



Available soil nutrients and water content affect leaf nutrient concentrations and stoichiometry at different ages of *Leucaena leucocephala* forests in dry-hot valley

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Received: 11 January 2018 / Accepted: 12 May 2018 / Published online: 14 June 2018
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Abstract

Purpose The carbon (C), nitrogen (N), and phosphorus (P) concentrations of leaves can reflect soil nutrient supply conditions and changes in soil. An understanding of species adaptability and nutrient use efficiency in extreme ecosystems can help land managers choose effective methods to improve management and community structure of introduced plants which may induce biological invasion and limit the regeneration of native species.

Materials and methods We selected the *Leucaena leucocephala* forests in three ages (9, 15, and 26 years old) in the Jiangjiagou Gully to study the relationships between (i) soil factors and forest age and (ii) leaf nutrient concentrations. Soil factors and leaf nutrients were measured in nine sampling quadrats of 10 × 10 m of each plot. We used ANOVA to examine differences in leaf variables and soil factors at different ages of *L. leucocephala* forest. Pearson's correlation analysis and linear regression analysis were conducted to identify the relationships between soil factors and leaf variables. Then, we used analysis of covariance to examine combined effects of forest ages and soil factors on leaf variables.

Results and discussion Leaf N was significantly correlated with available P, while leaf P was significantly correlated with both available P and available N. Leaf N and P had no significant relationship with soil total N and P. Leaf C:N:P stoichiometries had a higher significant correlation with total N, available N, and soil water content.

Conclusions Our findings illustrate that available N and available P are the main limitations for *L. leucocephala*, though available P imposed a stronger limitation than available N. Moreover, soil water content played an indispensable role on nutrient accumulation and the soil ecological environment. Our results provide useful information to improve *L. leucocephala* community structure and reduce soil degradation in a dry-hot valley.

Keywords Forest age · Leaf nutrients · *Leucaena leucocephala* · Soil factors · Stoichiometry

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1 Introduction

Soil nutrients are among the most important factors controlling plant growth and the structure of plant communities (Tilman 1986; Koerselman and Meuleman 1996). Also, forest type and age have a significant impact on terrestrial carbon (C), nitrogen (N), and phosphorus (P) cycles and their interactions (Tamm 1991; Cao et al. 2009), leading to altered C, N, and P stoichiometry and storage. Case studies have reported that negative or positive interactions exist among C, N, and P geochemical cycling (Cao et al. 2009; Gao et al. 2014), but to date, little attention has been paid to the reactions of these elements in plants to their environments, with the exception of simple element circulation in forest lands (Casper et al. 2000; Gallardo and Covelo 2005). Leaf nutrient concentrations can reflect the nutritional status of plants, controlled by soil fertility, water supply, precipitation, and temperature, as well as other environmental factors (Tana et al. 2006). For example, the N:P ratio of leaf can simply and accurately predict N or P limitation of plant growth (Koerselman and Meuleman 1996). In addition, plants can use biomass allocation strategies to adapt nutrient limitations in arid-hot grasslands (Yan et al. 2016), but we still know little about plant leaf responses to a similar severe environment, which may potentially limit our knowledge about the adaptive strategies of species to their living environment in population dispersal. It is therefore necessary to improve our understanding of the relationships between plants and soil that contributes to the growing body of knowledge on plant adaptability when describing functional differences between plants and their responses to environmental factors (Güsewell 2004; Miatto et al. 2016).

Stoichiometry is involved in all aspects of ecology, from gene level to ecosystem level, which includes food webs, nutrient cycling, and nutritional interactions (Downing and McCauley 1992; Urabe and Watanabe 1993; Elser and Urabe 1999). Global or large-scale stoichiometry researches—combined with molecular theory, growth rate hypothesis theory, and homeostasis theory—have been the focus of stoichiometry in recent years (Elser et al. 2009). Although much of this research focuses on differences among multi-scales, there is an increasing recognition that stoichiometry can be affected not only by soil nutrient supply but also by other environmental factors such as biological controls, rainfall, and temperature (Yu et al. 2010). Furthermore, many environmental factors interact with soil nutrients to affect stoichiometric variation in some extreme ecosystems. For example, Lü et al. (2012) found that plant internal nutrient translocation occurred in response to changes in N and water availability. Also, forest age can affect the spatial variation of soil stoichiometry (Wang et al. 2017). However, the question of whether forest age had a significant effect on leaf

nutrients and stoichiometry even after accounting for the effects of soil remains poorly addressed.

