ECOLOGICAL STOICHIOMETRIC CHARACTERISTICS OF LEAF, LITTER, AND SOIL IN EUCALYPTUS PLANTATIONS WITH DIFFERENT AGES IN SUBTROPICAL, SOUTH CHINA

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Abstract. Understanding the ecological stoichiometry in the growth of different stand ages of *Eucalyptus* plantations is essential to evaluate the effects of management practices on biogeochemical cycling in plantation forest ecosystems. The study examined the relationship between leaf, litter, and soil stoichiometry on 3-, 6-, 9- and 12-year-old *Eucalyptus grandis x urophylla* plantations in subtropical China. Results showed that (1) With increased stand age, the concentrations of TN (total nitrogen) and TP (total phosphorus) in leaf and litter increased gradually. Leaf TC (total carbon) concentration decreased gradually, litter TC concentration initially increased and then decreased, and the concentrations of TC and TN in soil were opposite. Soil TC and TN concentrations decreased with increasing soil depth. (2) The ratios of C:N, C:P, N:P were litter > leaf > soil. With increasing stand age, C:N and C:P of leaf and litter decreased gradually, while the ratios of C:N, C:P, N:P of soil fluctuated greatly. (3) There were significant negative correlations between the C, N of soil and litter P and significant positive correlation was between the leaf C:N and litter C:P. The main limiting element was P. The results of this study can provide a scientific basis for the management of *Eucalyptus grandis x urophylla* plantations.
Keywords: *C, N, and P stoichiometric, Eucalyptus plantation, stand age, soil depth*

Introduction

Ecological stoichiometry is a powerful indicator of energy flow, material cycling, and nutrient limitations throughout ecosystems (Elser et al., 2010). In forest ecosystems, the biogeochemical cycles of carbon (C), nitrogen (N), and phosphorus (P), are linked through the reactions during primary production, respiration, and decomposition (Finzi et al., 2011). C, N, and P are the primary chemical elements of all organisms and play a vital role in adjusting plant primary productivity, energy flow, material circulation, and predation (Elser, 2006). The dynamics of the concentrations and ratios involving C, N, and P are closely associated to organic matter mineralization, plant respiration, and photosynthesis (Sardans et al., 2012). For instance, N and P govern plant growth and several other biological processes in terrestrial ecosystems (Elser et al., 2007). The ratios of C:N and C:P represent the ability of plant to assimilate C while simultaneously absorbing N and P (Liu et al., 2021). Plant N:P ratio can influence the functioning of terrestrial vegetation. For example, N:P determines the growth of individual plants and serves as a useful indicator for the shift between N- and P- limitation (Sardans et al.,

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2012) Understanding shifts in C, N, and P stoichiometry improves our understanding of the potential impact nutrients have on ecosystem processes under environmental change.

In China, approximately 69 million hectares are allocated to plantations and equates to one-third of plantation area globally. Over 60% of plantations are distributed in the subtropics (Chen et al., 2019). Eucalyptus (*Eucalyptus* spp.), native to Australia and New Guinea, has been widely planted as fast-growing commercial trees in numerous tropical and subtropical countries (Zhou et al., 2020). Due to the rapid growth, high adaptability, and economic value of *Eucalyptus*, by the year 2010, 3.68×10^7 ha of *Eucalyptus* had been planted in plantations across southwest China (Pang et al., 2018). Previous studies report that *Eucalyptus* growth declines with age and the decline is associated with changes in stand structure, gross primary production, foliar respiration nutrient elements (Ryan et al., 2004; Fan et al., 2015). Analyzing the alterations in the ecological stoichiometry of *Eucalyptus grandis x urophylla* ecosystems unveils the connections and constraining impacts of nutrient elements on eucalyptus growth. However, few studies have focused on the correlations between the stoichiometry characteristics and plant growth in *Eucalyptus* plantations.

In the study, we investigate C, N, and P concentrations and ratios in leaf, litter, and soil on different *Eucalyptus grandis x urophylla* spp. stand ages (3-, 6-, 9-, 12-year old) in subtropical China. We hypothesized that: (1) the C, N, P concentrations and stoichiometric characteristics in leaf, litter, and soil would be influenced by stand ages. (2) the variations in soil C:N:P stoichiometric ratio across stand ages decrease with increase in soil depth, because the influence of little input on soil nutrient decreases with increase in soil layer. (3) The main limiting element was P in *Eucalyptus grandis x urophylla* plantations. Exploring ecological stoichiometry characteristics is important for developing vegetation recovery and management strategies in karst ecosystems.

