

康自佳, 吴福忠, 吴秋霞, 胡仪, 岳楷, 倪祥银. 米槠、杉木和马尾松凋落叶和凋落枝碳氮含量及归还特征[J]. 应用与环境生物学报, 2023, 29 (3): 639-646  
Kang ZJ, Wu FZ, Wu QX, Hu Y, Yue K, Ni XY. Concentrations and returns of carbon and nitrogen in foliar and twig litters of *Castanopsis carlesii*, *Pinus massoniana*, and *Cunninghamia lanceolata* [J]. *Chin J Appl Environ Biol*, 2023, 29 (3): 639-646

# 米槠、杉木和马尾松凋落叶和凋落枝 碳氮含量及归还特征

康自佳<sup>1</sup> 吴福忠<sup>1,2,3</sup> 吴秋霞<sup>1</sup> 胡仪<sup>1</sup> 岳楷<sup>1,2,3</sup> 倪祥银<sup>1,2,3</sup>✉

<sup>1</sup>福建师范大学地理科学学院 福州 350007

<sup>2</sup>福建师范大学湿润亚热带生态-地理过程教育部重点实验室 福州 350007

<sup>3</sup>福建三明森林生态系统国家野外科学观测研究站 三明 365002

**摘要** 大面积亚热带常绿阔叶林转换为马尾松 (*Pinus massoniana*) 和杉木 (*Cunninghamia lanceolata*) 人工林后, 土壤肥力衰退. 凋落叶和凋落枝是森林地上凋落物的主要组成部分, 其中部分碳 (C)、氮 (N) 经过分解归还土壤, 是土壤有机碳和养分的重要来源. 因此, 认识马尾松和杉木新鲜凋落叶和凋落枝C、N含量和归还特征对于揭示亚热带森林转换后土壤养分周转和肥力提升具有重要意义. 选取亚热带常绿阔叶林优势树种米槠 (*Castanopsis carlesii*) 和主要造林树种马尾松、杉木为研究对象, 分析其新鲜凋落叶和凋落枝产量、C和N含量及归还量的动态变化规律. 结果表明: 米槠、马尾松和杉木凋落叶、凋落枝产量和C、N含量及归还量均具有明显的季节动态变化, C、N含量总体上在夏季 (6-8月) 较高, 而凋落叶和凋落枝产量和C、N归还量总体上在4-5月和8-9月较高, 12月-次年1月较低. 米槠、马尾松、杉木凋落叶年凋落量分别为3 613、3 054和2 587 kg/hm<sup>2</sup>, 凋落枝年凋落量分别为881、2 135和1 228 kg/hm<sup>2</sup>. 总体上看, 凋落叶C、N含量高于凋落枝, 而C/N值低于凋落枝; 马尾松、杉木凋落叶和凋落枝C含量高于米槠, 但N含量低于米槠. 3个树种凋落叶和凋落枝每月的C归还量变化范围分别为5.18-210和0-205 kg/hm<sup>2</sup>, 凋落叶和凋落枝每月的N归还量变化范围分别为0.14-4.69和0-2.34 kg/hm<sup>2</sup>. 总之, 亚热带常绿阔叶林转换为马尾松、杉木人工林后, 凋落叶和凋落枝C、N含量和归还量的动态规律发生了显著改变, 马尾松和杉木凋落叶和凋落枝C含量和C/N值增加, 而N含量降低. 同时, 与米槠相比, 马尾松、杉木凋落叶和凋落枝较低的C、N归还量导致从地上凋落物输入的C和养分减少, 这可能是导致亚热带马尾松和杉木人工林土壤肥力下降的重要原因. (图8 表2 参37)

**关键词** 碳; 氮; 凋落物; 人工林; 亚热带森林

## Concentrations and returns of carbon and nitrogen in foliar and twig litters of *Castanopsis carlesii*, *Pinus massoniana*, and *Cunninghamia lanceolata*

KANG Zijia<sup>1</sup>, WU Fuzhong<sup>1,2,3</sup>, WU Qiuxia<sup>1</sup>, HU Yi<sup>1</sup>, YUE Kai<sup>1,2,3</sup> & NI Xiangyin<sup>1,2,3</sup>✉

<sup>1</sup> School of Geographical Sciences, Fujian Normal University, Fuzhou 350007, China

<sup>2</sup> Key Laboratory for Humid Subtropical Eco-Geographical Processes of the Ministry of Education, Fujian Normal University, Fuzhou 350007, China

<sup>3</sup> Sanming Forest Ecosystem National Observation and Research Station, Sanming 365002, China

**Abstract** Many broad-leaved subtropical forests have been converted to plantations (mainly *Pinus massoniana* and *Cunninghamia lanceolata*) in subtropical China, resulting in a substantial decline in soil fertility. Foliar and twig litter are the primary components of aboveground litter in forest ecosystems. Parts of carbon (C) and nitrogen (N) in foliar and twig litter can be returned to forest soils after progressive decomposition and are an important source of organic C and nutrients in forest soils. Therefore, a comprehensive understanding of C and N content and return dynamics in the foliar and twig litter of *P. massoniana* and *C. lanceolata* is of great significance for assessing soil nutrient turnover and fertility improvement after subtropical forest conversion. In this study, we collected fresh foliar and twig litter of *Castanopsis carlesii* (a dominant tree species in subtropical evergreen broad-leaved forests) in a natural *C. carlesii* forest, as well as *P. massoniana* and *Cunninghamia lanceolata* (two main planted trees in subtropical China) in their separate plantations over one year to assess the seasonal dynamics of litterfall, C and N concentrations, and return amounts, as well as their C/N ratios in

收稿日期 Received: 2022-04-22 接受日期 Accepted: 2022-09-06

国家自然科学基金项目 (32022056、31800521、32101509、32171641) 资助 Supported by the National Natural Science Foundation of China (32022056, 31800521, 32101509, 32171641)

✉通信作者 Corresponding author (E-mail: nixy@fjnu.edu.cn)

fresh foliar and twig litters. The results showed that not only the foliar and twig litterfall, but also the C and N concentrations and returns showed obvious seasonal dynamics in different months for all tree species studied. They were generally higher from April to May and August to September, and lower from December to January of the following year. Specifically, C and N concentrations were generally higher in summer (June to August). Moreover, the annual foliar litterfall were 3 613, 3 054, and 2 587 kg/hm<sup>2</sup> for *C. carlesii*, *P. massoniana*, and *C. lanceolata*, respectively, and the annual twig litterfall were 881, 2 135, and 1 228 kg/hm<sup>2</sup>, respectively, for the three studied litter species. The annual litterfall was greater in *C. carlesii* foliar litter than in the foliar litters of *P. massoniana* and *C. lanceolata*. Moreover, both C and N concentrations were greater in foliar litter than in the twig litter of the corresponding tree species, but the C/N ratios were lower in foliar litter than in twig litter. The C concentrations in the foliar litter of *C. lanceolata* and *P. massoniana* were significantly higher than those in *C. carlesii*, but the N concentrations were significantly lower than those in *C. carlesii* foliar litter. The C return from foliar litter of the three studied tree species showed a range of 5.18–210 kg/hm<sup>2</sup>, and those in twig litter showed a range of 0–205 kg/hm<sup>2</sup>. The N return of the three studied tree species were 0.14–4.69 kg/hm<sup>2</sup> for foliar litter and were 0–2.34 kg/hm<sup>2</sup> for twig litter. These results suggest that C and N concentrations and C/N ratios in the litter varied greatly among litter types, tree species, and the time period. The results suggest that the conversion of subtropical evergreen broad-leaved forests (i.e., *C. carlesii*) to *P. massoniana* and *C. lanceolata* plantations could lead to decreased C and N return from foliar and twig litter. Lower litter production and the associated lower nutrient returns are important biogeochemical reasons for the decline in plantation soil fertility in subtropical China.