Though facilitation and negative effects of exotic species are still debated (Rodriguez 2006), due to their better adaptations to a deteriorated environment compared to native plants, some exotic species have been successfully introduced in many studies to reduce soil erosion and accelerate land reclamation and rehabilitation in degraded lands (Hesp 1991; Bennett and Kruger 2013; Lin et al. 2017). For example, *Leucaena leucocephala*, a plant from southern Mexico and northern Central America, was introduced to Yunnan province, China, in 1981 (Lin et al. 2008). This species has strong environmental adaptability, and although it has been proven allelopathic to some native plants (Chou and Kuo 1986), it has become the most successful introduced species in Jinsha River dry-hot valley ecosystems (Lin et al. 2009). Recently, many researchers debate this plant due to the increasing area of its planting. On the one hand, the seedlings produced by its rapid spread dominated the understory, resulting in biological invasion and the decline of native species (Ma et al. 2006). Its root caused soil desiccation by stronger water-absorbing capacity than native species (Kang et al. 1999). On the other hand, benefits of planting this species include its ability to survive extreme environments, increase vegetation cover, and improve N fixation (Sanginga et al. 1988; Normaniza et al. 2008). Moreover, it controls gravitational erosion such as debris flow and landslides, while substituting for native woody species in supplying abundant firewood to local people through high root reinforcement and stump-sprouting capacity (Normaniza et al. 2008; Lin et al. 2009; Guo et al. 2014). Previous studies show differences in nutrient resorption efficiency at different ages of *L. leucocephala* forests (Deng et al. 2015), but do not consider how soil factors and forest age affect its leaf nutrients and stoichiometry. Here, we analyzed a data set containing C, N, and P concentrations in the forest soil and 1-year-old leaves of *L. leucocephala* at different ages. Our objective was to analyze the relationship between (i) soil factors and forest age and (ii) leaf C, N, and P concentrations to determine the main factors that affect the variation of leaf C, N, and P concentrations. Though the N:P ratio of leaf is used to predict plant nutrient limitation (Koerselman and Meuleman 1996), little is known about the role of N fixation ability in shaping plant adaptation to nutrient limitations. Therefore, in this study, we were also interested in knowing whether *L. leucocephala* was limited less by N than P due to its N fixation ability. This study may improve our understanding of introduced species adaptability, growth strategies, and nutrient cycling in extreme ecosystems and help land managers choose better ways to improve the management and community structure of the forests dominated by introduced plants.

2 Materials and methods

2.1 Study area

Our study area is the Jiangjiagou Gully located in Dongchuan District, Kunming city, Yunnan province (latitude 26° 13'–26° 17' N, longitude 103° 06'–103° 13' E) at an altitude between 1042 and 3269 m above sea level. According to vertical climate differences, Jiangjiagou Gully contains three strata: (1) the first, dominated by torrid red soil and calcic regosols, belongs to the dry-hot river valley ecosystem type at altitudes between 1042 and 1600 m and has a mean yearly rainfall of 600–700 mm, a mean annual temperature of 20 °C, and a mean annual potential evapotranspiration of 3700 mm year⁻¹; (2) the second, dominated by mountain red soil, belongs to the subtropical and sub-humid warm temperate ecosystem type at altitudes between 1600 and 2200 m and has a mean yearly rainfall of 700–850 mm, a mean annual temperature of 13 °C, and a mean annual potential evapotranspiration of 1700 mm year⁻¹; and (3) the third, dominated by mountain yellow-brown and brown soil, belongs to the humid warm temperate ecosystem type at altitudes of > 2200 m and has a mean yearly rainfall of 1200 mm, a mean annual temperature of 7 °C, and a mean annual potential evapotranspiration of 1350 mm year⁻¹. Historically, the main rainy season is between May and September and the dry season is between October and April.