Materials and methods

Study site

This study was conducted at Qipo Forest farm (22° 28’ - 22° 46’ N, 107° 59’ - 108° 18’ E) in Nanning city, Guangxi Zhuang autonomous region in southern China. The study area has a continental subtropical monsoon humid climate. The mean annual temperature is 21-22℃ and the coldest and hottest months are January (-2.6 ℃) and July (38.4℃), respectively. The average annual rainfall is 1200-1300 mm yr^{-1}. The potential annual evaporation capacity is 1600-1800 mm (Peng et al., 2021). The average annual sunshine is 1827 h. The main soil type is red soil and is 90% hilly landform. Understory species in the plantation are dominated by *Broussonetia papyrifera*, *Litsea cubeba*, *Rhodomyrtus tomentosa*, *Melicope pteleifolia*, *Rhus chinensis*, *Miscanthussinensis*, *Lygodium japonicum* (Peng et al., 2021).

Sampling method

In May 2020, 3-, 6-, 9- and 12-year-old *Eucalyptus grandis x urophylla* plantations was chosen in this study location, where the natural characteristics (elevation, Slope aspect, slope gradient, crown density, average diameter, height) of each stand age were relatively similar (*Table 1*). three plots with an area of 10 m × 10 m, were set for each stand age. A total of 12 plots were established. The geographical coordinates, elevation,

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slope aspect, slope gradient, crown density, average diameter, height of each plot was recorded (*Fig. 1; Table 1*).

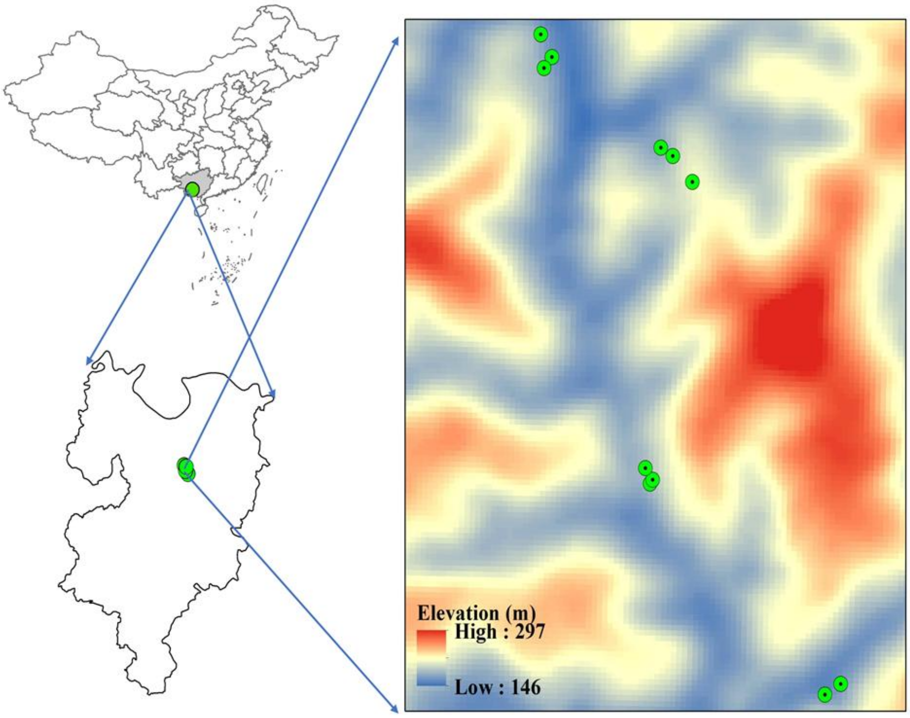

Figure 1. *Map of soil samples collecting locations*

Table 1. *Stand characteristics of different ages of Eucalyptus plantations (mean ± standard error)*