**Keywords** carbon; nitrogen; litter; plantation; subtropical forest

我国亚热带地区分布着全球同纬度地区面积最大的湿润季风性常绿阔叶林<sup>[1]</sup>。然而,在过去几十年里,大量天然林被转换为马尾松和杉木等人工林。据第九次全国森林清查数据显示,马尾松和杉木人工林已分别占我国人工林总面积的4.4%和17.3%<sup>[2]</sup>。虽然这些人工林在保障我国木材供应和山地生态安全等方面发挥了巨大作用,但已有大量研究表明,人工林连栽导致森林结构单一、土壤肥力下降、地力衰退等一系列问题<sup>[3-4]</sup>。因此,深入认识亚热带大面积常绿阔叶林转换为马尾松和杉木人工林后土壤肥力衰退机制对于我国南方亚热带森林可持续经营具有重要意义。

凋落物通过节律性归还地表,为土壤动物和微生物提供碳(C)和养分来源<sup>[5-9]</sup>,是连接地上植被与土壤之间物质循环的重要环节,对于维持森林养分循环和土壤肥力等生态系统功能具有重要意义<sup>[10-14]</sup>。凋落叶、凋落枝是凋落物的主要组成部分,且不同的凋落物类型具有不同的生产节律、产量和质量(quality),且可以进一步影响后续凋落物分解和养分释放过程<sup>[15]</sup>。凋落物中C、N是土壤微生物重要的C和养分来源,是驱动森林土壤养分周转和土壤有机质形成的重要纽带。以往的研究主要集中在森林凋落叶产量、养分含量及归还动态等方面,但对凋落枝的研究较少,因此,凋落叶和凋落枝中C、N含量及其归还规律调控着森林生态系统诸多生物地球化学过程,也是维持森林土壤肥力的关键因素之一<sup>[16-21]</sup>。

本研究拟解决的关键科学问题是:亚热带常绿阔叶林转换为马尾松和杉木人工林后,凋落叶、凋落枝产量和C、N含量及归还量是否显著降低。本研究以亚热带常绿阔叶林典型优势树种米槠和主要造林树种马尾松、杉木为研究对象,连续12个月收集其新鲜凋落叶和凋落枝,分析凋落物量和C、N含量及归还量的动态变化特征,揭示亚热带森林转换是否导致凋落物C、N归还量发生显著改变,以期为亚热带人工林土壤肥力衰退机制和森林可持续经营提供理论依据。

## 1 材料与方法

### 1.1 研究样地概况

研究区域位于福建三明森林生态系统国家野外科学观测研究站(26°19'N, 117°36'E),低山丘陵为主,平均海拔约300 m,坡度25-45°,属中亚热带季风气候,年平均气温19.3 °C,年平均降水量1 610 mm(主要集中于3-8月)(图1)。土壤以花岗岩发育的红壤为主,碳含量为22.7 g/kg,氮含量为1.4 g/kg,可溶性有机碳含量为56 mg/kg,土壤容重为1.04 g/cm<sup>3</sup>,多呈酸性<sup>[1]</sup>。1958年以前,研究样地内主要分布着以米槠为优势树种的常绿阔叶林,但在1976年大面积米槠常绿阔叶林经强度择伐后,一部分经天然更新形成米槠次生林,主要树种有米槠、闽粤栲(*Castanopsis fissa*)、罗浮栲(*Castanopsis fabri*)等,林下植被有油草(*Leptochloa chinensis*)、狗脊蕨(*Woodwardia japonica*)等。另一部分经皆伐、炼山后营造马尾松和杉木人工林,林下植被有芒萁(*Dicranopteris dichotoma*)、狗骨柴(*Tricalysia dubia*)、毛冬青(*Ilex pubescens*)、芒(*Miscanthus sinensis*)和蕨等草本植物(表1)。

### 1.2 样品采集与处理

本研究选取米槠次生林、马尾松人工林和杉木人工林3种森林类型,每种森林各设置3个20 m × 20 m样地,每个样地间距约800 m,且坡向、坡度和郁闭度相似<sup>[15]</sup>。每个样地内均随机布置5个0.7 m × 0.7 m凋落物收集框(孔径为1 mm,距离地面0.5 m),每月(雨季每半月收集,防止淋溶流失)收集并筛选出目标树种(米槠、马尾松、杉木)新鲜凋落叶和凋落枝,共连续收集12个月,带回实验室于80 °C烘干至恒重,计算凋落叶和凋落枝干重。将烘干的凋落叶和凋落枝样品研磨过筛,测定C、N含量。

### 1.3 样品分析

称取凋落叶干样品8-10 mg和凋落枝干样品10-12 mg,每个样品取3个重复。再称取2.5 mg乙酰苯胺(acetanilide)作为

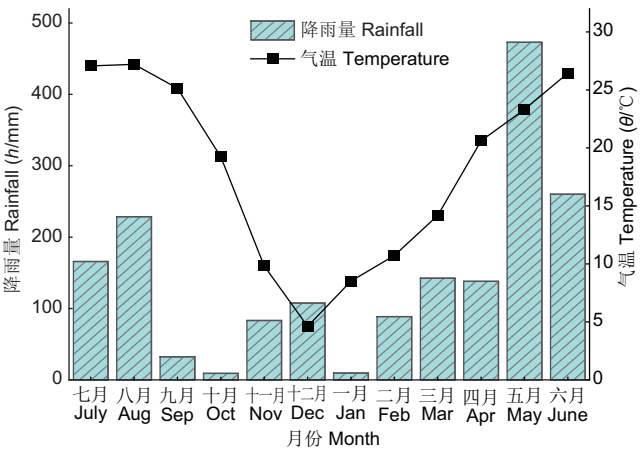


图1 研究样地逐月降水量和空气温度  
Fig. 1 Monthly precipitation and temperature at the sampling site

表1 研究样地的基本特征

| 参数<br>Parameter                            | 森林类型 Forest type                  |                                |                                      |
|--------------------------------------------|-----------------------------------|--------------------------------|--------------------------------------|
|                                            | 米槠<br><i>Castanopsis carlesii</i> | 马尾松<br><i>Pinus massoniana</i> | 杉木<br><i>Cunninghamia lanceolata</i> |
| 海拔 Altitude (h/m)                          | 330                               | 313                            | 301                                  |
| 坡度 Gradient (a/°)                          | 40                                | 38                             | 30                                   |
| 林龄 Stand age (t/a)                         | 45                                | 46                             | 46                                   |
| 平均树高<br>Mean tree height (h/m)             | 10.8                              | 18.3                           | 18.2                                 |
| 平均胸径<br>Mean DBH (d/cm)                    | 12.2                              | 18.3                           | 15.6                                 |
| 林分密度<br>Stand density (n/hm <sup>2</sup> ) | 3788                              | 1500                           | 2858                                 |

DBH: 树木胸径.  
DBH: Diameter at breast height.

标样, 使用Vario EL III 元素分析仪 (Elementar, 德国) 测定样品的C、N含量, 计算C/N比和归还量.

