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Citation for published version:
Zhou, L, Li, S, Jia, Y, Heal, KV, He, Z, Wu, P & Ma, X 2020, 'Spatiotemporal distribution of canopy litter and nutrient resorption in a chronosequence of different development stages of Cunninghamia lanceolata in southeast China', *Science of the Total Environment*, vol. 762, 143153.
https://doi.org/10.1016/j.scitotenv.2020.143153

Digital Object Identifier (DOI):
10.1016/j.scitotenv.2020.143153

Document Version:
Peer reviewed version

Published In:
Science of the Total Environment

Spatiotemporal distribution of canopy litter and nutrient resorption in a chronosequence of different development stages of *Cunninghamia lanceolata* in southeast China

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Running title: Canopy litter and nutrient retranslocation in Chinese fir plantations

Abstract

Canopy litter is an important component of coarse woody debris (CWD), which affects nutrient and carbon cycling in forest ecosystems. For marcescent plant species (characterized by dead branches and leaves remaining in the canopy for several years before abscission), nutrient resorption from senescing leaves is an important nutrient conservation strategy. However, investigating the ecological function of canopy litter is challenging due to its limited accessibility and also the heterogeneous canopy microclimate in terms of light transmission, temperature and moisture. We studied the spatiotemporal distribution of canopy litter mass and seasonal dynamics of leaf nutrients and nutrient resorption during senescence in the canopy along a chronosequence of Chinese fir [*Cunninghamia lanceolata* (Lamb.) Hook] plantations in southeast China. The dry mass weight of dead branches and dead leaves in the canopy significantly increased with stand stage (14.6, 14.2, and 17.4 t ha^{-1} for young, middle-aged, and mature stands respectively), accounting for high proportions of total aboveground litter of 85.7%, 79.1% and 80.0%, respectively, along with annual litterfall production (2.44, 3.75, and 4.34 t ha^{-1}, respectively). The canopy height distribution of dead branches and leaves also increased with stand age, ranging from 0-4 m in young stands, 3–8 m in middle-aged stands, to 4–10 m in mature stands. The seasonal pattern of canopy litter mass was the inverse of litterfall production: canopy litter mass peaked, whilst litterfall production was lowest in winter. Mean N, P, K, and Mg nutrient resorption efficiencies across stands at each stage were 53.8–58.9%, 64.0–68.9%, 85.0–90.2%, and 46.5–56.6%, respectively, while Ca was not retranslocated from senescing leaves. In summary, Chinese fir plantations retain large amounts of dead branches and leaves in the canopy from which at least ~50% of the nutrients N, P, K and Mg are recycled, representing an important nutrient conservation strategy that has evolved to adapt to nutrient-limited habitats. Canopy litter therefore plays an important role in these forest plantation ecosystems and should be protected instead of being removed from the canopy to the forest floor.

Key words: canopy litter, nutrient concentration, nutrient resorption, nutrient recycling, *Cunninghamia lanceolata* (Lamb.) Hook

1. Introduction

Nutrient resorption and litterfall kinetics may play an important role in modifying the return of nutrients to the soil and litterfall chemistry, thereby strongly influencing soil nutrient turnover and fertility. Nutrient resorption is the process by which nutrients are retranslocated from senescing organs to living or storage organs (Aerts, 1996). It is also a key nutrient conservation strategy in perennial plants and is frequently studied to understand the internal cycling of nutrients in plants (Brant and Chen, 2015; Zhou et al., 2016a). For example, mineral nutrients are absorbed in the tree crown before leaf shedding, which enhances the residence time of nutrients within plant tissues and improves internal nutrient recycling and use efficiency (Cleveland et al., 2013; Maillard et al., 2015; Yan et al., 2015). On average, perennial plants reabsorb more than half of leaf N and P pools during leaf senescence (Van Heerwaarden et al., 2003a). For example, Liu et al. (2014) investigated resorption of 13 nutrient elements in karst vegetation and reported that four nutrients (N, P, K and Mg) were resorbed in varying degrees from senescing leaves, with the extent of resorption increasing with decreasing concentrations of these nutrients in green leaves. Therefore, insights into nutrient resorption patterns are important for understanding nutrient cycling in forest ecosystems.

Nutrient resorption is usually quantified as resorption efficiency (RE), which is defined as the ratio between the amount of nutrients reabsorbed prior to leaf shedding and leaf nutrient content before the onset of leaf senescence (Huang et al., 2007). For planted forests worldwide, mean nitrogen and phosphorus RE values are 59.0% and 60.2%, respectively, with significantly lower nitrogen REs in tropical and subtropical forests (Jiang et al,. 2019). Differences in RE values reported are associated with leaf life span (evergreen vs. deciduous), leaf nutrient content, and soil nutrient availability (Yuan and Chen, 2015; Tsujii et al., 2017). For instance, nutrient RE is higher in deciduous species and graminoids than in evergreen species and forbs (Aert, 1996; Han et al. 2013). However, the relationship between nutrient RE and soil nutrient availability and leaf nutrient status is not clear-cut. Many studies have suggested that plants would resorb more nutrients in nutrient-poor environments (Tully et al. 2013; Yuan and Chen, 2015), but this has been disputed (Tang et al. 2013; See et al. 2015). In addition, whether and how nutrient resorption is regulated by plant nutrient status across different functional types and forest ecosystem remains unresolved (Vergutz et al. 2012; Zhou et al. 2016a).

The canopy litter (dead branches and leaves that remain attached to the trunk) is not only a component of the aboveground coarse woody detritus (CWD) pool, but also of the nutrient and carbon pool (Fonte and Schowalter, 2004; Yoshida and Hijii, 2006). In marcescent species, such as the conifers *Cryptomeria japonica* and *Pseudotsuga menziesii*, dead branches and leaves remain attached to the trunk within the canopy long after death (Ishii and Kadotani, 2006; Yoshida and Hijii, 2006). Some broad-leaved trees, such as *Populus euphratica*, *Fagus grandiflora* and many *Metrosideros* forests also retain brown leaves within the canopy for some time (Escudero and Arco, 1987; Shi et al., 2017). This results in accumulation of large amounts of dead branches and leaves in the canopy. For example, canopy litter (foliage, reproductive tissue and fine woody debris) accounted for 66–86% of the mass, 63–90% of the N, and 49–92% of the P returned annually in aboveground litter, dominating recycling of N and P in three Rocky Mountain forests (Laiho and Prescott, 1999). The canopy litter plays an important role in nutrient cycling through withdrawing nutrients from senescing tissues and providing litterfall to the forest floor (Prescott, 2002). However, the spatial and temporal distributions of canopy litter have not been reported in previous studies as they are difficult to estimate accurately (Ishii and Wilson, 2001; Ishii and Kadotani, 2006). Furthermore, the nutrient concentrations of leaves have been shown in agricultural crop plants to change substantially between senescence and death, significantly influencing the nutrient RE (Osaki and Shinano, 2001). Most previous studies of nutrient RE in trees have focused on comparing nutrient concentrations between green leaves and either senescent leaves or litterfall, but the changes in nutrient concentrations from leaf senescence to death are not well known across different stand development stages.

