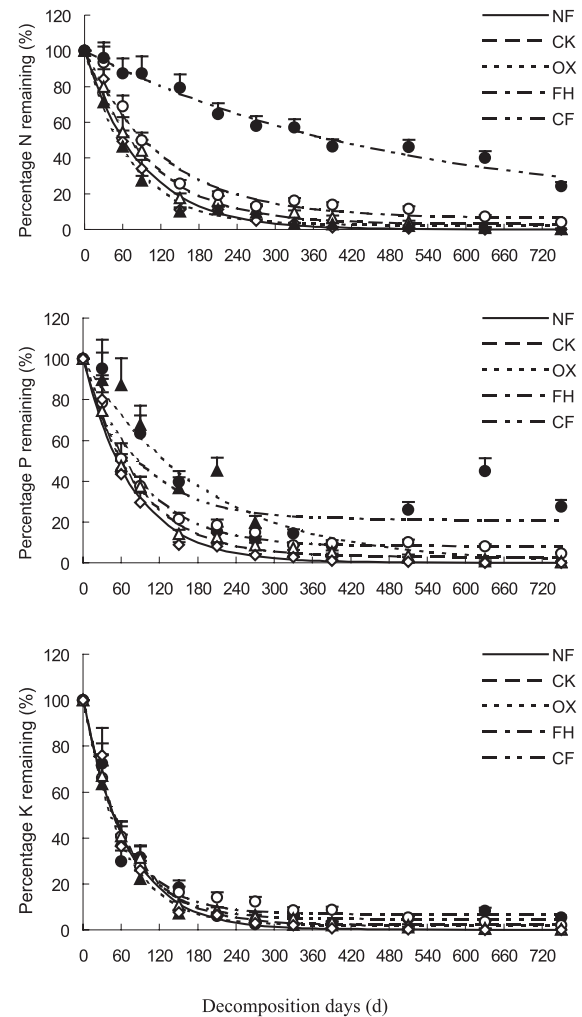

Figure 5. Percentages of N, P, and K remaining in the various leaf litters over a 750 day period. Same symbols as in Figure 3. Bars indicate + s.d., $n = 6$. Lines represent the fitted curves by the model $X_t = A + Be^{-kt}$.

Considering N dynamics under all the stands, *C. kawakamii* leaf litter in the NF showed the highest net release (98.2% of initial N content in the first year), and Chinese fir the lowest one (Fig. 5). Decrease in P stocks in all leaf types reflects net mineralization of this nutrient from the beginning. However, throughout the decomposition period different degrees of increase in P stock was recorded for leaves of Chinese fir and *O. xylocarpa* (Fig. 5). The tendency toward net release of K in all leaf litters was evident during the decomposition (Fig. 5).

The decay constant of N (k_N) ranged from 0.769 in Chinese fir to 4.978 in *O. xylocarpa*; the decay constant of P (k_P) ranged from 1.967 in the *O. xylocarpa* to 4.664 for *C. kawakamii* in the NF; and the decay constant of K (k_K) seemed very similar among these forests (5.250–5.992). The decay constants of nutrients during leaf-litter decomposition can be arranged in the sequence of $k_K > k_P > k_N$, except for leaf litter of *O. xylocarpa* where $k_K > k_N > k_P$. The annual, actual return of N and P through leaf-litter for *O. xylocarpa* and *C. kawakamii* in the CK were significantly higher than those in Chinese fir and *F. hodginsii* ($P < 0.05$). *C. kawakamii* in the CK actually returned the highest amount of K and Chinese fir the lowest (Tab. VI).

Table VI. Percentage of initial nutrient content decayed by the end of the 1st year (DR, $g \cdot g^{-1}$)[(1)] and annual, actual return (AAR, $kg \cdot ha^{-1} \cdot yr^{-1}$)[(2)] of N, P, and K by leaf-litter in the five forests.

Tree species	N		P		K	
	DR	AAR	DR	AAR	DR	AAR
Chinese fir	0.48	10	0.78	1.0	0.95	8.3
F. hodginsii	0.89	27	0.91	1.6	0.93	16
O. xylocarpa	0.97	53	0.86	4.2	0.98	16
C. kawakamii in the CK	0.95	49	0.96	3.7	0.97	40
C. kawakamii in the NF	0.98	39	0.99	3.0	0.99	32

[(1)] Calculated with the model: $X_t = A + Be^{-kt}$.
[(2)] Obtained by multiplying DR with the corresponding potential nutrient return through leaf fall (Tab. III).