1.4 数据处理与统计分析

使用双因素方差分析检验树种和凋落物类型对凋落物产量、C/N值和C、N含量及归还量的影响; 使用独立样本t检验比较年凋落量和C、N含量及C/N值在凋落叶和凋落枝之

间的差异显著性; 使用单因素方差分析及最小显著性差异法 (least significant difference, LSD) 对同一月份不同树种的C、N含量及C/N值进行事后检验, 对不同树种之间的凋落叶和凋落枝年凋落量、C和N含量及C/N值进行多重比较, 显著性水平设为 $P = 0.05$ . 以上数据分析在SPSS 21.0软件中进行.

2 结果与分析

2.1 凋落叶和凋落枝产量动态变化

凋落物类型对凋落叶和凋落枝产量具有显著影响 ( $P < 0.05$ , 表2). 米槠凋落叶和凋落枝产量高峰分别出现在4月和8月, 马尾松凋落叶和凋落枝产量高峰分别出现在11-12月和6-9月, 杉木凋落叶和凋落枝产量高峰分别出现在4月和9月 (图2). 3个树种凋落叶产量变化范围为11.4-2 259 kg/hm<sup>2</sup>, 凋落枝产量变化范围为0-454 kg/hm<sup>2</sup>. 米槠、马尾松、杉木凋落叶年凋落量分别为3 613、3 054和2 587 kg/hm<sup>2</sup>, 凋落枝年凋落量分别为881、2 135和1 228 kg/hm<sup>2</sup>, 米槠凋落叶年凋落量高于马尾松和杉木 (图3).

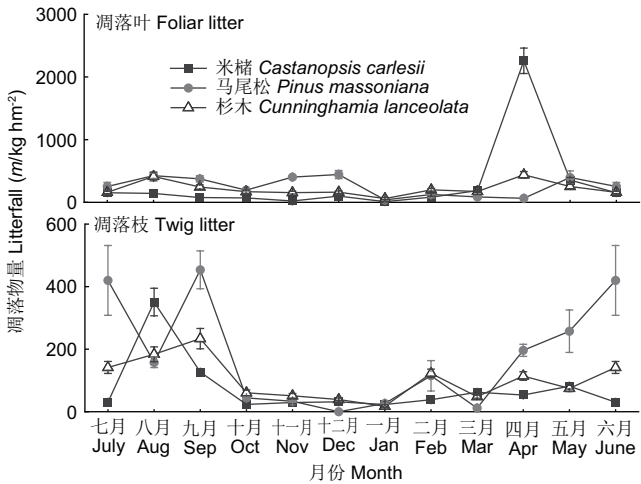


图2 米槠、马尾松、杉木凋落叶和凋落枝产量月动态. 数值为平均值±标准误差 (N = 3).

Fig. 2 The monthly dynamics of foliar and twig litterfall of *Castanopsis carlesii*, *Pinus massoniana* and *Cunninghamia lanceolata*. Values are mean ± standard errors (N = 3).

表2 树种和凋落物类型对凋落物产量、C/N值和C、N含量及归还量的双因素方差分析

Table 2 Two-way ANOVA analysis testing for the effects of tree species and litter types on the concentrations and return of carbon and nitrogen, the ratio of carbon to nitrogen and litterfall

| 变量 Variable                         | 变异来源 Source of variation            | 自由度 d <sub>f</sub> | F       | P       |
|-------------------------------------|-------------------------------------|--------------------|---------|---------|
| 碳含量 Carbon concentration            | 树种 Tree species                     | 2                  | 6.373   | < 0.010 |
|                                     | 凋落物类型 Litter type                   | 1                  | 25.099  | < 0.001 |
|                                     | 树种×凋落物类型 Tree species × Litter type | 2                  | 2.352   | 0.104   |
| 氮含量 Nitrogen concentration          | 树种 Tree species                     | 2                  | 172.486 | < 0.001 |
|                                     | 凋落物类型 Litter type                   | 1                  | 224.555 | < 0.001 |
|                                     | 树种×凋落物类型 Tree species × Litter type | 2                  | 12.524  | < 0.001 |
| 碳氮比 The ratio of carbon to nitrogen | 树种 Tree species                     | 2                  | 119.987 | < 0.001 |
|                                     | 凋落物类型 Litter type                   | 1                  | 195.248 | < 0.001 |
|                                     | 树种×凋落物类型 Tree species × Litter type | 2                  | 25.071  | < 0.001 |
| 凋落物产量 Litterfall                    | 树种 Tree species                     | 2                  | 0.254   | 0.777   |
|                                     | 凋落物类型 Litter type                   | 1                  | 4.490   | < 0.050 |
|                                     | 树种×凋落物类型 Tree species × Litter type | 2                  | 0.480   | 0.621   |
| 碳归还量 Carbon return                  | 树种 Tree species                     | 2                  | 4.375   | < 0.050 |
|                                     | 凋落物类型 Litter type                   | 1                  | 6.988   | < 0.050 |
|                                     | 树种×凋落物类型 Tree species × Litter type | 2                  | 0.431   | 0.652   |
| 氮归还量 Nitrogen return                | 树种 Tree species                     | 2                  | 1.297   | 0.281   |
|                                     | 凋落物类型 Litter type                   | 1                  | 25.116  | < 0.001 |
|                                     | 树种×凋落物类型 Tree species × Litter type | 2                  | 0.412   | 0.664   |



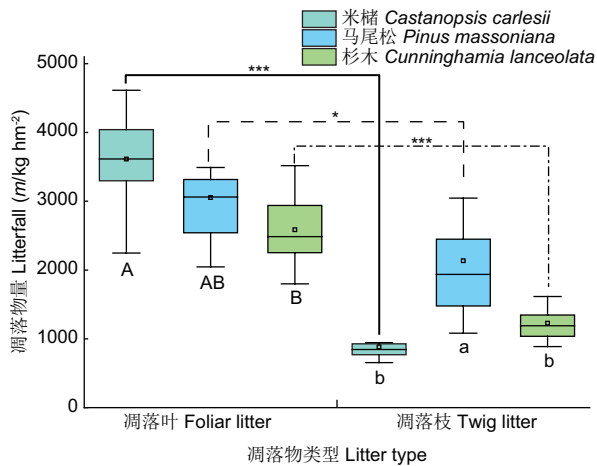


图3 米槠、马尾松、杉木凋落叶和凋落枝年凋落物量。数值为平均值±标准误差 ( $N = 3$ )。星号表示同一树种的凋落叶与凋落枝之间差异显著 (\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ )。不同大写字母和小写字母分别表示凋落叶、凋落枝年凋落量在不同树种之间差异显著 ( $P < 0.05$ )。

Fig. 3 Annual litterfall of foliar and twig litter of *Castanopsis carlesii*, *Pinus massoniana*, and *Cunninghamia lanceolata*. Values are mean  $\pm$  standard errors ( $N = 3$ ). Asterisks denote significant differences between foliar and twig litters for the same tree species (\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ). Different uppercase and lowercase letters denote significant ( $P < 0.05$ ) differences in annual litterfall among tree species for foliar and twig litters, respectively.