Chinese fir (*Cunninghamia lanceolata* (Lamb.) Hook) is an endemic coniferous species in China with high yield of timber and excellent wood quality. It has a planting history of more than 1000 years and is distributed across 17 provinces, ranging from 21°31′ to 34°03′ N, and 101°30′ to 121°53′ E (Yu, 2000). The planted area and stand volumes of Chinese fir account for 23.2% and 29.2% of the total plantation area and stand volume in China, respectively, the highest of any tree species (State Forestry Administration, 2014). Chinese fir is characterized by a canopy containing large amounts of dead leaves and branches which remain attached to the trunk for more than 4 years (Sheng and Fan, 2002) (Fig. S1). Previous studies reported that the mass of dead leaves and branches increased with stand stage from 0.70–1.26 t ha^{-1} in young stands to 6.51–9.43 t ha^{-1} in middle-aged stands (Sheng and Fan, 2002). In 10-year-old Chinese fir, the mass of dead branches and leaves in the canopy accounted for 95% of the total aboveground litter, and remained at ~50% even after substantial increase in litterfall production in trees >15-years-old (Liao et al., 1996). Several studies have demonstrated that the decay rates of dead branches and leaves in the canopy are much slower than litter decomposition on the forest floor, leading to less nutrient return than in forest soil (Zhang and Sheng, 2001; Gao et al., 2015). However, canopy litter mass and its spatiotemporal distribution in Chinese fir has not been quantified, due to the difficulty of sampling.

In a previous study conducted at Xinkou National Forest Farm, but at different locations and different-aged stands compared to this research and only comparing green and litterfall leaves, we showed that fresh Chinese fir leaves absorb 50% N and 70% P before litterfall to the forest floor (Zhou et al., 2016a). Similar values have been reported for *Larix spp.* (a dominant coniferous species in China), with resorption from senescing leaves of 72.6%, 69.7% and 44.7% of N, P and K, respectively, but not Mg and Ca (Yan et al., 2015). Lower N and P resorption efficiencies of 38% and 46%, respectively, reported for Chinese fir (Liu, 2014), perhaps arise from neglecting the leaf mass loss and leaf shrinkage during senescence (Van Heerwaarden et al., 2003a). Litter retention in the canopy is not only closely linked with litterfall production and nutrient input into soil, but also with internal nutrient recycling. Long retention times of litter in the canopy and translocation of nutrients to other tissues before senescence should potentially increase nutrient reuse efficiency (Escudero et al., 1992; Niinemets and Tamm, 2005). This may be an important adaptation strategy, which enables plants to use nutrients directly from senescent organs instead of absorbing them from soil nutrient pools, helping plants to survive in nutrient-deficient environments (Kobe et al., 2005; Lü et al., 2016).

We hypothesized that: (1) the spatiotemporal distribution of canopy litter varies significantly with chronosequence-development stages in Chinese fir plantations; (2)

nutrient concentrations of needles decreased from growth to senescence and varied seasonally; (3) foliar nutrient resorption varied among stand stages and seasons, and nutrients required in large quantities (such as N, P and K) would be resorbed more effectively than nutrients required in small amounts (such as Ca and Mg). The specific objectives of this study were to investigate the spatiotemporal dynamics of canopy litter mass and determine the nutrient (N, P, K, Ca, and Mg) RE and seasonal patterns of dead canopy leaves among young, middle, and mature aged Chinese fir plantations. Our results contribute towards a better understanding of plant adaptation strategies to nutrient availability, and forest nutrient cycling processes, including internal nutrient recycling and external fluxes.

2. Materials and methods

2.1 Study site

This study was conducted at Xinkou National Forest Farm (26°07′–27°13′ N, 117°27′–118°14′ E), Sanming City, Fujian province, China (Fig. S1). The elevation was ~205–500 m above sea level. The region is characterized by a subtropical monsoon climate with mean annual temperature of 17–19.4 °C, and mean annual precipitation of 1600–1800 mm. The mean annual evaporation is 1585 mm, mean annual relative humidity 81.0%, and the frost-free period is 240–300 days (Zhou et al. 2015). The soil was classified as Silty Oxisol (according to US Taxonomy), developed on sandstone and shale parent material.

The study area was originally covered by broad-leaved forests that have now been replaced by fast-growing Chinese fir plantations with a short rotation of typically 20–30 years (Wu, 1984). Three first-generation monoculture Chinese fir plantation stands of ages 8, 16 and 25 years (established in 2008, 2000 and 1991), representing young, middle, and mature ages, respectively, were selected for the study within a 2 km distance. The young and middle-aged stands face northeast and the mature stand is located on a southeast facing slope. All stands were established from seedlings planted in hand-dug holes after clear-cutting and burning of the existing forest. The young stage was unthinned, whilst the middle-aged and mature stands were thinned following the standard practice for Chinese fir plantations by removing alternate rows and cutting the crowns of thinned trees on site. The middle-aged stand was thinned in 2008, and the mature stand in 2000 and 2008. The dominant understory comprised shrubs and grasses, such as *Woodwardia japonica*, *Maesa japonica*, *Ilex pubescens*, *Selaginella doederleinii* and *Miscanthus floridulus*. In each stand, three permanent replicate plots (20 m × 20 m) were established. Soil properties across different developmental stages were: pH 4.24–4.58, soil organic matter 35.3–42.4 g kg^{-1}, bulk density 1.25–1.33 g cm^{-3} and C:N ratio 10.9–13.1.

2.2 Canopy litter biomass production

Canopy litter was collected in January, April, July, and October 2015. After measuring tree diameter at breast height (DBH), tree height, crown diameter and the height above ground of the lowest dead branch for all the trees in the plot (Table 1), 16 sample trees were tagged in each plot, of which a separate four trees were sampled on each date (Fig. S2). Above the lowest dead branch, all canopy litter was collected from each sample tree at 1-m height intervals for the young stage (from a ladder placed against the trunk), and 2-m intervals for the middle and mature stages (using branch clippers). If the canopy litter was too high to be accessed by these methods, it was collected by climbing the tree (Fig. S3). Plastic sheets were placed on the forest floor around each sample tree to collect any canopy litter detached during the canopy collection. The fresh weights of all samples of dead branches and dead leaves from each height interval were measured in the field. Sub-samples were taken to determine moisture content in the laboratory to allow the fresh weights to be converted to dry weight. Since there were no obvious branch gaps in the canopy, it was assumed that the distribution of canopy litter by height represents the original branch location and that there has not been substantial downwards movement of canopy litter.

Table 1. Plot characteristics in Chinese fir plantation stands at different development stages (young, middle and mature). Tree DBH, height, height above ground of lowest dead branch, and crown diameter are expressed as mean ± SE of all the trees in each plot.

Stage	Plot number	Year of planting	DBH (cm)	Tree height (m)	Height above ground of lowest dead branch (m)	Crown diameter (m)	Canopy density	Stand density (stem ha^{-1})	Slope (°) and aspect
Young	1	2008	8.78±0.22	7.69±0.13	0.09±0.01	2.44±0.06	0.9	1789	20° NE
	2	2008	11.1±0.22	9.25±0.11	0.13±0.01	3.08±0.06	0.8	2811	18° NE
	3	2008	11.5±0.25	9.50±0.14	0.14±0.01	3.29±0.07	0.8	2547	17° NE
Middle	1	2000	13.2±0.60	10.1±0.46	2.93±0.13	5.72±0.26	0.8	1775	29° NE
	2	2000	14.2±0.47	11.8±0.39	3.47±0.12	6.23±0.22	0.7	1880	28° NE
	3	2000	15.5±0.53	11.9±0.41	3.44±0.12	6.74±0.23	0.7	1802	26° NE
Mature	1	1991	18.9±0.72	15.3±0.59	5.72±0.22	8.58±0.33	0.6	1475	21° SE
	2	1991	20.9±0.62	17.4±0.52	9.95±0.30	9.52±0.28	0.5	1650	20° SE
	3	1991	21.5±0.62	17.4±0.45	9.09±0.27	8.72±0.26	0.5	1580	22° SE

2.3 Litterfall production

Litterfall was collected in litter traps (1 m × 1 m) installed at 1 m above the ground at five randomly selected locations in each plot in October 2014. Chinese fir litter was collected from each trap in January, April, July, and October 2015, with litter from other tree species or understory vegetation discarded. The fresh weight of the Chinese fir litter (unsorted leaves and twigs) was measured and sub-samples oven-dried at 80 °C for 48 h to a constant weight. Litterfall production (t ha^{-1}) was calculated as a dry weight taking account of the litter trap area and the moisture content of the fresh litterfall.