4. DISCUSSION

4.1. Litterfall

Litter production in forest ecosystem is determined by climatic condition, species composition, and successional stage [14, 37, 42]. The mean annual litterfall in the NF (11.01 $Mg \cdot ha^{-1}$) was in the upper part of the range recorded for subtropical evergreen broadleaved forests [9, 21, 23, 52] and even equivalent to or higher than that in some tropical rain forests elsewhere in the world [14, 24, 36, 37]. The range of litter production in the four plantations (5.47–9.54 $Mg \ ha^{-1} \cdot yr^{-1}$) was lower than that in the NF, but similar to that recorded in subtropical plantations [9, 21, 39, 52]. Furthermore, litterfall estimates in the CF and FH were higher than in other coniferous forests from temperate and warm temperate regions [6, 16, 17]. The higher diversity of tree species, the larger pools of soil organic C and total N, and the larger total (CK + other species) stand volume (563.5 $m^3 \cdot ha^{-1}$) in the NF compared with monoculture plantations (Tab. I) may explain the higher litterfall in the NF [11, 22, 50]. Significant differences were also observed between average annual litterfall production in plantations of CF, FH, OX, and CK (Tab. II), which could be partly due to the characteristics of the species. In general, broadleaved trees had higher litterfall production than that of coniferous trees in subtropics [9, 24, 41, 45]. This general trend was however not observed in this study.

For the OX, CK, and NF, one peak of litterfall was observed in the spring (March or April) over the 3-year period, when most of old leaves were replaced by new ones. This rhythm of physiological leaf senescence fits with similar studies of evergreen broadleaved forests [9, 21, 23]. Regarding litterfall pattern of FH forest (Fig. 2), the peak in December may be associated with shed of needles induced by low temperature stress. Available studies concerning Chinese fir plantations mostly showed that this conifer yielded two maximum litterfall [21, 39, 46], whereas our study showed other maxima (Fig. 2); this was perhaps due to the highest actual evapotranspiration (AET) and slow-growth characteristic of Chinese fir in the period [39, 50]. Year-to-year variations in litter production and litterfall pattern for the five forests may be related to annual change in environmental parameters, especially air temperature and rainfall [14, 21, 23].

4.2. Potential nutrient return through litterfall

Mean annual, potential returns of P and K through litterfall in NF (6.6 and 51 $kg \cdot ha^{-1}$) were higher than those of subtropical broadleaved forests, e.g., a subtropical rain forest in Hexi (3.8 and 41 $kg \cdot ha^{-1}$) [52], a primary *Lithocarpus xylocarpus* forest in Ailao mountain (1.7 and 29 $kg \cdot ha^{-1}$) [9], an old-growth evergreen broadleaved forest in Dinghu mountain (5.9 and 42 $kg \cdot ha^{-1}$) [44], and a *Castanopsis eyrei* forest in Wuyi mountain (1.4 and 13 $kg \cdot ha^{-1}$). By contrast, the amounts of return of N, Ca, and Mg in NF fall in the range of subtropical broadleaved forests (N: 36–128 $kg \cdot ha^{-1}$; Ca: 26-47 $kg \cdot ha^{-1}$; Mg: 5.5–15 $kg \cdot ha^{-1}$) [9, 23, 44, 52]. The potential nutrient input from the CK and OX lied in the range of subtropical broadleaved forests, except that of K in the CK [9, 23, 44, 52]. Compared with the CK, the OX had much lower return of K and Mg. The CF had potential input of N and P close to those of pure Chinese fir plantations in Tianlin (39 $kg \cdot ha^{-1}$ and 2.0 $kg \cdot ha^{-1}$) [21] and in Huitong (37 $kg \cdot ha^{-1}$ and 2.2 $kg \cdot ha^{-1}$) [39]. The annual, potential returns of N and K in the FH were higher than those in the CF and the two other Chinese fir plantations in Tianlin and Huitong, while those of P seems very similar [21, 39]. The CF and FH potentially returned much more Ca, and less N and P, to the forest floor than the three other broadleaved forests (Tab. III), which was in agreement with the results of Tian et al. (1989) [39]. N and P are the major limiting nutrients for tree growth in many subtropical forests because of high soil acidity; hence the relative high return of N and P through litterfall makes the broadleaved species more advantageous over conifers in nutrient supply, especially in the surface soil horizons [49].

4.3. Leaf-litter decomposition

At a regional scale with similar climatic conditions, litter decomposition rates are primarily controlled by litter quality [1, 2, 19]. Rapid mass loss in the earlier stage might be largely associated with easily decomposed carbohydrates, while the relatively slow mass loss in the later stage is perhaps due to the accumulation of more recalcitrant compounds, such as lignin and cellulose [2, 36]. The higher amounts of water soluble compounds in OX, CK, and NF were associated to an increase in the decomposition rate; 150 days after the onset of decomposition, the % of initial leaf dry weight remaining amounted to 11.7%,

14.0%, and 9.4% for leaves of *O. xylocarpa*, and *C. kawakamii* in the CK and in the NF, respectively (Fig. 3). There were no significant relationships between initial concentrations of alcohol-soluble compounds, cellulose, hemicellulose, coarse protein, and decay rates of various leaf litters. As Tripathi and Singh (1992) [40], we also found a positive effect of water-soluble substances on initial litter decomposition ($P < 0.05$, $r = 0.712$).