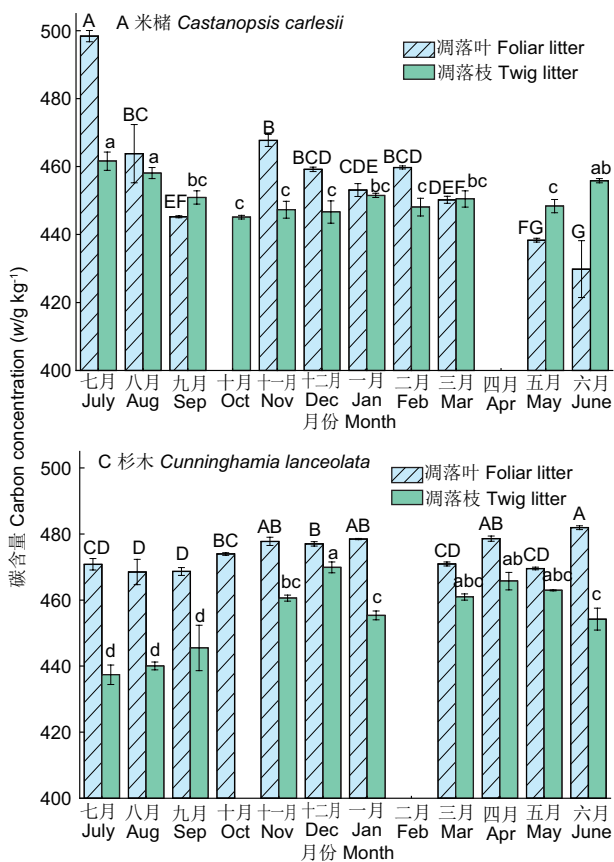


图4 米槠、马尾松、杉木凋落叶和凋落枝C含量 (A, B, C) 及其在不同树种和凋落物类型之间的差异 (D)。数值为平均值±标准误差 ( $N = 3$ )。星号表示凋落叶与凋落枝之间差异显著 (\*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ )。不同大写字母和小写字母分别表示凋落叶、凋落枝C含量在不同月份或不同树种之间差异显著 ( $P < 0.05$ )。

Fig. 4 Carbon concentrations in foliar and twig litters of *Castanopsis carlesii*, *Pinus massoniana*, and *Cunninghamia lanceolata* (A, B, C), and difference among tree species and litter types (D). Values are mean  $\pm$  standard errors ( $N = 3$ ). Asterisks denote significant differences between foliar and twig litters for the same tree species (\*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ). Different uppercase and lowercase letters denote significant ( $P < 0.05$ ) differences in carbon concentration among month/tree species for foliar and twig litters, respectively.

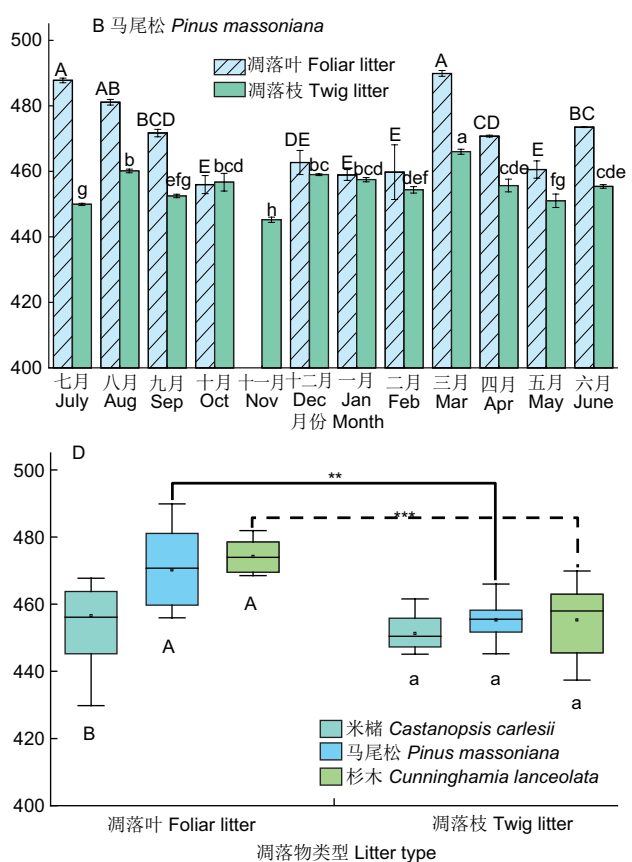
## 2.2 凋落叶和凋落枝C含量及归还量

树种、凋落物类型对凋落叶和凋落枝C含量均具有显著影响 ( $P < 0.01$ , 表2)。3个树种凋落叶和凋落枝C含量在不同月份之间均具有显著差异 ( $P < 0.01$ ) (图4)。米槠凋落叶和凋落枝C含量高峰均出现在7月 (图4A), 马尾松凋落叶和凋落枝C含量高峰均出现在3月 (图4B), 杉木凋落叶和凋落枝C含量高峰分别出现在6月和12月 (图4C)。3个树种凋落叶C含量变化范围为430-498 g/kg, 凋落枝C含量变化范围为437-470 g/kg, 米槠凋落叶和凋落枝C含量低于马尾松和杉木 (图4D)。

树种、凋落物类型对凋落叶和凋落枝C归还量均具有显著影响 ( $P < 0.05$ , 表2)。米槠凋落叶和凋落枝C归还量高峰分别出现在5月和8月, 马尾松凋落叶和凋落枝C归还量高峰分别出现在8月和9月, 杉木凋落叶和凋落枝C归还量高峰分别出现在4月和9月 (图5)。3个树种凋落叶C归还量变化范围为5.18-210 kg/hm<sup>2</sup>, 凋落枝C归还量变化范围为0-205 kg/hm<sup>2</sup>。

## 2.3 凋落叶和凋落枝N含量及归还量

树种、凋落物类型及其交互作用对凋落叶和凋落枝N含量均具有显著影响 ( $P < 0.001$ , 表2)。3个树种凋落叶和凋落枝N含量在不同月份之间均具有显著差异 ( $P < 0.01$ ) (图6)。米槠凋落叶和凋落枝N含量高峰分别出现在7月和6月 (图6A), 马尾松凋落叶和凋落枝N含量高峰分别出现在6月和3月



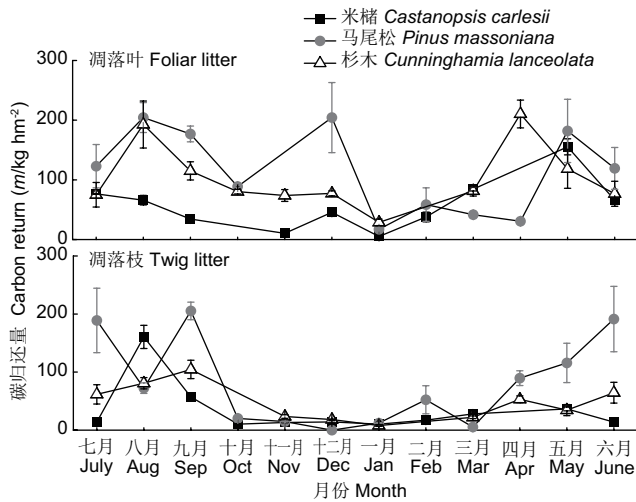


图5 米槠、马尾松、杉木凋落叶和凋落枝C归还量的月动态. 数值为平均值±标准误 ( $N=3$ ).

Fig. 5 Monthly dynamics of carbon return from foliar and twig litters of *Castanopsis carlesii*, *Pinus massoniana*, and *Cunninghamia lanceolata*. Values are mean  $\pm$  standard errors ( $N=3$ ).

(图6B), 杉木凋落叶和凋落枝N含量高峰分别出现在9月和8月(图6C). 3个树种凋落叶N含量变化范围为4.94-14.2 g/kg, 凋落枝N含量变化范围为3.06-9.37 g/kg, 米槠凋落叶和凋落枝N含量高于马尾松和杉木(图6D).