2.4 Needle sampling and nutrient analysis

Chinese fir needles were also sampled from the same sample trees from which canopy litter was collected and at the same times in January, April, July, and October 2015. Chinese fir leaves form a new node annually, therefore, the apex needles in the first node are <1-year old, while needles further along the shoot are perennial. At least 10 shoots were collected from each sample tree from different aspects and heights in the canopy. Five categories of needles [<1-year-old, 1-year-old, perennial, senesced (brown), and dead (yellow)] were collected separately from each shoot (Fig. S4). Senesced needles are brown and not completely dry; dead needles are completely dry and yellow, without signs of deterioration (Wright and Westoby, 2003). All the needles in the same category were mixed to form a composite sample. All the samples were first oven-dried at 105 °C for 15 min to deactivate enzymes and then at 80 °C for at least 48 h to constant weight (Zou et al., 2015). Dried samples were ground uniformly using a grinder, sieved to <1.0 mm and then stored in brown glass bottles before nutrient concentration determination. Total N was determined using combustion in an ELEMENTAT Vario EL III analyzer (Germany) at Fujian Agriculture and Forestry University (Zhou et al., 2015). High purity glutamic acid containing 9.52% N was used as a standard to calibrate the instrument. It was also analyzed every 10 samples as a quality control check, with instrument performance deemed acceptable if the measured value was ±10% that of the standard. For each plant sample, a 0.1 g subsample was digested using HNO_3-H_2SO_4 solution (volume ratio 5:1). Total P in the digests was measured using the molybdenum-antimony colorimetric method with a 723A spectrophotometer (AOXI Instruments, Shanghai, China) (He et al., 2003). The absorbance of the solution was determined in a 1-cm cell at 700 nm, using ultrapure water as the blank. Total K, Ca, and Mg were determined using atomic absorption spectrophotometry (AAS) (Puxi Instruments, Beijing, China) (Institute of Soil Academia Sinica, 1978).

2.5 Resorption efficiency

Nutrient resorption efficiency (RE), the proportional withdrawal of nutrients during leaf senescence, was calculated using Equation 1 (Han et al., 2013; Zhou et al., 2016a):

$$RE = \left(1 - \frac{Nutrient_{yel}}{Nutrient_{gre}} \times \mathrm{MLCF}\right) \times 100 \quad (1)$$

where $Nutrient_{yel}$ and $Nutrient_{gre}$ are nutrient concentrations (N, P, K, Ca, and Mg) of yellow and <1-year-old needles, respectively. Considering that leaf mass decreases during senescence, a mass loss correction factor (MLCF) was used to compensate for the underestimation of RE. Here the MLCF for needles was 0.65, determined in a previous study of Chinese fir trees conducted nearby at different locations within Xinkou National Forest Farm (Zhou et al., 2016a).

2.6 Statistical analysis

The data are presented as means ± SE. A three-way analysis of variance (ANOVA) was used to test the effects of canopy strata (height sampled above the ground), stand age, season, and their interactions on the dry mass of canopy litter. Fixed factors were canopy strata, stand stage and season. A one-way ANOVA was used to compare the dry mass differences among seasons in the same vertical strata or among vertical strata in the same season. Means were compared using LSD post-hoc tests ($P < 0.05$). All statistical analyses were performed using SPSS 17.0 software package for Windows (SPSS Inc., Chicago, IL, USA).

3. Results

3.1 Spatiotemporal distribution of canopy litter and annual litterfall production

Canopy strata, stand age, and season all had significant effects ($P < 0.001$) on canopy litter mass (Table 2). The interactions between stand age and canopy height, and canopy strata and season were also significant ($P < 0.001$ and $P < 0.01$, respectively). There were no significant interaction effects between all three factors. The mean masses of the dead leaves and dead branches in the canopy of Chinese fir trees were

14.6, 14.2, and 17.4 t ha^{-1} for the young, middle-aged and mature stages, respectively (Fig. 1). The height of dead branches and leaves in the tree canopy increased with stand age: 0–4 m in the young stand, 3–8 m in the middle-aged stand, and 4–10 m in the mature stand (Fig. 2). In the young stand, most canopy litter mass was at 0–3 m height above the ground, accounting for 78.6% of total canopy litter mass. For the middle-aged stand, the majority of the canopy litter mass was at 4–8 m height, accounting for 75.1% of total canopy litter production. In the mature stand, most canopy litter was at 6–10 m height, accounting for 77.7% of the total canopy litter mass.

Table 2. Three-way analysis of vertical strata (df = 6), season (df = 3), stand stage (df = 2) and their interaction on canopy litter mass of attached dead branches and leaves of Chinese fir plantations at different development stages. *P* values in bold indicate significant factors and their interactions.

Values	*df*	*F*	*P*
Stand stage	2	227.643	**<0.001**
Season	3	12.490	**<0.001**
Vertical strata	6	1353.813	**<0.001**
Stand stage × Season	6	0.750	0.610
Stand stage × Vertical strata	1	1584.753	**<0.001**
Season × Vertical strata	18	2.211	**0.003**
Stand stage × Season × Vertical strata	3	0.643	0.588