Forest age/year	Longitude	Latitude	Elevation (m)	Slope aspect	Slope gradient	Crown density	Average diameter (cm)	Height (m)
3	108.1916	22.6883	163	North-west	15°	0.4	8.27 ± 0.15	8.33 ± 0.33
	108.1918	22.6878	120	West	20°	0.5	8.2 ± 0.31	9.67 ± 0.33
	108.1916	22.6876	188	North-west	17°	0.4	8.2 ± 0.12	8.01 ± 0.12
6	108.1984	22.6749	172	North-west	18°	0.4	12.87 ± 0.47	14.67 ± 0.33
	108.1980	22.6747	170	North-west	18°	0.3	12.97 ± 0.39	14.56 ± 0.58
	108.1981	22.6757	168	West	9°	0.5	12.67 ± 0.17	14.76 ± 0.59
9	108.1940	22.6790	187	North-east	9°	0.5	12.5 ± 0.29	18.67 ± 0.67
	108.1941	22.6791	185	North-east	8°	0.4	13.4 ± 0.49	19.67 ± 0.67
	108.1939	22.6794	186	South-east	11°	0.5	15.03 ± 0.32	21 ± 0.58
12	108.1943	22.6860	198	North-east	18°	0.7	19.6 ± 0.83	22.67 ± 0.33
	108.1946	22.6858	184	North-west	10°	0.8	19.83 ± 0.44	23.33 ± 0.33
	108.1950	22.6853	206	West	15°	0.7	19.8 ± 0.45	23.02 ± 0.58

With each plot (10 m × 10 m) in 3-, 6-, 9- and 12-year-old *Eucalyptus grandis x urophylla* plantations, five well-developed Eucalyptus were selected according to diagonal placement for collecting the leaves, litter and soil samples. Leaves of the lower crown layer were collected from four directions of east, south, west, and north; and the leaf samples from the five trees were evenly mixed into one simple. The undecomposed litter on the ground surface was collected in a 1 × 1 m sample square under the

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corresponding five Eucalyptus stands, and the litter from the five trees was evenly mixed into one sample. Soil was collected from 0-20 cm, 20-40 cm, 40-60 cm depths using the diagonal method in the corresponding five sample plots where the litter was collected, and the five soil samples were evenly mixed into one sample.

All leaf and litter materials were dried to a constant mass at 75℃ for 72 h. Dried materials were then ground, passed through a 1- mm mesh sieve, and stored for analysis. Soil samples were collected using 4.0 cm diameter soil cores from 0-20 cm, 20-40 cm, 40-60 cm depths in each plot. The soil samples were put in a polyethylene bag and shipped to a laboratory for soil chemical analysis. In the laboratory, the roots, stones, and other debris were removed by hand. Soil samples were then air-dried, sieved through a 60- mesh sieve (0.25 mm diameter) before chemical analysis.

Laboratory analysis

Total N and C concentrations were measured using an elemental analyzer (Vario MAX CN, Elementar, Germany). Total P concentration was measured using the molybdenum blue colorimetric method after the samples were digested in a solution of H_2SO_4 and H_2O_2 (Li et al., 2018). The units (g kg^{-1}) of SOC, TC, TN and TP concentrations were transformed to mol kg^{-1}. The C:N, C:P and N:P ratios were calculated as molar ratios (atomic ratio) with the SOC:TN, SOC:TP and TN:TP ratios for soil samples, and TC:TN, TC:TP, and TN:TP ratios for leaf and litter sample.

Statistical analysis

One-way analysis of variance (ANOVA) was performed in conjunction with Tukey's test to analysis the concentrations and ratios of C, N, and P characteristics in leaf, litter, soil. Relationships among concentrations and ratios of C, N, and P characteristics in leaf, litter, soil were determined by correlation analysis. Tukey's test at the 0.05 significance level was used to compare means. All statistical analyses were performed with SPSS 20.0 (SPSS Inc., Chicago, IL, USA).

Results

C, N, and P concentrations characteristics

The concentrations of TC in leaf, litter, and soil in *Eucalyptus grandis x urophylla* plantations varied from 418.28 to 448.89 g kg^{-1}, 464.92 to 480.23 g kg^{-1} and 8.38 to 32.97 g kg^{-1}, respectively. Significant differences among the different stand ages were found ($P < 0.05$). Leaf TC concentration tended to decline with plantation age and was significantly lower in the 12-year-old plantations compared to the 3-year-old plantations. Litter TC concentration initially increases and then decreases with plantation age (*Fig. 2*). Soil TC concentration gradually decreased with increased soil depth, but initially decreases and then increases at the same depth from 3-year-old to 12-year-old plantations (*Table 2*; *Fig. 2*).