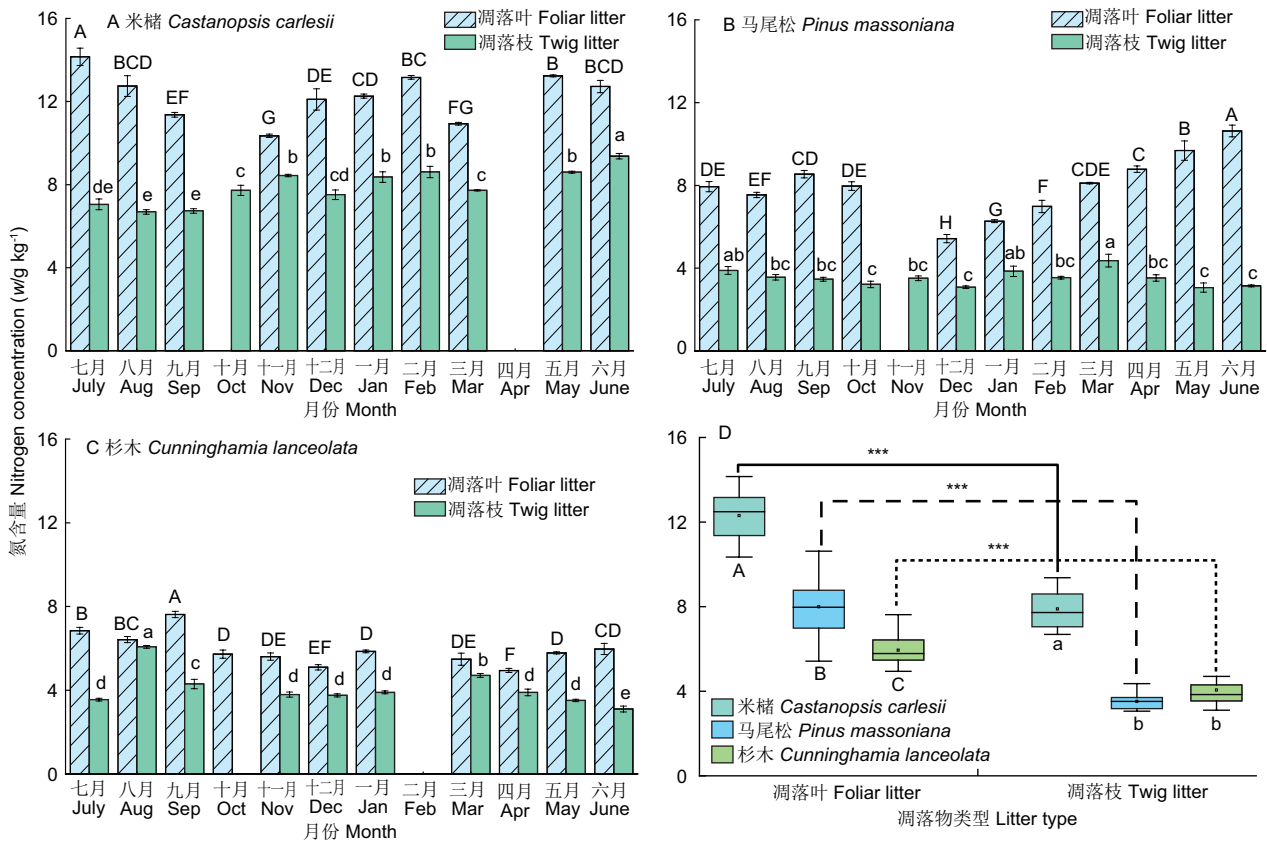


图6 米槠、马尾松、杉木凋落叶和凋落枝N含量(A, B, C)及其在不同树种和凋落物类型之间的差异(D). 数值为平均值±标准误 ( $N=3$ ). 星号表示凋落叶与凋落枝之间差异显著 (\*\*\*) ( $P < 0.001$ ). 不同大写字母和小写字母分别表示凋落叶、凋落枝N含量在不同月份或不同树种之间差异显著 ( $P < 0.05$ ).

Fig. 6 Nitrogen concentrations in foliar and twig litter of *Castanopsis carlesii*, *Pinus massoniana*, and *Cunninghamia lanceolata* (A, B, C), and difference among different tree species and litter types (D). Values are mean  $\pm$  standard errors ( $N=3$ ). Asterisks denote significant differences between foliar and twig litters for the same tree species (\*\*\*) ( $P < 0.001$ ). Different uppercase and lowercase letters denote significant ( $P < 0.05$ ) differences in nitrogen concentration among months/tree species for foliar and twig litters, respectively.

凋落物类型对凋落叶和凋落枝N归还量具有显著影响 ( $P < 0.001$ , 表2). 米槠凋落叶和凋落枝N归还量高峰分别出现在5月和8月, 马尾松凋落叶和凋落枝N归还量高峰分别出现在5月和7月, 杉木凋落叶和凋落枝N归还量高峰均出现在8月(图7). 3个树种凋落叶N归还量变化范围为0.14-4.69 kg/hm<sup>2</sup>, 凋落枝N归还量变化范围为0-2.34 kg/hm<sup>2</sup>.

## 2.4 凋落叶和凋落枝C/N比

树种、凋落物类型及其交互作用对凋落叶和凋落枝C/N值均具有显著影响 ( $P < 0.001$ , 表2). 3个树种凋落叶和凋落枝C/N值在不同月份之间均具有显著差异 ( $P < 0.01$ ) (图8). 米槠凋落叶和凋落枝C/N值高峰分别出现在11月和8月(图8A), 马尾松凋落叶和凋落枝C/N值高峰均出现在12月(图8B), 杉木凋落叶和凋落枝C/N值高峰分别出现在4月和6月(图8C). 3个树种凋落叶C/N值变化范围为33.1-97.0, 凋落枝C/N值变化范围为48.7-149, 米槠凋落叶和凋落枝C/N值低于马尾松和杉木(图8D).

## 3 讨论

不同树种凋落物产量季节动态存在很大差异. 米槠、杉木凋落叶和凋落枝产量在4月和8、9月达到高峰, 马尾松凋落枝产量在9月也出现高峰, 这可能是由于植物生理和气候因素的综合影响<sup>[22]</sup>. 本研究区降水主要集中在3-8月, 雨季初期(3-4

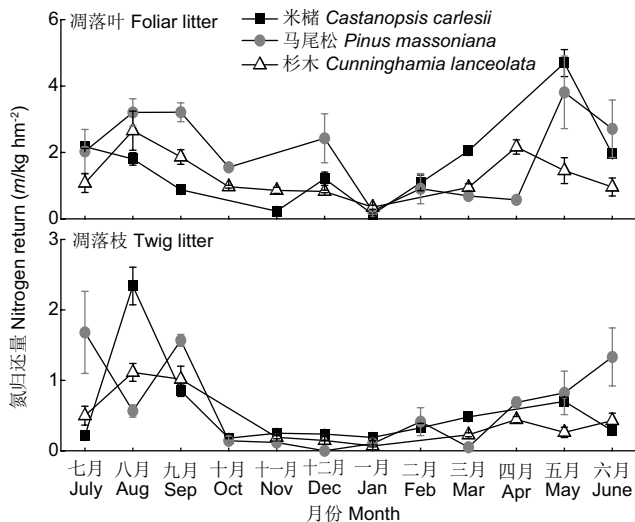


图7 米槠、马尾松、杉木凋落叶和凋落枝N归还量月动态。数值为平均值±标准误 (N=3)。

Fig. 7 Monthly dynamics of nitrogen returns from foliar and twig litters of *Castanopsis carlesii*, *Pinus massoniana*, and *Cunninghamia lanceolata*. Values are mean  $\pm$  standard errors (N = 3).

