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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 \( xt = A + B e^{-kt} \), 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 \( xt = A + Be^{-kt} \), 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 \( k_K > k_N > k_P \).

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 dynamiqne des N, P et K associée à la décomposition de la litière ont été étudiées 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·ha−1 pour OX, 9,54 Mg·ha−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 \( xt = A + Be^{-kt} \), la constante de décomposition de la matière \( k \) varie de 1,157 en CF à 4,619 en OX. La concentration initiale en ligneine et le rapport ligneine/N présente une corrélation négative significative avec \( k \) (\( r = -0.916, P = 0.011; r = -0.473, P = 0.041 \)) alors que la concentration initiale de N montre une faible corrélation positive (\( r = 0.225, P = 0.038 \)). En utilisant le modèle \( xt = A + Be^{-kt} \), la constante de décomposition de N (\( k_N \)) varie de 0,769 en 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 (\( k_K \)) apparait très similaire pour ces forets (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 \( k_K > k_N > k_P \).
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 Dianyun 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 occurring 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.

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
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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. Subsamples 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 K2Cr2O7-H2SO4 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 H2SO4-HClO4, 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 arc sine 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.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>CF</th>
<th>FH</th>
<th>OX</th>
<th>CK</th>
<th>NF(2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean tree age(3) (years)</td>
<td>33</td>
<td>33</td>
<td>33</td>
<td>33</td>
<td>~150</td>
</tr>
<tr>
<td>Mean tree height (m)</td>
<td>21.9</td>
<td>21.4</td>
<td>18.4</td>
<td>18.9</td>
<td>24.3</td>
</tr>
<tr>
<td>Mean tree diameter at breast height (cm)</td>
<td>23.3</td>
<td>21.6</td>
<td>17.2</td>
<td>24.2</td>
<td>42.2</td>
</tr>
<tr>
<td>Stand density (stem·ha−1)</td>
<td>1117</td>
<td>975</td>
<td>1109</td>
<td>875</td>
<td>255</td>
</tr>
<tr>
<td>Stand volume(4) (m³·ha−1)</td>
<td>425.91</td>
<td>379.57</td>
<td>209.01</td>
<td>412.43</td>
<td>398.31</td>
</tr>
<tr>
<td>Standing biomass of forest floor(5) (Mg·ha−1)</td>
<td>3.15</td>
<td>2.65</td>
<td>7.22</td>
<td>7.44</td>
<td>7.72</td>
</tr>
<tr>
<td>Soil (A horizon, 0–20 cm depth)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bulk density (g·cm−3)</td>
<td>1.20</td>
<td>1.13</td>
<td>1.15</td>
<td>1.10</td>
<td>0.93</td>
</tr>
<tr>
<td>Organic C (mg·g−1)</td>
<td>16.9</td>
<td>17.7</td>
<td>17.5</td>
<td>17.1</td>
<td>26.4</td>
</tr>
<tr>
<td>Total N (mg·g−1)</td>
<td>1.12</td>
<td>1.37</td>
<td>1.29</td>
<td>1.12</td>
<td>1.88</td>
</tr>
<tr>
<td>Total P (mg·g−1)</td>
<td>0.29</td>
<td>0.35</td>
<td>0.30</td>
<td>0.31</td>
<td>0.36</td>
</tr>
<tr>
<td>C/N ratio</td>
<td>15.1</td>
<td>12.9</td>
<td>13.6</td>
<td>15.3</td>
<td>14.0</td>
</tr>
<tr>
<td>Hydrolyzable N (mg·g−1)</td>
<td>0.110</td>
<td>0.118</td>
<td>0.125</td>
<td>0.115</td>
<td>0.136</td>
</tr>
<tr>
<td>Available P(6) (µg·g−1)</td>
<td>4.7</td>
<td>5.6</td>
<td>6.8</td>
<td>5.9</td>
<td>7.6</td>
</tr>
</tbody>
</table>

(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 H2SO4, and then their concentration were determined using (NH4)6Mo7O24-KSbOC4H4O6-C6H8O6 method.

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

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.

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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 arc sine 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.
Table II. Quantity (kg·ha⁻¹·yr⁻¹) and proportion in the total (% in parentheses) of litterfall in the five forests.