Due to severe soil and water loss, as well as deforestation by humans for farmland and firewood, Jiangjiagou Gully became a typical debris flow basin, leading to serious ecological degradation and destruction of native plants (Lin et al. 2014). Vegetation restoration and protection measures including planting saplings, aerial seeding, and natural reforestation have been launched to improve vegetation cover. In 1988, *L. leucocephala* was planted across about 6000 m² with 1-year-old seedlings, at a density of 1 m apart with 1.5 m between rows, and at altitudes between 1300 and 1400 m. Up to 2014, seed dispersal increased the area of *L. leucocephala* cover, which led to the development of an unevenly aged forest with a total area of about 1.5 ha.

2.2 Sample plots and experimental design

Three sample plots with similar natural conditions, as seen in Fig. 1 and Table 1, were selected consisting of 9-year-old, 15-year-old, and 26-year-old *L. leucocephala* forests to study the relationship between soil factors and forest age and leaf nutrients and stoichiometry. All three adjacent experimental plots have calcic regosols and are located near Dongchuan debris flow observation research station, which is downstream of the Jiangjiagou Gully. Plot 1 developed from bare land to a *L. leucocephala* forest planted with 1-year-old seedlings in 1988. Plots 2 and 3 also developed from bare land and were populated in 1999 and 2005 by seed dispersal from *L.*

leucocephala planted in 1988. In plot 1, the average diameter at breast height (DBH) and height of *L. leucocephala* trees are 10.21 cm and 12.2 m, respectively, with about 2366 stems per hectare. In plot 2, average DBH is 7.43 cm and average height is 9.7 m, with about 3033 stems per hectare. In plot 3, average DBH and height are 5.28 cm and 7.4 m, respectively, with about 4400 stems per hectare. Canopy density was about 60% at each plot. However, understory plant species and cover varied as follows: in plot 1, *Dodonaea viscosa* and *Heteropogon contortus* dominated the understory layer with cover of about 80%; in plot 2, *Agave achilleoides* and *Themeda Japonica* dominated with cover of about 25%; in plot 3, *L. leucocephala* seedlings and *H. contortus* dominated with cover of about 20%. In all plots, nine sampling quadrats of 10 × 10 m were randomized on the northeast slope of each plot. We investigated plant species quantity, cover of each plant species (including trees, shrubs, and herbs), grass height, and the height and average crown diameter (calculated in the direction of north-south and west-east) of shrubs and trees among all quadrats in August 2014.