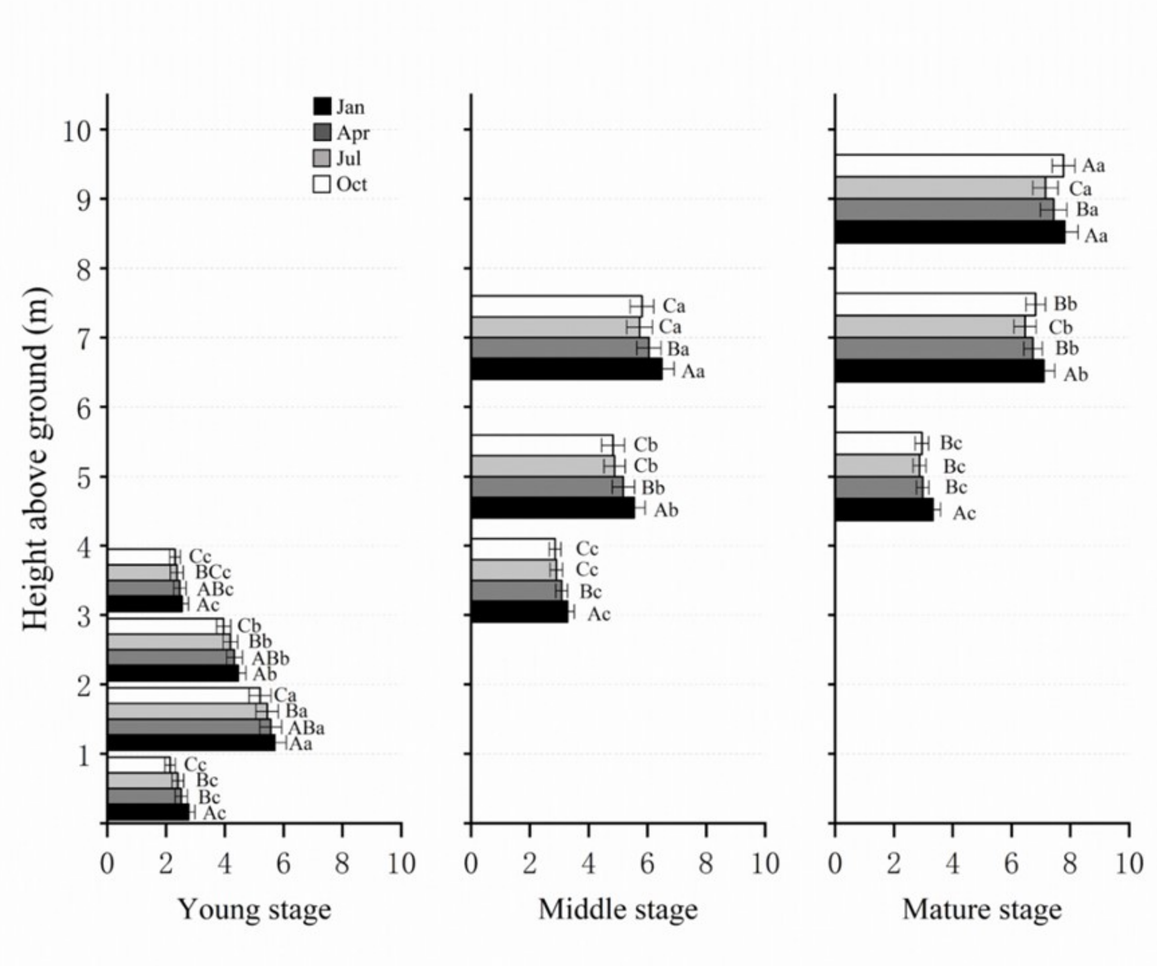

Fig. 1. Vertical and seasonal distribution of dry mass of attached dead branches and leaves in the canopy among young, middle and mature stage *C. lanceolata* plantations in southern China (t ha^{-1}). Horizontal bars are means ± SE (n=3). Different uppercase letters indicate significant differences between seasons for the same vertical strata (P<0.05). Different lowercase letters indicate significant differences between vertical strata in the same season (P<0.05).

The total mass of canopy litter was significantly higher during the winter (January): 15.5, 15.3, and 18.2 for the young, middle, and mature stage stands, respectively (Fig. 1). The lowest total mass of canopy litter was 13.6 and 13.5 t ha^{-1} during autumn (October) for the young and middle stage stands, respectively, and 16.5 t ha^{-1} during the summer (July) for the mature stand. The seasonal dynamics of litterfall production were in the order autumn > spring > summer > winter for all stand stages (Fig. 2). The total annual litterfall production was 2.44, 3.75, and 4.34 t ha^{-1} for young, middle-aged, and mature stands, respectively. The canopy litter mass comprised 85.7%, 79.1%, and 80.0% of the total mass, including the annual litterfall production, in the three different stages of Chinese fir plantations.

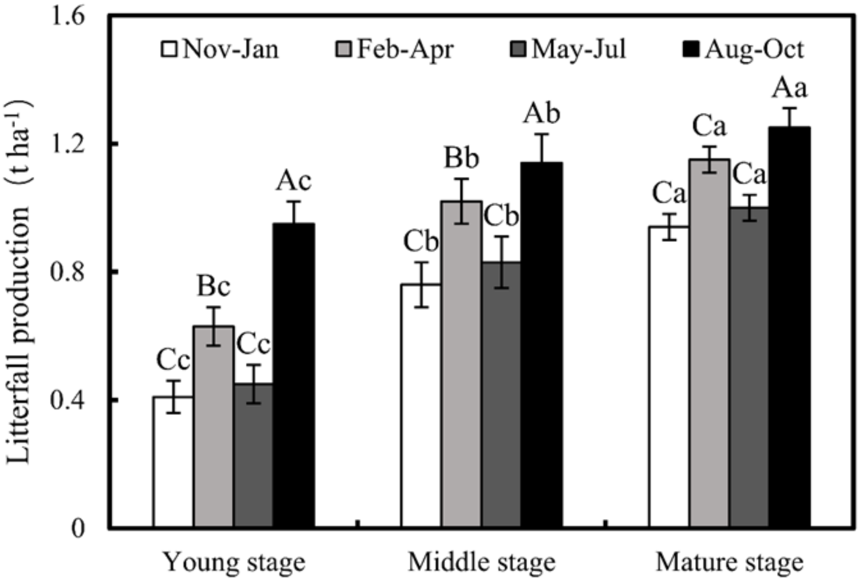

Fig. 2. Seasonal dynamics of litterfall production (t ha^{-1}) of Chinese fir plantations at different developmental stages. Vertical bars are means ± SE (n = 3). Different uppercase letters indicate significant differences between seasons for the same stage (*P*<0.05). Different lowercase letters indicate significant differences between stages for the same season (*P*<0.05).

3.2 Variation of leaf nutrient concentrations during senescence and shedding

Nutrient concentration (N, P, K, Ca and Mg) varied significantly with stand stage, leaf level, and season (Table 3, $P < 0.01$). There were also significant interaction effects for all nutrients studied between stand stage and needle categories, and needle categories and seasons ($P < 0.01$). N, P, K and Mg concentrations showed a significant downward trend with leaf senescence and shedding, while Ca concentrations displayed the opposite trend (Fig. 3). Concentrations of N, P, K, and Mg were highest in the <1-year-old needles at 12.2–16.9 g kg^{-1}, 0.93–1.13 mg g^{-1}, 6.55–6.83 g kg^{-1}, and 1.83–2.54 g kg^{-1}, respectively. Concentrations of N, P, K, and Mg were lowest in the litterfall needles at 6.96–9.96 g kg^{-1}, 0.44–0.53 g kg^{-1}, 0.74–1.24 g kg^{-1}, and 1.30–1.89 g kg^{-1}, respectively. In contrast, the highest Ca concentrations were in yellow (dead) needles (5.62–8.32 g kg^{-1}), and the lowest were in the <1-year-old needles (2.24–3.68 mg g^{-1}). All the needles from different categories and stand stages showed similar seasonal patterns. N and P concentrations were lowest in January, increased from April to July and decreased again. The seasonal variation in Ca concentrations showed the opposite trend, being highest in January and lower in July. K and Mg concentrations were highest in October and lowest in April.