<table>
<thead>
<tr>
<th>Forest type</th>
<th>Leaf</th>
<th>Leaves from other trees(1)</th>
<th>Subtotal of leaves</th>
<th>Small branches</th>
<th>Branches from other trees(1)</th>
<th>Subtotal of branches</th>
<th>Flowers</th>
<th>Fruits</th>
<th>Miscellaneous</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>CF</td>
<td>3 188 ± 424</td>
<td>3 188 ± 424a</td>
<td>3 167 ± 62a</td>
<td>1 367 ± 25a</td>
<td>1 367 ± 62a</td>
<td>1 367 ± 62a</td>
<td>79 ± 2.2a</td>
<td>582 ± 137ab</td>
<td>5 468 ± 431a</td>
<td></td>
</tr>
<tr>
<td>FH</td>
<td>4 778 ± 497</td>
<td>4 778 ± 497b</td>
<td>1 374 ± 127b</td>
<td>1 374 ± 127b</td>
<td>1 374 ± 127ab</td>
<td>258 ± 26b</td>
<td>289 ± 53a</td>
<td>592 ± 121ac</td>
<td>7 291 ± 767b</td>
<td></td>
</tr>
<tr>
<td>OX</td>
<td>3 775 ± 215</td>
<td>3 775 ± 215a</td>
<td>1 228 ± 51b</td>
<td>1 228 ± 51b</td>
<td>1 228 ± 51b</td>
<td>8.5 ± 1.8c</td>
<td>25 ± 11b</td>
<td>650 ± 72a</td>
<td>5 687.50 ± 229.54a</td>
<td></td>
</tr>
<tr>
<td>CK</td>
<td>6 865 ± 159a</td>
<td>6 865 ± 159c</td>
<td>2 132 ± 357c</td>
<td>2 132 ± 357c</td>
<td>2 132 ± 357c</td>
<td>13 ± 9cd</td>
<td>142 ± 154a</td>
<td>386 ± 42b</td>
<td>9 538 ± 532c</td>
<td></td>
</tr>
<tr>
<td>NF</td>
<td>5 400 ± 274</td>
<td>1 171 ± 249</td>
<td>2 982 ± 393d</td>
<td>2 982 ± 393d</td>
<td>2 982 ± 393d</td>
<td>253 ± 16a</td>
<td>662 ± 337c</td>
<td>1 032 ± 138d</td>
<td>11 008 ± 529d</td>
<td></td>
</tr>
</tbody>
</table>

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 NF and decreased in the order: NF > CK > FH > OX > CF.

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 (\( P > 0.05 \)). 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.

3.4. Leaf-litter decomposition

The regressions describing decay rates over time were significant for all forests (\( P < 0.05 \)). 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 fir. 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 C. kawakamii (18%) and C. kawakamii (18%).
Figure 2. Monthly variations in total litterfall in the five forests. Bars indicate ± s.d., n = 15.


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
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.

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

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

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: \( X_t = A + Be^{-kt} \).

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Dry matter</th>
<th>Nutrient contents</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
</tr>
<tr>
<td>Chinese fir</td>
<td>0.119</td>
<td>0.881</td>
</tr>
<tr>
<td><em>F. hodginsii</em></td>
<td>0.128</td>
<td>0.872</td>
</tr>
<tr>
<td><em>O. xylocarpa</em></td>
<td>0.035</td>
<td>0.965</td>
</tr>
<tr>
<td><em>C. kawakamii</em> in the CK</td>
<td>0.032</td>
<td>0.968</td>
</tr>
<tr>
<td><em>C. kawakamii</em> in the NF</td>
<td>0.000</td>
<td>1.000</td>
</tr>
</tbody>
</table>

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

**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 $X_t = A + Be^{-kt}$. 

$$\frac{dN}{dt} = k_N N - \frac{N}{t}$$

$$\frac{dP}{dt} = k_P P - \frac{P}{t}$$

$$\frac{dK}{dt} = k_K K - \frac{K}{t}$$

$X_t = A + Be^{-kt}$
4. DISCUSSION

4.1. Litterfall

Litterfall 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·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·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 m3·ha–1) in the NF compared with monoculture plantations in Dinghu mountain (5.9 and 42 kg·ha–1) [44], and a Castanopsis eyrei forest in Wuyi mountain (1.4 and 13 kg·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·ha–1; Ca: 26–47 kg·ha–1; Mg: 5.5–15 kg·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 potential input of N and P in the CK and OX was close to those of pure Chinese fir plantations in Tianlin (39 kg·ha–1·yr–1) [21] and in Huitong (37 kg·ha–1·yr–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].

4.2. Potential nutrient return through litterfall

Mean annual, potential returns of P and K through litterfall in NF (6.6 and 51 kg·ha–1) were higher than those of subtropical evergreen broadleaved forests, e.g., a subtropical rain forest in Hexi (3.8 and 41 kg·ha–1) [52], a primary Lithocarpus xylocarpus forest in Ailao mountain (1.7 and 29 kg·ha–1) [19], an old-growth evergreen broadleaved forest in Dinghu mountain (5.9 and 42 kg·ha–1) [44], and a Castanopsis eyrei forest in Wuyi mountain (1.4 and 13 kg·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·ha–1; Ca: 26–47 kg·ha–1; Mg: 5.5–15 kg·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 potential input of N and P in the CK and OX was close to those of pure Chinese fir plantations in Tianlin (39 kg·ha–1·yr–1) [21] and in Huitong (37 kg·ha–1·yr–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%.
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].

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 broadleaves 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 broadleaves 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 broadleaves more effective in the actual returns of these two nutrients than conifers, which indicates that broadleaves 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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REFERENCES


Litterfall, nutrient return and leaf-litter decomposition