2.3 Field sampling

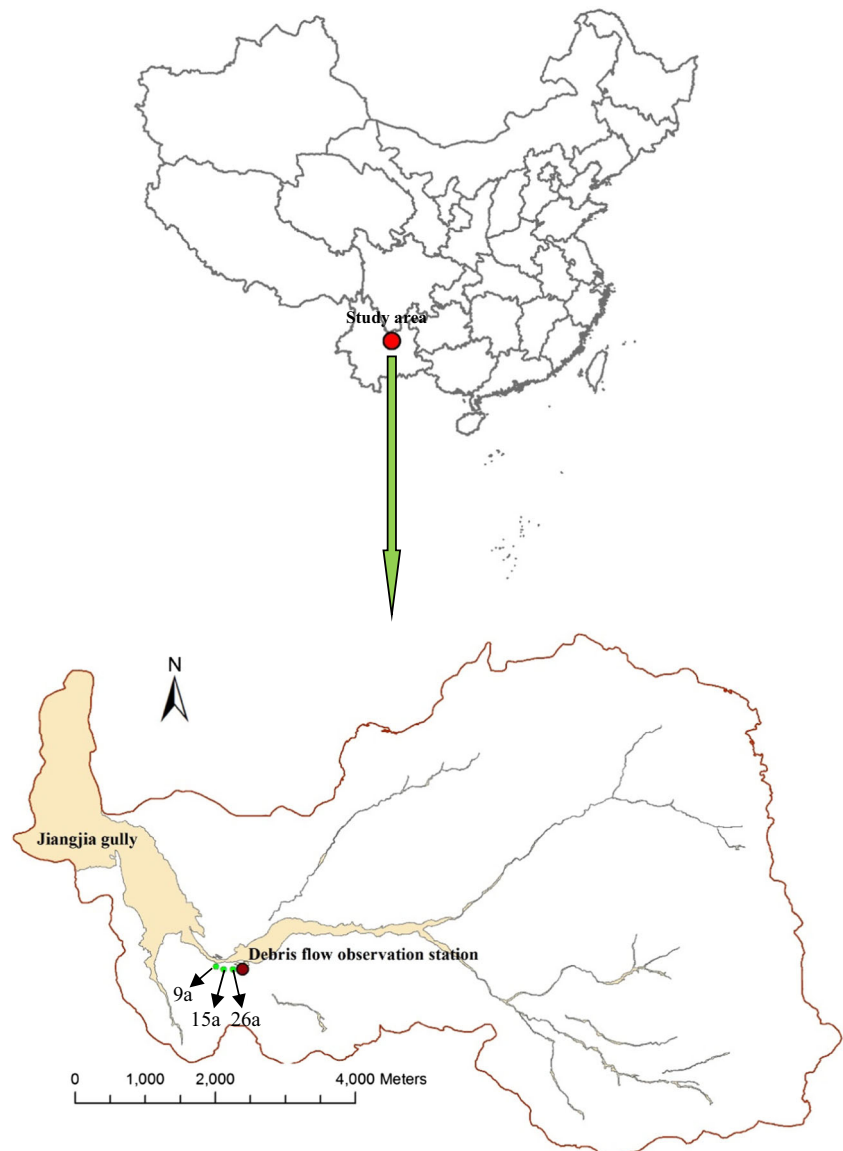
2.3.1 Soil sampling and analysis

Soil samples were collected during the growing season in August 2014. In each selected quadrat, at least five surface soil samples from the depth of 0–20 cm were taken randomly, weighed, and mixed before taking a 20-g sub-sample for determining soil water content with a soil water-measuring instrument (TZS-I, China). No precipitation occurred for 8 days before sampling in each quadrat. After being transported to the laboratory, each soil sample was air-dried, disaggregated, and passed through a 0.149-mm screen. Soil available N and available P were analyzed by using alkaline hydrolysis diffusion and hydrochloric acid-sulfuric acid extraction. Soil organic carbon (SOC) was measured using the K₂Cr₂O₇ volumetric dilution heating method (Nelson and Sommers 1982). Total N was determined using the Kjeldahl procedure (Gallaher et al. 1976). Total P was measured by the ammonium molybdate method after persulfate oxidation (Schade et al. 2003). Alkaline hydrolyzable N (AN) was measured using the ISNT method (Khan et al. 2001). To measure available P, we used the sodium bicarbonate Olsen method (Pierzynski 2000).

2.3.2 Leaf collection and analysis

In each quadrat, we chose a third-level (from the main stem) branch from sunny aspect in all *L. leucocephala*. After selecting 20 complete and healthy fresh leaves from each third-level branch, we mixed them in a bag as a representative sample. In total, nine bags of mixed leaf samples were

Fig. 1 Geographic location of the Jiangjiagou Gully selected as the study area and the distribution of 9-, 15-, and 26-year-old *L. leucocephala* forests



collected from nine quadrats in each plot. The samples were oven-dried for 30 min at 90 °C, and then oven-dried at 65 °C and weighed. C concentrations were determined using the $K_2Cr_2O_7$ volumetric dilution heating method (Nelson and Sommers 1982). N concentrations were measured using the micro-Kjeldahl method (Gallaher et al. 1976). P concentrations were measured using the ammonium molybdate method after persulfate oxidation (Schade et al. 2003).

2.4 Statistical analysis

A one-way ANOVA in conjunction with the least significant difference (LSD) test ($\alpha = 0.05$) was used to examine sources of variation between leaf C, N, and P concentrations and soil factors at different ages of *L. leucocephala* forests. Pearson's correlation analysis and linear regression analysis were conducted to identify the relationships between (i) C, N, and P

Table 1 Location, abiotic conditions (elevation, exposure, and slope), and two mean attributes (DHB and height of all the trees sampled in each site) of the plots studied to analyze the nutrient concentrations in different ages of *L. leucocephala* forests

Age (a)	Longitude	Latitude	Elevation	Exposure	Slope (°)	Average height (m)	Average DBH (cm)
9	103° 08' 01"	26° 14' 41"	1399.1	NE	28.5	7.4 ± 1.24	5.28 ± 0.74
15	103° 07' 60"	26° 14' 43"	1352.4	NE	33.9	9.7 ± 1.66	7.43 ± 0.62
26	103° 07' 49"	26° 14' 53"	1314.9	NE	26.8	12.2 ± 1.78	10.21 ± 0.86

concentrations and stoichiometric ratios of leaf and (ii) soil factors. Analysis of covariance (ANCOVA) was used to examine the combined effects of forest ages and soil factors on leaf variables. Statistical analyses were performed using R language (Version 3.4.1).