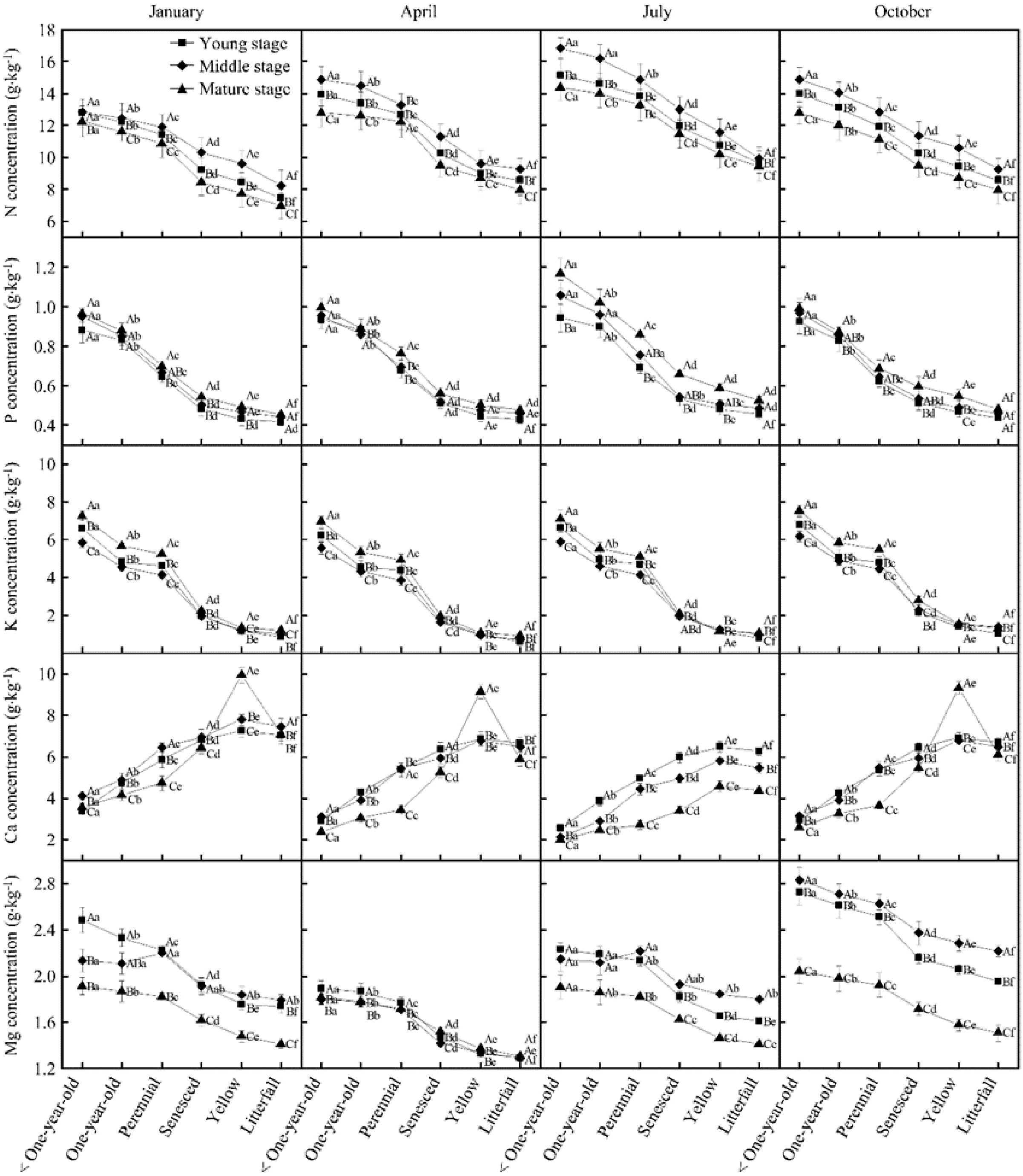

Fig. 3. Nutrient concentrations (N, P, K Ca and Mg) in the different categories of needles sampled in the canopy (<1-year-old needles, 1-year-old needles, perennial needles, senesced needles, yellow (dead) needles) and in litterfall needles at various seasons among young, middle and mature stage *C. lanceolata* plantations in southern China. Note different y-axis scales between figures. Different uppercase letters indicate significant differences between stages for the same needle category in each season ($P<0.05$). Different lowercase letters indicate significant differences between needle categories for the same stage in each season ($P<0.05$).

3.3 Nutrient resorption efficiency of needles during senescence in the canopy

During leaf senescence, N, P, K, and Mg were strongly resorbed, with the resorption efficiency (RE) varying significantly among stand stage and seasons (apart from for season for Mg). There were also significant interactions between the two variables (except Mg, Table 4). Overall, across stand stages, the REs of different nutrients were in the order K > P > N > Mg, at 85.0–90.2%, 64.0–68.9%, 53.8–58.9%, and 46.5–56.6%, respectively (Fig. 4). In contrast, Ca concentrations in needles were enriched during leaf senescence in all stand stages. N and Mg resorption efficiencies were highest in the young stand (58.4% and 52.8%, respectively), followed by the mature (46.7% and 50.1%, respectively), and the middle-aged stand (45.1% and 46.5%, respectively). P resorption efficiency was in the order, young stand (70.0%) > middle-aged stand (67.8%) > mature stand (66.2%). K had the largest resorption efficiency at 86.5–88.5% in all three stands.

It is noteworthy that nutrient RE varied significantly between seasons. N resorption efficiency was highest in April for young and middle-aged stands, and in January for the mature stand. P resorption efficiency was highest in April for young and mature stands, and in July for the middle-aged stand. K resorption efficiency was highest in April and lowest in October for each of the three stands. Mg resorption efficiency showed a similar trend in all stand ages of April > October > January > July.

Table 3. Three-way analysis of stand stage (df = 2), needle categories (df = 5), season (df =3) and their interaction on nutrient concentration (N, P, K, Ca, Mg) of different needle categories of Chinese fir plantations at different development stages. *P* values in bold indicate significant factors and their interactions.

Values	N concentration		P concentration		K concentration		Ca concentration		Mg concentration	
	F	P	F	P	F	P	F	P	F	P
Stand stage	6143.548	**< 0.01**	1.106	0.334	1946.781	**< 0.01**	200.388	**< 0.01**	519.069	**< 0.01**
Needle categories	3440.240	**< 0.01**	1375.376	**< 0.01**	48541.201	**< 0.01**	4350.938	**< 0.01**	460.773	**< 0.01**
Season	5720.779	**< 0.01**	21.521	**< 0.01**	692.002	**< 0.01**	954.066	**< 0.01**	852.737	**< 0.01**
Stand stage ×Needle categories	294.374	**< 0.01**	6.185	**< 0.01**	248.380	**< 0.01**	323.598	**< 0.01**	10.893	**< 0.01**
Stand stage × Season	656.548	**< 0.01**	2.134	0.053	17.700	**< 0.01**	64.847	**< 0.01**	114.785	**< 0.01**
Needle categories × Season	7.287	**< 0.01**	3.524	**< 0.01**	3.399	**< 0.01**	5.503	**< 0.01**	2.499	**< 0.01**
Stand stage × Needle categories × Season	5.622	**< 0.01**	1.062	0.392	2.993	**< 0.01**	4.717	**< 0.01**	1.928	**< 0.01**

Table 4. Two-way analysis of stand stage (df = 2), season (df = 3) and their interaction on nutrient resorption efficiency (N, P, K, Ca, Mg) of Chinese fir plantations at different development stages. *P* values in bold indicate significant factors and their interactions.

Values	N resorption efficiency		P resorption efficiency		K resorption efficiency		Ca resorption efficiency		Mg resorption efficiency	
	F	P	F	P	F	P	F	P	F	P
Stand stage	8912.653	**< 0.001**	36.701	**< 0.001**	343.190	**< 0.001**	2902.120	**< 0.001**	9.770	**0.001**
Season	133.390	**< 0.001**	4.505	**0.012**	549.263	**< 0.001**	420.285	**< 0.001**	2.195	0.115
Stand stage ×Season	48.938	**< 0.001**	3.024	**0.024**	21.726	**< 0.001**	70.357	**< 0.001**	1.305	0.293

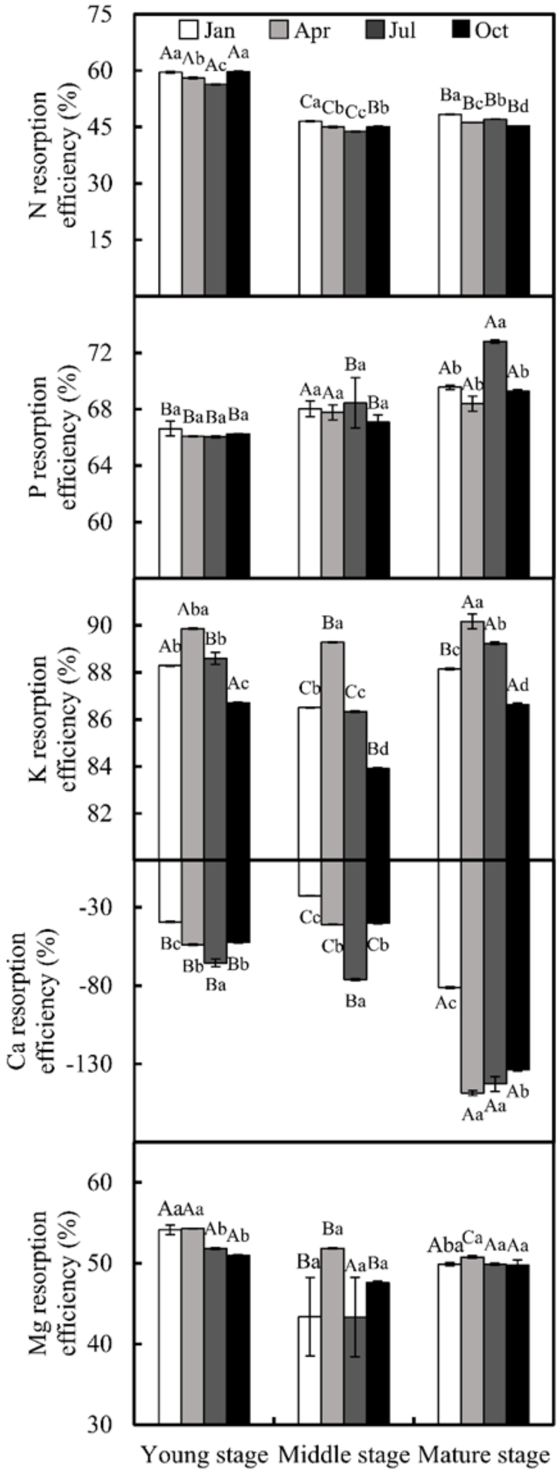

Fig. 4. Nutrient resorption efficiency (N, P, K Ca and Mg) from senescent leaves in canopy litter of young, middle and mature stage *C. lanceolata* plantations in southern China. Columns are means ± SE (n=3). Different uppercase letters indicate significant differences between stages in the same season (P<0.05). Different lowercase letters indicate significant differences between seasons for the same stage (P<0.05).