Nutrient and lignin concentrations of litter could be more important in determining the rate of decomposition [1, 8, 38]. However, k of the various leaf litter in this study was not highly correlated with the initial N concentration ($r = 0.225$, $P = 0.038$); it is possible that N concentration was not a limiting factor for decomposition in these forests. Lignin is an interfering factor in the degradation of cellulose and other carbohydrates, as well as proteins, and thus high initial levels of lignin may slow decomposition rates [5, 13, 35, 38]. Initial lignin concentration showed significantly negative correlations with k ($r = -0.916$, $P = 0.011$). There was an inverse relationship between lignin/N ratios and decay constants ($r = -0.473$, $P = 0.041$). Many previous workers also have found such negative relationships [1, 7, 35, 38].

4.4. Nutrient dynamics of decomposing leaf litter

Nutrient concentrations are known to vary to some extent during the decomposing period and between leaf litter types [4, 5, 15, 31]. The increase in N concentration (Fig. 4) followed by a decline over time as observed in this study is similar to the patterns found in other studies [4, 5, 25, 35]. A concentration increase in the early stage of decomposition was also found in leaf litter of Chinese fir, *F. hodginsii* and *O. xylocarpa* for P, which was also observed in some other studies [1, 28, 35].

A negative exponential pattern for nutrient release from decomposing leaf litter was found in the five forests (Fig. 5), characterized by an initial rapid and a subsequent slow release phase, which was in agreement with the results reported by Jamaludheen and Kumar (1999) [15]. However, this pattern differed from the generalized tri-phasic model proposed by Berg and Staaf (1981) [3]. Among the nutrients, K had the most rapid rate of release (Tab. V). Of the initial amount of K, 30–52% was lost from decomposing leaf litter during the first 60 days compared with a weight loss of 14–48%; and the values of k_K were much higher than those of k (Tab. V). This indicated initial leaching loss of K because of its solubility. Release of N began at once for all leaf litter types without net accumulation, suggesting that N was not a limiting factor for microorganisms because the initial N concentrations in these leaf-litters was relatively high compared to other studies [1, 28, 35]. The N/P ratios in fresh leaf litter of *O. xylocarpa* and Chinese fir were higher compared with other leaf litter (Fig. 6). As 10 is the ideal N/P ratio for decomposers [42], the highest initial N/P ratio in the OX indicated that P could be more limiting in the leaf-litter decomposition in the OX than in other forests. Moreover, the five forests had low soil P availability [51] and thus P release from litterfall could play an important control of site productivity. Nutrient release through litter decomposition may cause improvement in soil fertility. Details regarding changes in soil nutrient status in the five forests are presented elsewhere [49].
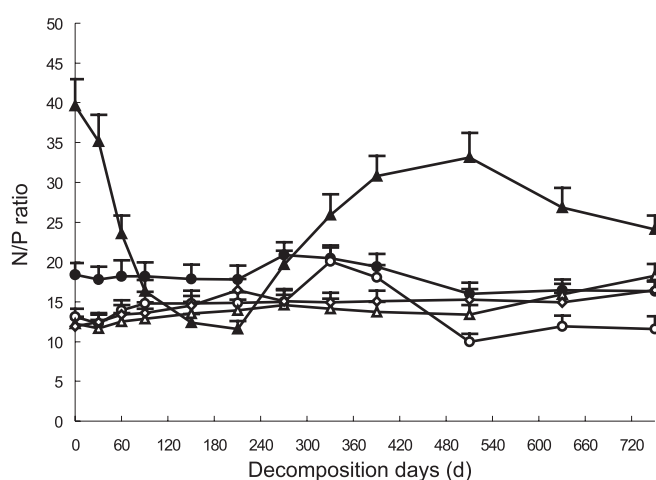

Figure 6. Changes of N/P ratios in various leaf litter over a 750 day period. Same symbols as Figure 3. Bars indicate + s.d., $n = 6$.

5. CONCLUSION

C. kawakamii, not only in natural forest, but also in monoculture plantations, exhibited higher annual litterfall than coniferous plantations, while *O. xylocarpa* showed a relatively low litter production close to Chinese fir. Generally, broadleaved forests had higher annual, potential return of N and P, and lower return of Ca than coniferous ones. While the amount of potential return of K and Mg show no clear trend between broadleafs and conifers. Initial lignin concentration and initial lignin/N ratio were found in significant relations with decay rate of leaf litter. Compared with those of conifers, leaf-litters of broadleafs had less recalcitrant materials and faster decay rate for dry matter, as well as faster actual release of N. *O. xylocarpa* was found more P-limiting than other forests in the leaf decomposition. The higher potential returns and decay constants of N and/or P make the broadleafs more effective in the actual returns of these two nutrients than conifers, which indicates that broadleafs are more promising species instead of Chinese fir for afforestation, since N and P are the major limiting nutrients for most subtropical forests of China.

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