The concentrations of TN in leaf, litter, and soil in Eucalypt plantations varied from 16.49 to 17.99 g kg^{-1}, from 8.85 to 10.03 g kg^{-1} and from 0.73 to 2.02 g kg^{-1}, respectively. Significant difference among the different ages were found ($P < 0.05$). Leaf TN concentration initially increases and then decreases. Litter TN concentrations increased with stand age. Similar with soil TC, soil TN concentration gradually decreased with increased soil depth, but initially decreases and then increases at same depth ($P < 0.05$) (*Fig. 2*).

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Table 2. *The concentrations and ratios of TC, TN, and TP in soil in different ages of Eucalyptus plantations (mean ± standard error)*

Forest age/year	Soil depth/cm	TC (g kg^{-1})	TN (g kg^{-1})	TP (g kg^{-1})	C:N	C:P	N:P
3	0-20	32.97 ± 2.86Aa	1.88 ± 0.07Aa	0.68 ± 0.14	20.43 ± 0.97	130.94 ± 15.27Aa	6.5 ± 1.01
	20-40	22.42 ± 2.85Ba	1.38 ± 0.15Ba	0.66 ± 0.15	18.89 ± 0.81	92.4 ± 9.37Ba	4.95 ± 0.66
	40-60	13.05 ± 3.75Aa	0.96 ± 0.13Ba	0.6 ± 0.22	15.36 ± 2.22	59.67 ± 8.89Ba	4.05 ± 0.8
6	0-20	20.14 ± 1.61Ab	1.51 ± 0.24Ab	0.72 ± 0.04	15.72 ± 1.25	72.66 ± 10.17Ab	4.7 ± 1.02
	20-40	8.84 ± 0.41Bb	0.85 ± 0.02Bb	0.66 ± 0.03	12.14 ± 0.33	34.65 ± 0.01Bb	2.86 ± 0.08
	40-60	6.98 ± 0.46Bb	0.73 ± 0.01Bb	0.65 ± 0.04	11.16 ± 0.53	27.81 ± 3.35Bb	2.48 ± 0.18
9	0-20	23.63 ± 5.09Ab	1.34 ± 0.21Ab	0.54 ± 0.03	20.36 ± 1.98	112.87 ± 20.85Aa	5.47 ± 0.63
	20-40	11.89 ± 3.49Bb	0.76 ± 0.12Bb	0.58 ± 0.1	17.65 ± 2.41	59.56 ± 23.42Bb	3.14 ± 0.85
	40-60	8.38 ± 1.48Bb	0.64 ± 0.07Bb	0.46 ± 0.02	15.03 ± 1.23	47.03 ± 7.03Ba	3.1 ± 0.26
12	0-20	32.7 ± 0.41Aa	2.02 ± 0.07Aa	0.7 ± 0.12	18.96 ± 0.46	129.36 ± 25.13Aa	6.89 ± 1.51
	20-40	18.74 ± 0.72Ba	1.28 ± 0.08Ba	0.58 ± 0.1	17.08 ± 0.51	89.14 ± 18.39Ba	5.28 ± 1.24
	40-60	10.89 ± 0.74Aa	0.91 ± 0.14Ba	0.53 ± 0.06	14.39 ± 1.8	53.67 ± 6.23Ba	3.95 ± 0.94

Different capital letters indicated that the parameters were significantly different among different soil layers at the same age ($P < 0.05$), different lowercase letters indicated that the parameters were significantly different among different ages in the same soil layer ($P < 0.05$)