4. Discussion

4.1 Spatiotemporal distribution of canopy litter

Our results verified the first hypothesis that the attached dead leaves and branches in the canopy of Chinese fir plantations at different development stages varied significantly among vertical strata and seasons (Table 2). Canopy litter of Chinese fir in the study stands was 14.2–17.4 t ha^{-1}, accounting for 79.1%–85.7% of both canopy biomass and annual litterfall production. The canopy litter mass of the mature stand was much lower than reported for other tree species in previous studies, e.g., 33-year-old *Cryptomeria japonica* stand (34 t ha^{-1}), but that of the young stand was much higher than in a 16-year-old *C. japonica* stand (3.6 t ha^{-1}) (Miyaura and Hozumi, 1989; Yoshida and Hijii, 2006). Compared to our results, much lower canopy litter masses have been reported in other studies of Chinese fir. For example, a 13-year-old Chinese fir plantation in Jiangxi Province, China, had a canopy litter mass of 4.12 t ha^{-1} (Zhang and Sheng, 2001), whilst Zheng (1997) reported canopy litter masses of ~8.0 t ha^{-1}, 3.5 t ha^{-1} and 5.5 t ha^{-1} in 10-, 15-, and 19-year-old Chinese fir stands, respectively, and it increased as soil quality improved. Liao et al. (1996) found that Chinese fir retained large amounts of dead branches and leaves for up to 10 years, with a small amount of litterfall production (canopy litter: 7.52 t ha^{-1}; litterfall production: 0.475 t ha^{-1}). Litterfall production was higher in >15-year-old stands, whilst the canopy litter biomass was only 1.69 and 2.62 t ha^{-1} for 15- and 19-year-old stands, respectively (Liao et al., 1996). The large variation in estimates of canopy litter mass reported in the literature may be attributed to differing stand stages, site climate, and sample size and methods. In other studies, a smaller number of trees were sampled and lower forest productivity (and thus litterfall production) is expected due to cooler and drier conditions compared to our site.

The canopy dead branches and leaves mainly occupied heights of 0–4 m, 3–8 m, and 4–10 m in the canopy of young, middle-aged, and mature stands, respectively, and the canopy litter occurred predominantly in the lower parts of the canopy in the young stand. Several possible factors may be responsible for the large mass of canopy litter and vertical distribution pattern of dead branches and leaves. First, the lower foliage is shaded by upper branches and leaves of adjacent trees after canopy closure (>5-year-old stands) (Zhang and Sheng, 2001). Most branches and leaves die from lack of sunshine instead of physiological causes. The dead branches and leaves remain attached to the trunk for several years with a slow decomposition rate, if not detached by wind or snow. Second, the canopy litter may continue to accumulate living leaves because Chinese fir leaf longevity is ~4–5 years (Ma et al., 2007) and the fast-growth and stemwood formation periods of Chinese fir are 5–12 years and 13–19-years, respectively (Tian et al., 2002). Third, Zhang and Sheng (2001) reported that dead branches and leaves in the lower canopy may decay more rapidly due to greater moisture and abundant microbial communities than in the upper canopy, which could lead to an increase in the vertical height of occurrence of canopy litter as developmental stage increases for Chinese fir.

Our results showed that the seasonal mass dynamics of canopy litter were inverse to those of litterfall production (Figs. 2 and 3). The death of branches and leaves occurred all year, but the canopy litter mass of Chinese fir peaked in winter (15.3–18.2 t ha^{-1}), while litterfall production was lowest in winter. Furthermore, the mass of dead branches and leaves in the canopy was much larger relative to that of litterfall production, accounting for 79.1%–85.7% of total litter mass including litterfall production, which indicated that the death rate (litter input to canopy) was much higher than the litterfall rate (litter output from the canopy to the soil). Assuming that the litterfall rate equals the canopy litter death rate, the turnover rate of the canopy litter was 0.17, 0.26, and 0.25 t year^{-1} for the young, middle-aged, and mature stands of Chinese fir plantations studied, respectively. The actual turnover rates of canopy litter are likely to be much lower. Yoshida and Hijii (2006) reported the average turnover rate of canopy litter was 0.17 year^{-1} (0.21 t year^{-1} for canopy leaf litter and 0.09 t year^{-1} for canopy branch litter) for *C. japonica* forests. Assuming the rates of litterfall input to soil and the output to the deeper soil layers are approximately equal, litter accumulating on the soil surface would be replaced after about 0.63, 0.60, and 0.80 years in the young, middle-aged, and mature stands, respectively (Fig. 5).