3 Results

3.1 Leaf nutrient concentrations and stoichiometric ratios

Leaf C concentration varied across different ages of *L. leucocephala* forests (Fig. 2(a)). Significantly lower leaf C concentration was found in the 26-year-old *L. leucocephala* forest. Fifteen-year-old and 26-year-old forests' N and P concentrations were significantly higher than that of the 9-year-old forest (Fig. 2(b, c)).

Figure 2 also summarizes the statistics of stoichiometric ratios. The results show that the highest C:P ratio was observed in the 9-year-old forest and the lowest was in the 26-year-old forest. C:P ratio was significantly higher in the 9-

year-old forest than in the 15-year-old and 26-year-old forests (Fig. 2(d)). The C:N ratio, varying from 8.61 to 10.44, was significantly higher in the 9-year-old and 15-year-old forests than in the 26-year-old forest (Fig. 2(e)). However, the N:P ratio of leaves had no significant differences among three ages of *L. leucocephala* forest (Fig. 2(f)).

3.2 Soil factors and correlation analysis

SOC and total N (TN), varying from 27.01 to 41.70 g kg⁻¹ and from 2.71 to 4.11 g kg⁻¹ respectively, were significantly higher in 9-year-old and 15-year-old forests than in 26-year-old forests (Fig. 3(a, b)). However, total phosphorous (TP) had no significant difference among three ages (Fig. 3(c)). Available P and soil water content were significantly higher in 9-year-old and 25-year-old forests than in the 15-year-old forest (Fig. 3(e, f)). Available N was significantly higher in the 9-year-old forest than in the 26-year-old forest, but there was no significant difference between the 9-year-old forest and the 15-year-old forest or the 15-year-old and the 26-year-old forest.

Fig. 2 The C, N, and P concentrations and stoichiometry in different ages of *Leucaena leucocephala* forests. The box plots show the 75th and 25th percentiles (box), and the highest and lowest observations. The different small letters of highest point show the different forest ages that reached significant level ($p < 0.05$), and the lowest value below the box plots was the average value