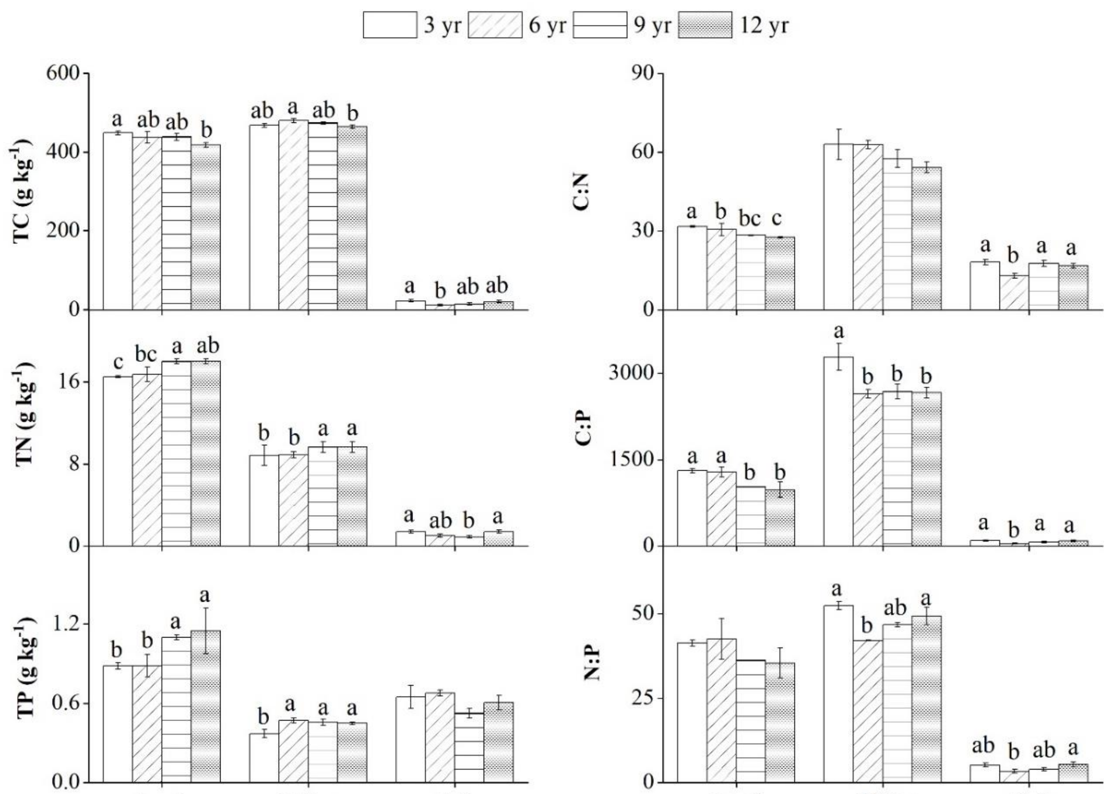

Figure 2. *The concentrations and ratios of TC, TN, and TP in leaf, litter, and soil in different ages of Eucalyptus plantations (mean ± standard error). Different letters indicated that the parameters were significantly different among different ages (P < 0.05) in leaf, litter, and soil in different ages of Eucalyptus plantations*

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The concentrations of TP in leaf, litter, and soil in Eucalypt plantations varied from 0.88 to 1.15 g kg^{-1}, from 0.37 to 0.47 g kg^{-1} and from 0.46 to 0.72 g kg^{-1}, respectively. TP concentration for leaf and litter increased with stand age ($P < 0.05$). However, no significant differences were found between different stand ages for soil TP concentration.

C, N, and P stoichiometry characteristics

For leaf, litter, and soil in Eucalypt plantations, the C:N ratio varied from 27.6 to 31.75, from 54.22 to 62.91 and from 14.39 to 20.43, respectively. The C:P ratio varied from 978.44 to 1312.17, 2647.28 to 3282.05, 34.65 to 130.94, respectively. The N:P ratio varied from 35.39 to 42.55, 42.08 to 52.36, 2.48 to 6.5, respectively. Ratios of C:N and C:P for leaf and litter decreased with increased stand age ($P < 0.05$). N:P ratio in litter decreased and then increased ($P < 0.05$), but N:P ratio in leaf was not significantly different. At the same depth, the C:P ratio initially decreased and then increased with increased stand age. At the same stand age, C:P ratio decreased with increased soil depth ($P < 0.05$), while ratios of C:N and N:P were not significantly different in different soil layers and stand ages (*Fig. 2*).

Relationships between leaf, litter and soil stoichiometry

Leaf and litter TN was significantly and positively correlated with TP ($P < 0.05$). Litter TP was negatively correlated with soil TC and TN ($P < 0.05$). Soil C was significantly and positively correlated with N ($P < 0.05$) (*Fig. 3*). Leaf C:N ratio and litter C:N ratio were significantly and positively correlated with litter C:P ($P < 0.05$). Leaf and soil C:P was significantly and positively correlated with N:P ($P < 0.05$) (*Fig. 4*).