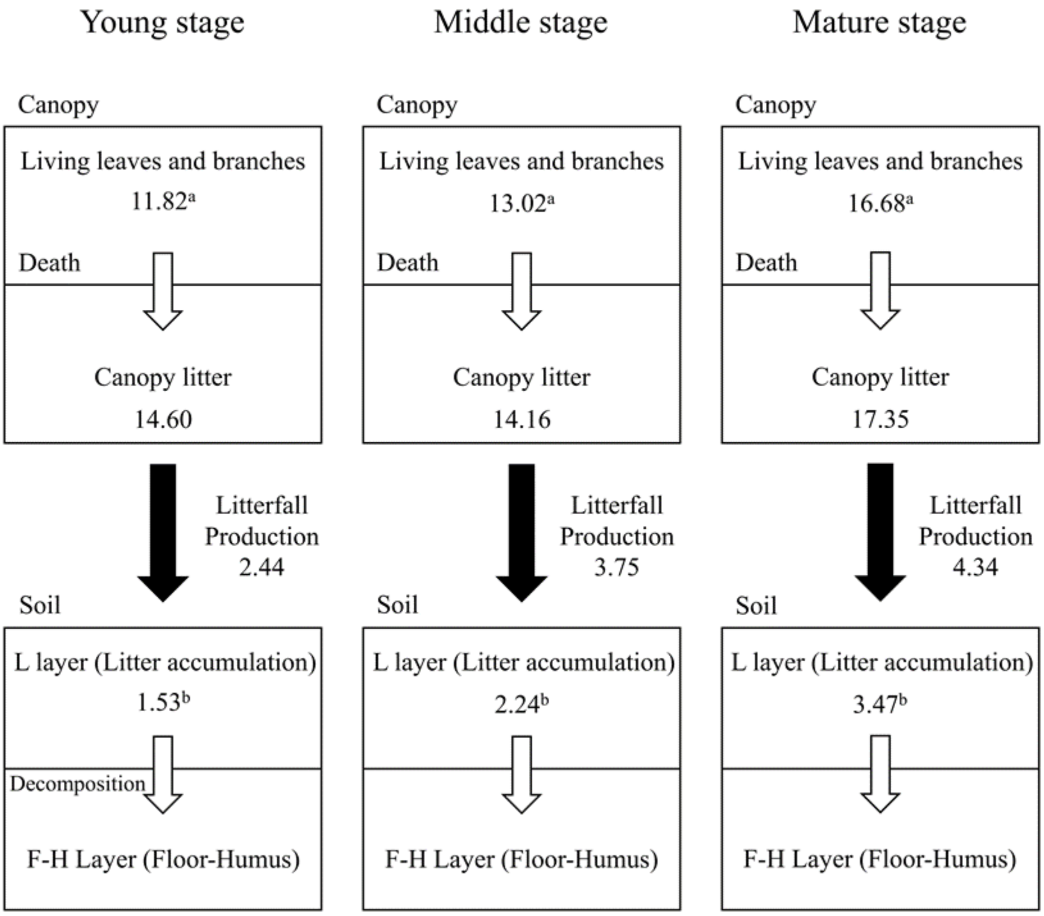

Fig. 5. Estimates of litter flow in young, middle and mature *C. lanceolata* plantations based on results from this study and other studies. The biomass of living branches and leaves and the mass of dead branches and leaves in the canopy is expressed as t dry wt ha^{-1}, and the amount of transfer (litterfall) is expressed as t dry wt ha^{-1} a^{-1}. ^{a} indicates data from Ma et al. (2002); ^{b} indicates data from Zhou et al. (2012).

4.2 Variation and seasonality in nutrient concentrations of needles in the canopy

We partly confirmed the second hypothesis that nutrient (N, P, K, Mg) concentrations of needles decreased from growth to senescence and varied seasonally. In contrast, Ca concentrations increased, in agreement with Viers et al. (2013), which may be explained by the relative immobility of Ca involved in the structure and physiological processes of cell membranes (Fircks et al., 2001). We found that nutrient concentration was significantly affected not only by the needle type but also by season. The highest leaf N and P concentrations in different categories of Chinese fir needles were measured in the summer (July) samples. A similar tendency has been observed in other conifers, such as *Pinus sylvestris* (Regina and Tarazona, 2001). In the growing season (summer), intense mitotic activity companied by cellular growth requires more nutrients for protein synthesis, in particular N and P (Arneth et al., 1996). The highest Ca and K concentrations in Chinese fir needles occurred in January and October, consistent with *Juniperus phoenicea* species (Kutbay et al. 2005). Due to the relative immobility of Ca, as noted already, it usually accumulates in plant tissues during the growing season, with peak concentrations occurring at the end of the growing season (Hepler, 2005).

In our study, fresh foliar (<1-year-old) nutrient concentrations (mean values of the three development stages are N: 14.0 g kg^{-1}; P: 0.98 g kg^{-1}; K: 6.55 g kg^{-1}; Ca: 2.86 g kg^{-1}; Mg: 2.08 g kg^{-1}) were lower than those in broadleaved species (such as *S. superb*, *Castanopsis sclerophylla schott*, *Eucalyptus grandis*), implying that nutrient cycling is more conserved in coniferous species (Huang et al., 2007; Li et al., 2009; Wang et al., 2010). The fresh foliar N and P concentrations in our study were lower than the critical nutrient concentrations in a global study (N: 18.6 g kg^{-1} and P: 1.21 g kg^{-1}) (Han et al. 2005), which further indicated that the Chinese fir plantations studied were both N- and P-limited. Lower nutrient concentrations and higher nutrient use efficiency in Chinese fir plantations might be important adaptation mechanisms for nutrient conservation in nutrient deficient soil conditions (Diehl et al., 2003).

4.3 Nutrient resorption efficiency of needles in the canopy

We partly verified the third hypothesis that nutrient RE varied among stand stages and seasons (Table 4). Many previous studies have focused on N and P resorption, overlooking other nutrients that are also important for forest productivity. In our study, leaf N and P nutrient RE (50.1% and 68.0%, respectively) in the canopy of Chinese fir during senescence were of a similar magnitude to the mean values reported for planted forests of 59.0% and 60.2% (Jiang et al., 2019), but slightly lower than in our previous study in the same area in 10-, 22-, and 34-year-old Chinese fir (57% and 75%, respectively).

The average RE of K and Mg was 85.0–90.2% and 46.5–56.6% respectively, and Ca was accumulated in the senescing leaves. The higher RE values for N, P and K may be explained by their large requirement as well as their mobility, in alignment with our third hypothesis. Ca is stable and not easily resorbed, as demonstrated by many studies (e.g., Viers et al., 2013). In our previous study, we found nutrient REs were most affected by leaf nutrient status and stoichiometric control rather than soil nutrient status (Zhou et al., 2016a). Leaf shedding patterns may also affect nutrient resorption from senescing leaves. Milla et al. (2005) reported that species that shed leaves gradually throughout the year have significantly lower K resorption efficiency than species that shed leaves over a short time period, such as Mediterranean perennials. Thus, many factors influence the nutrient resorption process from senescing leaves to other plant tissues. Which processes are dominant will likely be influenced by the relative status of leaf and soil nutrient conditions in the ecosystem.

In our previous study, we estimated the mass of senescent branches and senescent leaves and determined their nutrient concentrations (Zhou et al., 2016b). Based on these, in our study, the nutrient contents of senescent branches and leaves in the canopy for N, P, K, and Mg were 102–125, 5.00–6.39, 19.2–26.9, and 18.2–25.8 kg ha^{-1} a^{-1}, respectively, much higher than our previous estimates of total annual nutrient return from Chinese fir plantations (young, mature and over-mature stage) to the soil layer (N: 39.3–62.0, P: 1.30–1.63, K: 16.0–22.4 kg ha^{-1} a^{-1}) (Zhou et al., 2015). The decline in plantation productivity in successive plantings would be greatly eased if these nutrients could be absorbed directly from senescent organs before shedding (Farooq et al., 2019). From the N, P, K, and Mg REs estimated in the present study for the different development stages, nutrient resorption is 68.8–77.0, 4.54–6.30, 14.9–20.2, and 10.4–13.3 kg ha^{-1} a^{-1}, respectively. We previously reported that the nutrient turnover rate (storage/return) for Chinese fir plantations (7.44, 10.4, and 12.0 years for young, mature and overmature stage, respectively) increases as stand development stage increases (Zhou et al., 2016b). Long nutrient turnover time, relatively small litterfall production and low litterfall quality (higher C:N ratio and low P content) could slow the rate of nutrient cycling within Chinese fir plantations and soil fertility recovery, and thus reduce forest productivity (Zhou et al., 2015, 2016 a,b).

There are two major reasons why nutrient turnover rate is slow for Chinese fir. Firstly, litterfall production of Chinese fir is much lower than in many broad-leaved evergreen species, such as *Castanopsis kawakamii* (11.0 t ha^{-1} a^{-1}), *Altingia gracilipes* (6.4 t ha^{-1} a^{-1}), and *Tsoongiodendron odorum* (6.3 t ha^{-1} a^{-1}). Secondly, the decomposition rate of Chinese fir litter is slow, due to the poor litter quality which has a high C:N ratio (62.5) and lignin content (Wang et al. 2007, 2009), restricting nutrient recovery. Several studies have reported that the decomposition rate of Chinese fir litterfall on the forest floor is 3–5 times that in the canopy and suggested that knocking the canopy litter off onto the forest soil would be an effective measure to maintain plantation productivity (Zhang et al., 2001; Gao et al., 2015). However, in our study, the dead attached leaves and branches were characterized by high nutrient resorption capacity during needle senescence and death, which could greatly improve nutrient utilization by intra-tree cycling and decrease the dependence on soil nutrients. This is an important nutrient conservation strategy in response to the changes in nutrient availability.