月)温度升高且降雨增加,米槠进入生长期开始集中换叶,此时米槠凋落叶产量较高;而雨季末期(8月)气温降低且降雨减少,树种生长期即将结束,大量衰老叶片脱落,此时马尾松

和杉木凋落叶、凋落枝产量较高。前期长达10年(2010-2019年)的凋落物产量监测表明,米槠凋落叶和凋落枝年平均产量高于马尾松、杉木<sup>[15]</sup>。而本研究监测持续12个月,发现米槠凋落叶产量高于马尾松、杉木,而凋落枝产量低于马尾松、杉木。这可能是凋落物产量年际动态差异所致,长期来看,米槠凋落叶和凋落枝产量高于马尾松、杉木。

凋落叶和凋落枝C、N含量及C/N值在不同月份之间差异显著,这是由于米槠、马尾松和杉木在习性、物候等存在种间差异。凋落叶和凋落枝C、N含量总体上在3月和6-7月较高,而在10-12月和4-5月较低,这可能与植物叶片养分重吸收有关。研究发现,夏季温度与植物叶片N重吸收效率呈显著负相关性<sup>[23]</sup>。本研究区夏季(6-8月)气温较高,植物叶片N重吸收效率较低,大量养分留存在衰老叶片中,此时凋落叶N含量较高;春季(3-5月)气温上升,树木萌发新叶,大量衰老叶片在脱落前把养分转移给新叶生长,而秋季(9-11月)气温下降,部分衰老叶片脱落,一些养分被重吸收并储存在新叶中,此时凋落叶N含量较低<sup>[19]</sup>。不同树种凋落物C、N含量及C/N值差异显著。本研究中,马尾松和杉木凋落叶和凋落枝C含量以及C/N值均高于米槠,但N含量低于米槠。研究发现,针叶树种的C含量高于阔叶树种,N含量低于阔叶树种<sup>[24-25]</sup>。由于不同树种的生物学特性不同,马尾松比大多数树种更耐瘠薄<sup>[26]</sup>,为了减少养分流失,马尾松叶和枝在凋落之前进行养分转移和重吸收<sup>[27]</sup>,杉木也可通过养分重吸收在其叶和枝枯死前转移养分

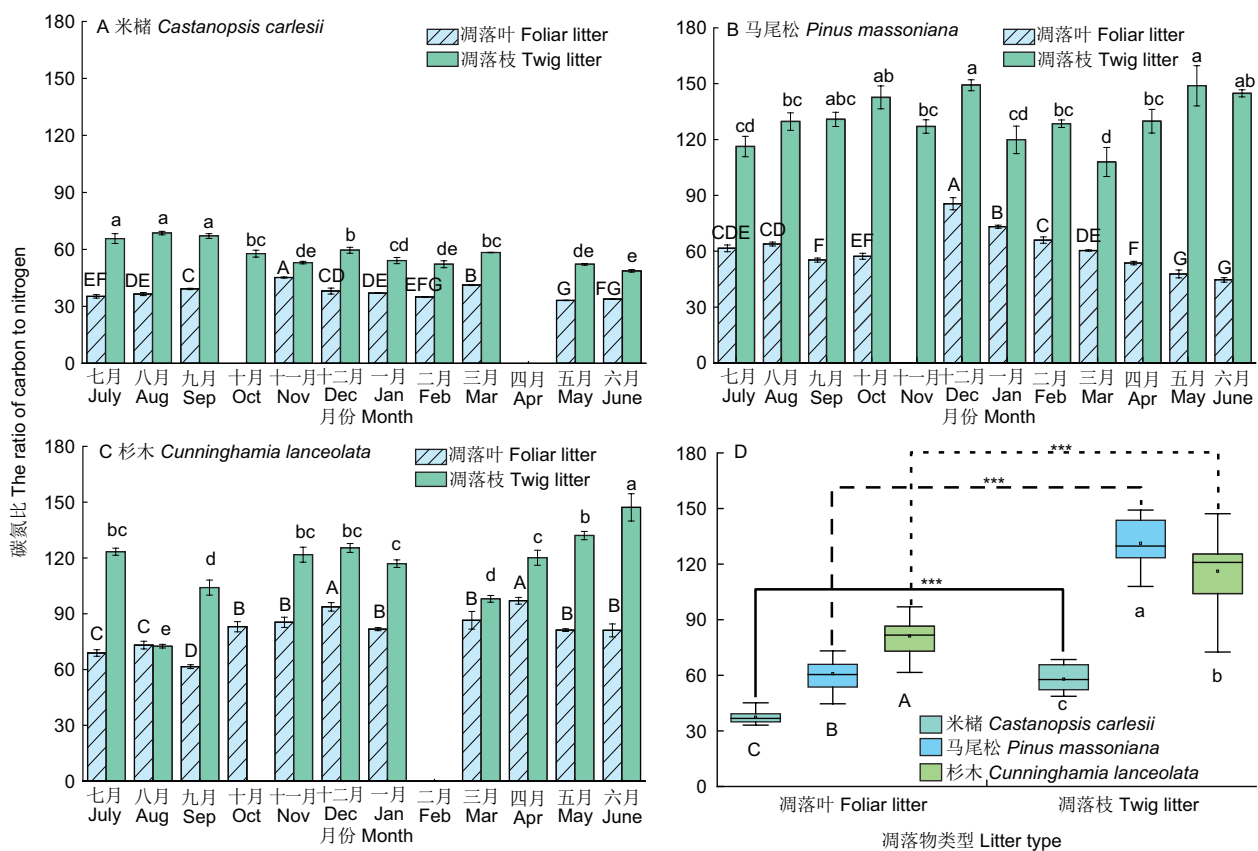


图8 米槠、马尾松、杉木凋落叶和凋落枝C/N值(A, B, C)及其在不同树种和凋落物类型之间的差异(D)。数值为平均值±标准误 (N=3)。星号表示凋落叶与凋落枝之间差异显著 (\*\*\*)  $P < 0.001$ 。不同大写字母和小写字母分别表示凋落叶、凋落枝C/N值在不同月份或不同树种之间差异显著 ( $P < 0.05$ )。

Fig. 8 The ratio of carbon to nitrogen in foliar and twig litter of *Castanopsis carlesii*, *Pinus massoniana*, and *Cunninghamia lanceolata* (A, B, C), and difference in among different tree species and litter types (D). Values are mean  $\pm$  standard errors (N = 3). Asterisks denote significant differences between foliar and twig litters for the same tree species (\*\*\*)  $P < 0.001$ . Different uppercase and lowercase letters denote significant ( $P < 0.05$ ) differences in the ratio of carbon to nitrogen among month/tree species for foliar and twig litters, respectively.