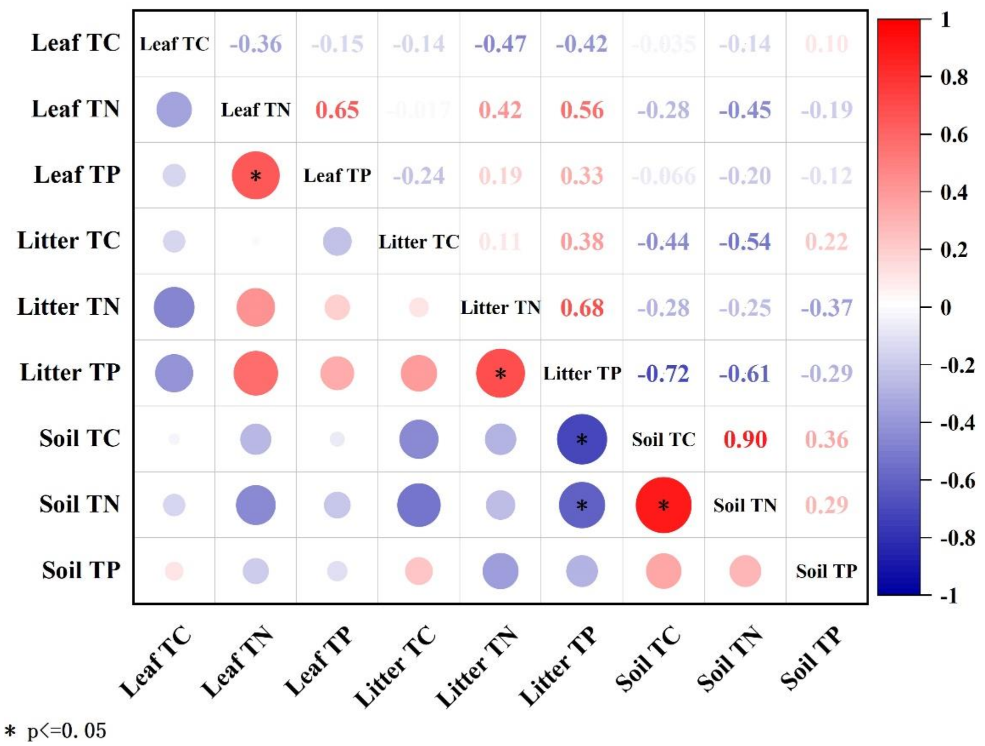

***Figure 3.** Correlation between concentrations of C, N, and P in leaf, litter, and soil in Eucalyptus plantations*

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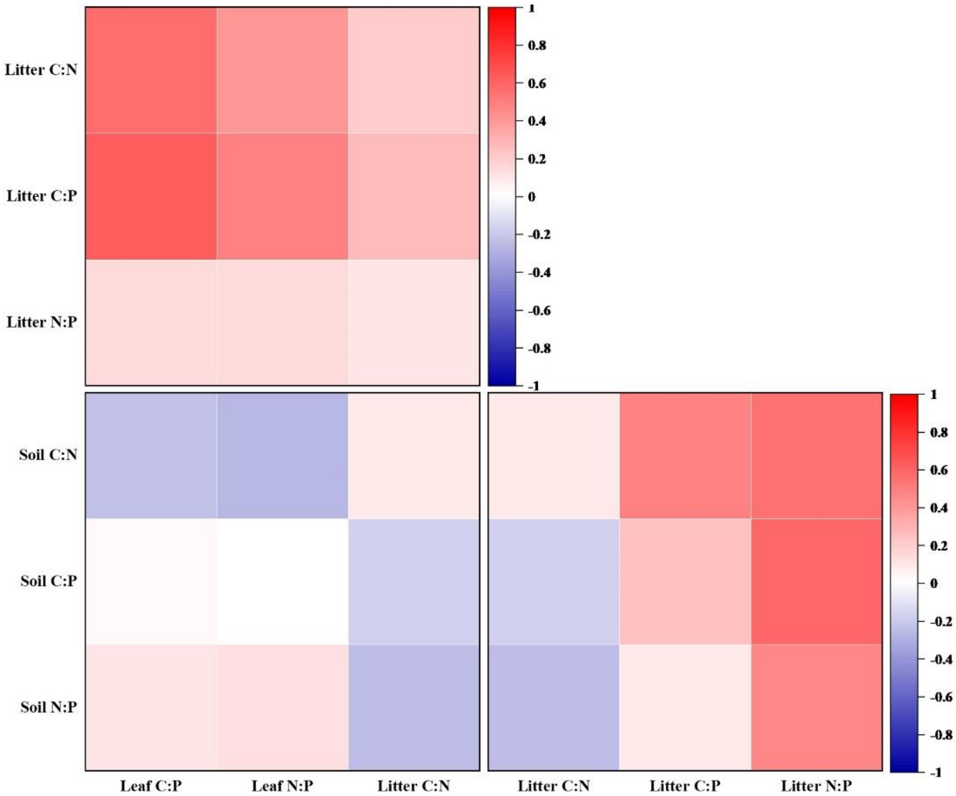