4.4 Implications for nutrient cycling in Chinese fir

This study examined the spatiotemporal dry mass of canopy litter and leaf nutrient resorption prior to death in Chinese fir plantations at different development stages. Large masses of dead leaves and branches were measured in the canopy of 14.6, 14.2, and 17.4 t ha^{-1}, comprising 85.7%, 79.1%, and 80.1% of the total canopy mass of young, middle-aged, and mature stands, respectively, including litterfall production. Apart from for Ca, we found that the extensive canopy litter contained the highest concentration of nutrients that were retranslocated to other plant tissues before needles senesced. The N, P, K, and Mg resorption efficiencies across development stages were high, at 53.8–58.9%, 64.0–68.9%, 85.0–90.2%, and 46.5–56.6%, respectively. Canopy pruning is an important silvicultural practice for many tree plantations. However, for Chinese fir, the lower litterfall production and slower litter decomposition rate results in less nutrient input over a longer time, which delays soil fertility recovery. Our results showed that Chinese fir is characterized by large amounts of dead attached leaves and branches remaining in the canopy for many years, and by high nutrient resorption efficiencies, which decrease the dependence on soil nutrients, especially in nutrient-deficient soil. The characteristics of Chinese fir canopy litter could be considered to have evolved as a nutrient conservation strategy to maximize within tree nutrient recycling. Therefore, maintaining dead leaves and branches in the canopy might be an important influence on nutrient cycling in subtropical plantation forests, and should inform pruning and management decisions.

5. Conclusions

Large amounts of dead branches and leaves accumulated in the canopy of Chinese fir plantations at young, middle-aged and mature development stages. The canopy litter occupied different canopy strata, and the vertical height increased with stand age. The seasonal dynamics of canopy litter mass were almost inverse to those of litterfall production. Macronutrient (N, P, K Ca, and Mg) concentrations varied greatly with leaf growth, senescence, and abscission among the three development stages. N, P, K, and Mg were resorbed during leaf senescence with resorption efficiency of 53.8–58.9%, 64.0–68.9%, 85.0–90.2%, and 46.5–56.6%, respectively. The nutrient contribution of resorption of these four nutrients is estimated at 68.8–77.0, 4.54–6.30, 14.9–20.2, and 10.4–13.3 kg ha^{-1} a^{-1}, respectively. This implies the retention of dead branches and leaves in the canopy may have evolved in Chinese fir as a strategy to conserve nutrients in response to nutrient-deficient soil.

Author Contributions

Lili Zhou: Conceptualization, Investigation, Writing - original draft, Formal analysis. **Shubin Li:** Investigation, Writing - review & editing. **Yayun Jia:** Investigation, Formal analysis. **Kate V. Heal:** Writing - review & editing. **Zongming He:** Investigation, Formal analysis. **Pengfei Wu:** Investigation. **Xiangqing Ma:** Conceptualization, Supervision, Writing - review & editing.

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments:

We thank Xinkou Experimental Forest Farm, Sanming, China, for field assistance. We thank Xinyang Yan, Xinding Liu and Fengze Han for laboratory assistance. We appreciate Editage [http://online. editage. cn/] for English language editing. We also thank two anonymous reviewers for constructive suggestions. This study was supported by the National Natural Science Foundation of China (31800532), the Forestry Science and Technology Project of Fujian Province (No. 16, 2019), the National Natural Science Foundation of Fujian Province (2018J05059), and the National Key Research and Development Plan (2016YFD0600301). The feedback from two anonymous reviewers was invaluable in improving the manuscript.

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Supplementary Material

Spatiotemporal distribution of canopy litter and nutrient resorption in a chronosequence of different development stages of *Cunninghamia lanceolata* in southeast China

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Number of pages: 4

Number of figures: 4

Fig. S1. Location of Xinkou National Forest Farm and of the different development-stage Chinese fir plantations studied.

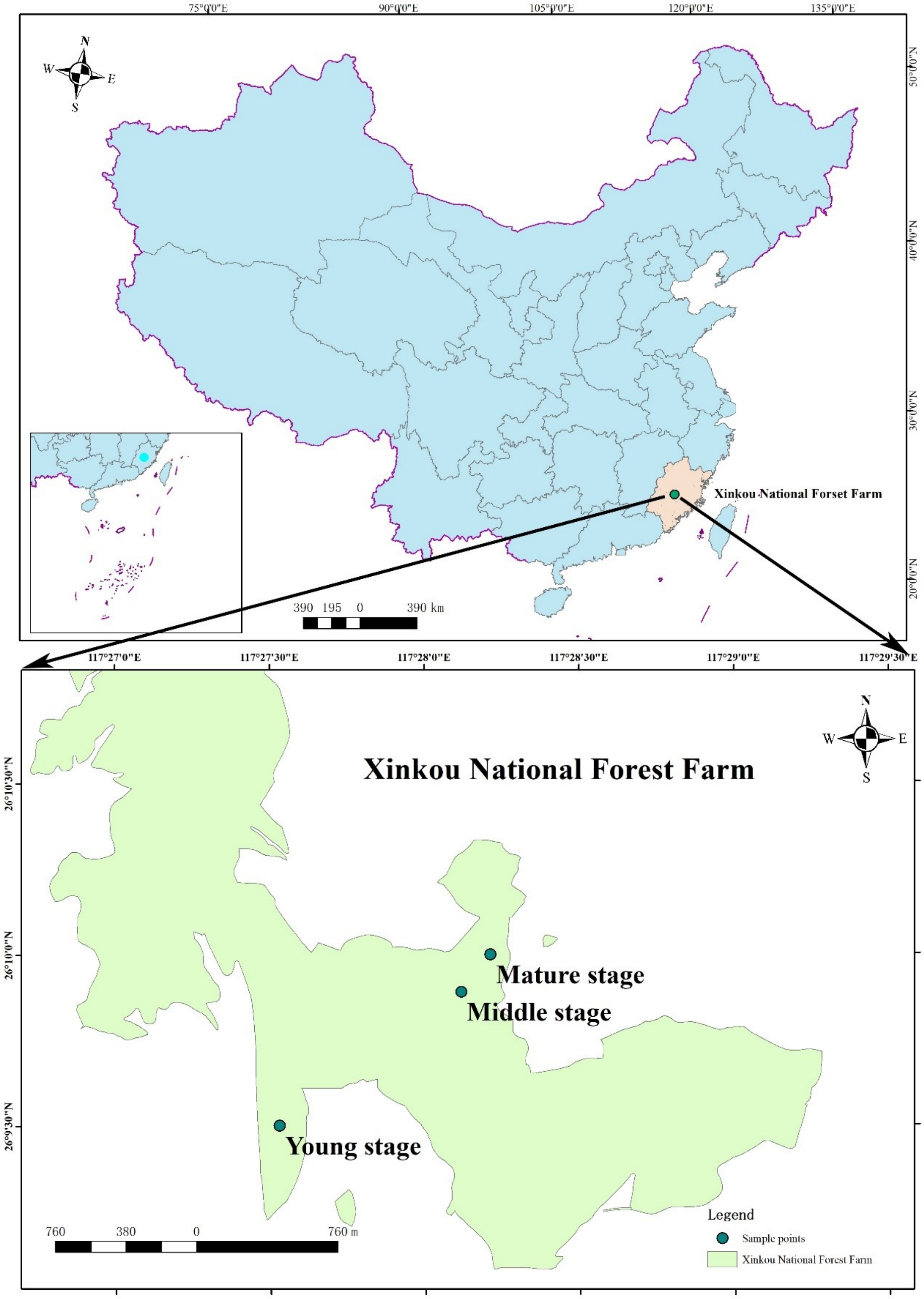

Fig. S2. Dead branches and leaves in the canopy of middle-age Chinese fir trees at the study site.

Fig. S3. Collection of dead branches and leaves from the tree canopy using clippers (left) and climbing (right).

Fig. S4. Five categories of needles [<1-year-old, 1-year-old, perennial, senesced (brown), and yellow] were collected from each shoot.