至新鲜叶片<sup>[28]</sup>。已有研究表明,养分重吸收效率与叶面积、比叶面积呈显著负相关,针叶树种比阔叶树种的养分重吸收率更高<sup>[29]</sup>。植物叶片寿命、衰老持续时间越长,从衰老叶中转移的养分就越多<sup>[30]</sup>。杉木叶和枝枯死后,宿存在树干上的时间较长,其养分重吸收效率较高<sup>[31]</sup>。这可能使马尾松、杉木凋落叶和凋落枝N含量普遍低于米楮,导致人工林凋落物的养分输入减少。

凋落物C、N归还量主要受凋落物产量、C和N含量的影响,而归还的C和养分通过分解进入碎屑食物网和微生物网络,这对于土壤有机质形成和养分周转至关重要<sup>[18, 32]</sup>。凋落物量、C/N比等指标会影响凋落物分解和养分归还,C/N值反映凋落物基质质量并影响凋落物分解进程,通常C/N值较低的凋落物分解较快<sup>[33]</sup>。研究发现,N含量较低会限制微生物生长,不利于凋落物分解<sup>[34-35]</sup>。亚热带地区的降水主要集中在3-8月,淋溶对春夏凋落物分解贡献很大,使其快速分解释放养分<sup>[36]</sup>。本研究中,马尾松、杉木人工林改变了凋落物产量的季节动态,其凋落物产量在8-9月出现峰值,此时温湿度条件相对较差,淋溶对凋落物分解的作用不明显<sup>[37]</sup>,较低的N含量以及较高的C/N值,其分解速率较慢,从凋落物中分解释放的养分减少。

## 4 结论

米楮、马尾松、杉木凋落叶和凋落枝产量、C和N含量及归还量均具有明显的季节动态变化。同一树种凋落叶产量和C、N含量高于凋落枝,而C/N值低于凋落枝。米楮凋落叶产量高于马尾松和杉木,但C含量较低、N含量较高。凋落叶和凋落枝C、N归还量由于受凋落物产量和C、N含量的影响,总体来看,马尾松、杉木凋落叶和凋落枝C、N归还量低于米楮。综上所述,亚热带地带性常绿阔叶林转换为马尾松、杉木人工林后,凋落叶和凋落枝C、N含量和归还量的动态规律发生了显著改变,C含量和C/N值增加,而N含量降低。同时,马尾松、杉木凋落叶和凋落枝较低的C、N归还量导致从地上凋落物输入的C和养分减少,这可能是亚热带马尾松和杉木人工林土壤肥力下降的重要原因。本研究从凋落物中养分归还的角度为亚热带马尾松和杉木人工林土壤肥力衰退机制提供了一定的理论依据。由于本研究未开展凋落物分解实验,仅测定了1年的凋落叶和凋落枝C、N含量,尚难精确计算3个树种凋落叶和凋落枝C、N归还后实际分解了多少进入土壤,准确量化不同树种凋落物C和养分归还及分解过程对于深入认识亚热带马尾松和杉木人工林土壤肥力提升机制具有重要意义。

## 参考文献 [References]

- Yang YS, Wang LX, Yang ZJ, Xu C, Xie JS, Chen GS, Lin CF, Guo JF, Liu XF, Xiong DC, Lin WS, Chen SD, He ZM, Lin KM, Jiang MH, Lin TC. Large ecosystem service benefits of assisted natural regeneration [J]. *J Geophys Res: Biogeosci*, 2018, **123** (2): 676-687
- 国家林业和草原局. 中国森林资源报告2014-2018 [M]. 北京: 中国林业出版社, 2019 [National Forestry and Grassland Administration. China Forest Resources Report 2014-2018 [M]. Beijing: China Forestry Publishing House, 2019]
- 杨玉盛, 俞新妥, 邱仁辉, 傅瑞树, 陈光水. 不同栽杉代数根际土壤肥力及生物学特性变化[J]. 应用与环境生物学报, 1999, **5** (3): 254-258 [Yang YS, Yu XT, Qiu RH, Fu RS, Chen GS. Variation of rhizospheric soil fertility under different Chinese fir rotations [J]. *Chin J Appl Environ Biol*, 1999, **5** (3): 254-258]
- 夏丽丹, 于姣姣, 邓玲玲, 李小艳, 周垂帆, 徐永兴. 杉木人工林地力衰退研究进展[J]. 世界林业研究, 2018, **31** (2): 37-42 [Xia LD, Yu JD, Deng LL, Li XY, Zhou CF, Xu YX. Researches on soil decline of Chinese fir plantation [J]. *World For Res*, 2018, **31** (2): 37-42]
- Lladó S, López-Mondéjar R, Baldrian P. Drivers of microbial community structure in forest soils [J]. *Appl Microbiol Biotechnol*, 2018, **102** (10): 4331-4338
- Lladó S, López-Mondéjar R, Baldrian P. Forest soil bacteria: diversity, involvement in ecosystem processes, and response to global change [J]. *Microbiol Mol Biol Rev*, 2017, **81** (2): e00063-16
- Liao JH, Wang HH, Tsai CC, Hseu ZY. Litter production, decomposition and nutrient return of uplifted coral reef tropical forest [J]. *For Ecol Manag*, 2006, **235** (1): 174-185
- 林波, 刘庆, 吴彦, 何海. 森林凋落物研究进展[J]. 生态学报, 2004, **23** (1): 60-64 [Lin B, Liu Q, Wu Y, He H. Advances in the studies of forest litter [J]. *Chin J Ecol*, 2004, **23** (1): 60-64]
- Li HL, Crabbe MJC, Xu FL, Wang WL, Niu RL, Gao X, Zhang P, Chen HK. Seasonal variations in carbon, nitrogen and phosphorus concentrations and C:N:P stoichiometry in the leaves of differently aged *Larix principis-rupprechtii* Mayr. plantations [J]. *Forests*, 2017, **8** (10): 373-373
- Bai SH, Dempsey R, Reverchon F, Blumfield TJ, Ryan S, Cernusak LA. Effects of forest thinning on soil-plant carbon and nitrogen dynamics [J]. *Plant Soil*, 2017, **411** (1-2): 437-449
- Reich PB, Tjoelker MG, Machado JL, Oleksyn J. Universal scaling of respiratory metabolism, size and nitrogen in plants [J]. *Nature*, 2006, **439** (7075): 457-461
- 张萍, 章广琦, 赵一娉, 彭守璋, 陈云明, 曹扬. 黄土丘陵区不同森林类型叶片-凋落物-土壤生态化学计量特征[J]. 生态学报, 2018, **38** (14): 5087-5098 [Zhang P, Zhang GQ, Zhao YP, Peng SZ, Chen YM, Cao Y. Ecological stoichiometry characteristics of leaf-litter-soil interactions in different forest types in the Loess hilly-gully region of China [J]. *Acta Ecol Sin*, 2018, **38** (14): 5087-5098]
- Sun X, Shen Y, Schuster MJ, Searle EB, Chen JH, Yang GW, Zhang YJ. Initial responses of grass litter tissue chemistry and N:P stoichiometry to varied N and P input rates and ratios in Inner Mongolia [J]. *Agric Ecosyst Environ*, 2018, **252** (1): 114-125
- 聂阳意, 陈坦, 吕茂奎, 张康靖, 曾敏, 邓翠, 任寅榜, 谢锦升. 植被恢复过程中芒萁覆盖对侵蚀红壤氮组分的影响[J]. 生态学报, 2018, **38** (19): 6964-6971 [Nie YY, Chen T, Lü MK, Zhang KJ, Zeng M, Deng C, Ren YB, Xie JS. Effects of *Dicranopteris dichotoma* coverage on nitrogen components during the vegetation restoration process in eroded red soil [J]. *Acta Ecol Sin*, 2018, **38** (19): 6964-6971]
- Ni XY, Lin CF, Chen GS, Xie JS, Yang ZJ, Liu XF, Xiong DC, Xu C, Yue K, Wu FZ, Yang YS. Decline in nutrient inputs from litterfall following forest plantation in subtropical China [J]. *For Ecol Manag*, 2021, **496** (1): 119445
- 向云西, 陈胜魁, 潘萍, 欧阳勋志, 宁金魁, 李琦. 马尾松叶片-凋落物-土壤的碳氮磷化学计量特征[J]. 森林与环境学报, 2019, **39** (2):