Figure 4. *Correlation between C:N, C:P, N:P in leaf, litter, and soil in Eucalyptus plantations*

Discussion

The leaf C concentration (435.89 g kg^{-1}) at the study site was lower than the global mean for leaf C concentration (464 g kg^{-1}) (Elser et al., 2000a, b), Karst forest in China (496.15 g kg^{-1}) (Yu et al., 2014), and the *Eucalyptus* plantation in Leizhou Peninsula in China (444.4-463.21 g kg^{-1}) (Xu et al., 2018). This indicates leaf C concentrations vary greatly at different regional scales. The leaf N concentration (17.23 g kg^{-1}) at our study site was lower than the global mean leaf N concentration (20.6 g kg^{-1}) (Elser et al., 2000b), China (20.2 g.kg^{-1}) (Han et al., 2005), and *Eucalyptus* plantation in Leizhou Peninsula in China (18.06-20.6 g kg^{-1}) (Xu et al., 2018). This may be because the study area has a subtropical continental monsoon climate. More rainfall results in increased leaching of available nitrogen in the region, this is not conducive to plant absorption and utilization of available nitrogen. The leaf P concentration (1.0 g kg^{-1}) was consistent with the mean leaf P for China (1.21 g kg^{-1}) (Han et al., 2005) and the *Eucalyptus* plantation in Leizhou Peninsula in China (0.93-1.17 g kg^{-1}) (Xu et al., 2018). Leaf P concentrations are consistent among these different scales because the growth of terrestrial plants in China is generally limited by P element (Han et al., 2005). Leaf C concentration decreases with increasing stand age. *Eucalyptus* in the young and middle-aged stands have a rapid growth stage of stem volume, the dry matter is synthesized and then the growth rate slows down. The growth rate of middle and older-aged *Eucalyptus* is faster and more rRNA is needed for protein synthesis. Thus, the concentrations of leaf N and P increases with increasing stand age.

In this study, the average concentrations of C, N and P in litter of *Eucalyptus grandis x urophylla* plantation are 471.78 g kg^{-1}, 9.37 g kg^{-1} and 0.44 g kg^{-1}, respectively. This

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result is similar with *Eucalyptus* plantation on the Leizhou Peninsula, China (Xu et al., 2018) and lower than the average value in the Changbaishan, Dinghushan, Xishuangbanna and Qianyanzhou, China (508.16 g kg^{-1}, 10.85 g kg^{-1}, 0.46 g kg^{-1}, respectively) (Wang et al., 2011). The average C concentrations of litter in the 6 yr stand is significantly higher than other stages. This may be because the crown density of 6 year *Eucalyptus grandis x urophylla* plantation is the highest, the light transmission ability is weak, and the litter decomposition rate is low. The concentrations of N and P in leaf and litter increases with increasing stand age. Soil C and N concentrations initially decrease and then increase with increasing of stand age and decrease with increasing of soil depth. The soil C and N concentrations increase with increasing of stand age. This is due to the C and N mainly being derived from litter, understory vegetation diversity increased with increasing of *Eucalyptus grandis x urophylla* plantation stand age. The increase of litter and root exudates was beneficial for soil C and N input. Soluble organic carbon from the top soil is washed into the lower soil layer by rain (Zhao et al., 2019). Thus, soil C concentration decreased with increasing soil depth. Soil P is not significantly different among different soil layers in our study. This might be because unlike the main sources and changing trends of soil C and N, soil P element is a sedimentary mineral element with a low mobility in soil (Zhang et al., 2021).