- 120-126 [Xiang YX, Chen SK, Pan P, Ouyang XZ, Ning JK, Li Q. Stoichiometric traits of C, N and P of leaf-litter-soil system of *Pinus massoniana* forest [J]. *J For Environ*, 2019, **39** (2): 120-126]
- 17 邹秉章. 亚热带主要森林类型凋落物量和土壤养分的关系[J]. 福建林业科技, 2019, **46** (3): 8-12 [Zou BZ. Relationship between litterfall production and soil nutrients in main subtropical forest types [J]. *J Fujian For Sci Technol*, 2019, **46** (3): 8-12]
- 18 Cotrufo MF, Soong JL, Horton AJ, Campbell EE, Haddix ML, Wall DH, Parton WJ. Formation of soil organic matter via biochemical and physical pathways of litter mass loss [J]. *Nat Geosci*, 2015, **8** (10): 776-779
- 19 蒲悦, 毛绘友, 刘群, 庄丽燕, 杨开军, 徐振锋. 四川盆地西缘峨眉含笑-喜树混交林凋落物量及碳氮磷动态特征[J]. 应用与环境生物学报, 2019, **25** (2): 262-267 [Pu Y, Mao HY, Liu Q, Zhuang LY, Yang KJ, Xu ZF. Dynamic characteristics of C, N, and P and leaf litterfall in a *Michelia wilsonii* and *Camptotheca acuminata* mixed forest on the western edge of the Sichuan Basin [J]. *Chin J Appl Environ Biol*, 2019, **25** (2): 262-267]
- 20 蒋龙, 徐振锋, 吴福忠, 谭波, 游成铭, 李汉森, 刘一霖, 彭永翔, 曾合州, 杨万勤. 亚热带3种典型常绿森林土壤和植物叶片碳氮磷化学计量特征[J]. 应用与环境生物学报, 2019, **25** (4): 759-767 [Jiang L, Xu ZF, Wu FZ, Tan B, You CM, Li HS, Liu YL, Peng YX, Zeng HZ, Yang WQ. Stoichiometric characteristics of C, N, and P in soil and plant leaves in three typical evergreen forest types in subtropical zone [J]. *Chin J Appl Environ Biol*, 2019, **25** (4): 759-767]
- 21 Miao RH, Ma J, Liu YZ, Liu YC, Yang ZL, Guo MX. Variability of aboveground litter inputs alters soil carbon and nitrogen in a coniferous-broadleaf mixed forest of central China [J]. *Forests*, 2019, **10** (2): 188
- 22 官丽莉, 周国逸, 张德强, 刘菊秀, 张倩媚. 鼎湖山亚热带常绿阔叶林凋落物量20年动态研究[J]. 植物生态学报, 2004, **28** (4): 449-456 [Guan LL, Zhou GY, Zhang DQ, Liu JX, Zhang QM. Twenty years of litter fall dynamics in subtropical evergreen broad-leaved forests at the Dinghushan forest ecosystem research station [J]. *Chin J Plant Ecol*, 2004, **28** (4): 449-456]
- 23 Nordell KO, Karlsson PS. Resorption of nitrogen and dry matter prior to leaf abscission: variation among individuals, sites and years in the *Mountain birch* [J]. *Funct Ecol*, 1995, **9** (2): 326-333
- 24 Aerts R, Chapin FS III. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns [J]. *Adv Ecol Res*, 1999, **30** (1): 1-67
- 25 Liu CJ, Berg B, Kutsch W, Westman CJ, Ilvesniemi H, Shen XH, Shen GR, Chen XB. Leaf litter nitrogen concentration as related to climatic factors in Eurasian forests [J]. *Glob Ecol Biogeogr*, 2006, **15** (5): 438-444
- 26 Pan P, Zhao F, Ning JK, Zhang L, Ouyang XZ, Zang H. Impact of understory vegetation on soil carbon and nitrogen dynamic in aerially seeded *Pinus massoniana* plantations [J]. *PLoS ONE*, 2018, **13** (1): e0191952
- 27 张秋芳, 谢锦升, 陈奶寿, 陈坦, 吕茂奎, 张浩, 杨玉盛. 生态恢复对马尾松叶片化学计量及氮磷转移的影响[J]. 生态学报, 2017, **37** (1): 267-276 [Zhang QF, Xie JS, Chen NS, Chen T, Lü MK, Zhang H, Yang YS. Effects of ecological restoration on stoichiometric characteristics and nutrient resorption efficiency of *Pinus massoniana* foliage [J]. *Acta Ecol Sin*, 2017, **37** (1): 267-276]
- 28 吕中诚, 康文星, 黄志宏, 赵仲辉, 邓湘雯. 不同林龄杉木组织迁移养分的再利用[J]. 植物生态学报, 2019, **43** (5): 458-470 [Lü ZC, Kang WX, Huang ZH, Zhao ZH, Deng XW. Reuse of retranslocated nutrients in tissues of *Chinese fir* in plantations of different ages [J]. *Chin J Plant Ecol*, 2019, **43** (5): 458-470]
- 29 周丽丽, 钱瑞玲, 李树斌, 董博微, 陈宝英, 潘辉. 滨海沙地主要造林树种叶片功能性状及养分重吸收特征[J]. 应用生态学报, 2019, **30** (7): 2320-2328 [Zhou LL, Qian RL, Li SB, Dong BW, Chen BY, Pan H. Leaf functional traits and nutrient resorption among major silviculture tree species in coastal sandy site [J]. *J Appl Ecol*, 2019, **30** (7): 2320-2328]
- 30 Kimmins JP. Evaluation of the consequences for future tree productivity of the loss of nutrients in whole-tree harvesting [J]. *For Ecol Manage*, 1976, **1** (1): 169-183
- 31 张家城, 盛炜彤. 杉木人工林树上宿存枯死枝、叶在冠层与在枯枝落叶层分解的比较研究[J]. 林业科学, 2001, **37** (6): 2-10 [Zhang JC, Sheng WT. The study on decay of dead branches and leaves on living trees taken from crown into litter environment in a *Chinese fir* plantation, compared with decay in canopy [J]. *Sci Silva Sin*, 2001, **37** (6): 2-10]
- 32 Du NN, Li WR, Qiu LP, Zhang YJ, Wei XR, Zhang XC. Mass loss and nutrient release during the decomposition of sixteen types of plant litter with contrasting quality under three precipitation regimes [J]. *Ecol Evol*, 2020, **10** (7): 3367-3382
- 33 Cepáková Š, Frouz J. Changes in chemical composition of litter during decomposition: a review of published <sup>13</sup>C NMR spectra [J]. *J Soil Sci Plant Nutr*, 2015, **15** (3): 805-815
- 34 Adair EC, Parton WJ, Del grosso SJ, Silver WL, Harmon ME, Hall SA, Burke IC, Hart SC. Simple three-pool model accurately describes patterns of long-term litter decomposition in diverse climates [J]. *Glob Chang Biol*, 2008, **14** (11): 2636-2660
- 35 Taylor BR, Parsons WFJ, Parkinson D. Decomposition of *Populustremuloides* leaf litter accelerated by addition of *Alnuscrispa* litter [J]. *Can J For Res*, 1989, **19** (5): 674-679
- 36 Campbell EE, Parton WJ, Soong JL, Paustian K, Hobbs NT, Cotrufo MF. Using litter chemistry controls on microbial processes to partition litter carbon fluxes with the litter decomposition and leaching (LIDEL) model [J]. *Soil Biol Biochem*, 2016, **100** (1): 160-174
- 37 Zhang HC, Yuan WP, Dong WJ, Liu SG. Seasonal patterns of litterfall in forest ecosystem worldwide [J]. *Ecol Complex*, 2014, **20** (1): 240-247