The mean values of C:N (44.3) and C:P (1987.7) of *Eucalyptus grandis x urophylla* leaf are higher than the global terrestrial leaf (22.5 and 496.16, respectively) (Elser et al., 2000b). This indicates that N and P utilization rates are low in *Eucalyptus grandis x urophylla* plantations. Leaf N:P ratios are used to indicate N-limitation or P-limitation in ecosystems, N:P ratios < 14 suggest N limitation, N:P ratios > 16 suggest P limitation. With an N:P ratio between 14 and 16, plant growth is co-limited by N and P together. Our study shows *Eucalyptus grandis x urophylla* is limited by Han et al. (2005) reported that in China ecosystems were limited by P by measuring > 735 plant species.

The ecological stoichiometry characteristics of C, N and P in litter is influenced by soil nutrient supply and plant nutrient utilization. When the supply of elements in the soil to the plants is lacking, the plant reabsorbs nutrients from the litter and the ecological stoichiometry characteristic of litter changes (Franklin and Agren, 2002). In our study, the C:N and C:P ratios in litter are higher than leaf and soil, which was consistent with Zeng et al. (2015). Studies have shown when the C:N of litter was lower than 40, mineralized decomposition and the net release of N begin to occur in litter. Additionally, the lower the C:N and C:P, the faster the decomposition rate (Sun et al., 2019). In our study, the C:N in litter is lower than 40, indicating decomposition mineralization of the litter and the release of N were relatively fast. The N:P is an important index restricting the decomposition of litter and low N:P ratios are beneficial to the decomposition of litter (Pan et al., 2011). In our study, the N:P in litter is higher than the global ratio, which tempered the decomposition of the litter at the study site. Soil C:P is important for plant growth and development and indicates the potential for P release and the absorption and fixation of P from the environment (Zeng et al., 2015). In our study, the C:P in soil (78.61) is lower than global forests (81.9) (Tian et al., 2010), indicating soil P is severely limited. Soil C:P ratio initially decreases and then increases with increasing forest age. This indicates soil P availability first increased and then decreased. In addition, soil C:P decreases with increasing soil depth and is primarily controlled by the relatively stable soil P along the soil profile. Soil N:P ratio (4.55) was

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lower than the average of terrestrial ecosystems in China (5.2) (Tian et al., 2010). The study area is located in red soil and the soil storage of P is greater, which inhibits plants from absorbing and utilizing P, and the availability of soil P is low (Zeng et al., 2013).

Soil is the substrate for plant growth and contains the main source of nutrients for plant growth and development. Plants fix C via photosynthesis in the leaf to synthesize organic matter. The organic matter then returns to the soil via litter decomposition or nutrient transfer. Therefore, the differences in the concentrations and stoichiometry characteristics of the C, N, and P in leaf, litter, and soil are important to understand (Ladanai et al., 2010). In our study, the concentration of N was significantly and positively correlated with P in leaf and litter, the concentration of C was significantly and positively correlated with N in soil. The concentration of P was significantly and positively correlated with C and N in litter. We suggest C and N in the soil are mainly obtained from litter and organic matter formed by plant root decomposition.

Conclusions

This study explored leaf, litter, and soil stoichiometry in different stand ages of *Eucalyptus* plantations. The results indicated leaf C, N, and P stoichiometric characteristics differed among different ages and the differences may be caused by changes in litter return and soil nutrients. In the *Eucalyptus* plantations, the N and P concentrations in leaf and litter increased with increasing of forest age, while the C concentration decreased with decreasing forest age. Soil C, N, and P initially decreased and then increased with the increasing forest age, while ratios of C:N, C:P, N:P in leaf was opposite. The ratios of C:N, C:P, N:P in litter and soil fluctuated greatly. P might be a limiting factor for the growth of *Eucalyptus* in the study region. The results of this study can provide a scientific basis for the management of *Eucalyptus* plantations.

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Conflict of interests. The authors declare that they have no competing interests.

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