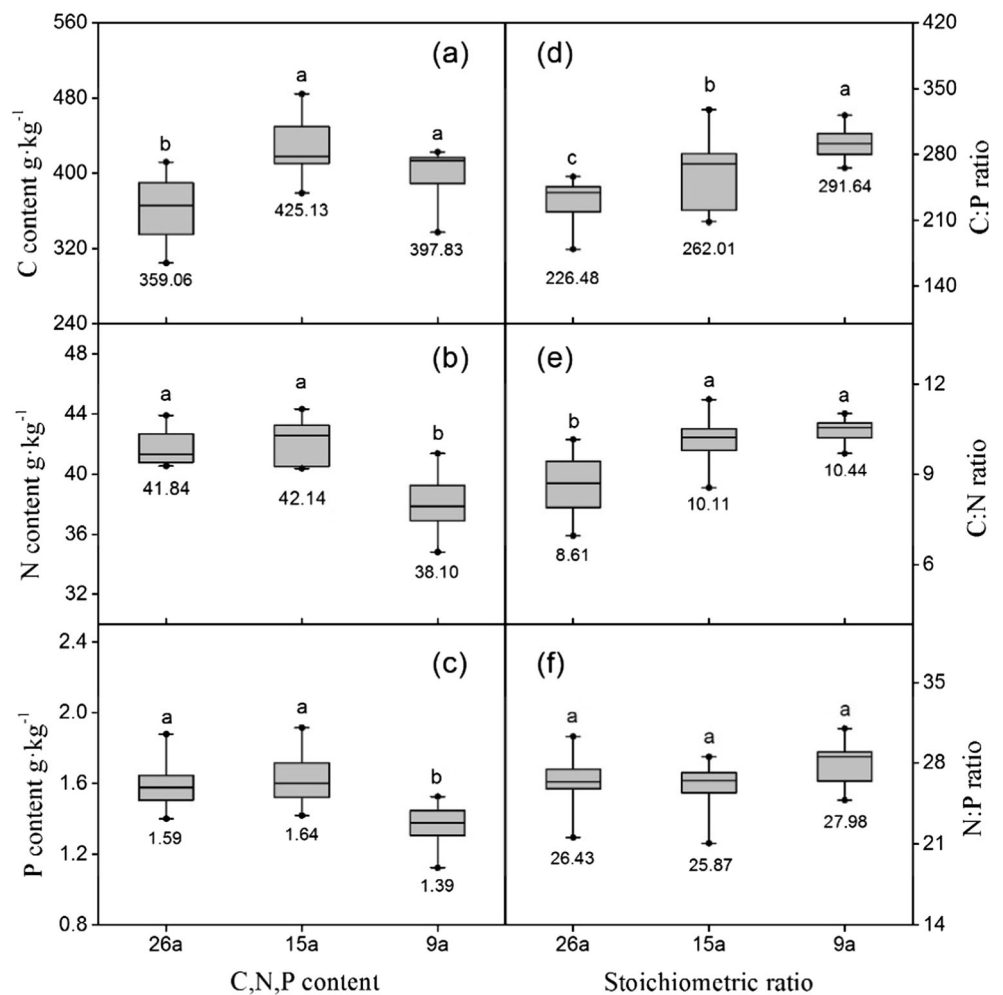
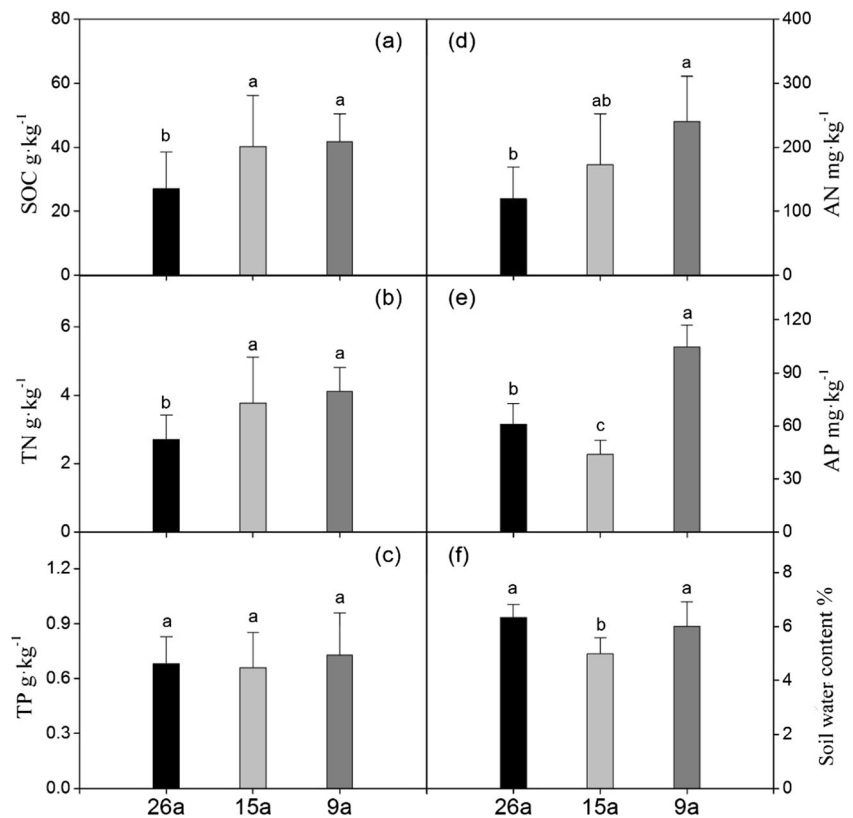


Fig. 3 Descriptive statistics of soil attributes including SOC, TN, TP, available nitrogen (AN), available phosphorus (AP), and soil water content in different ages of *L. leucocephala* forests. The different letters mean significant difference ($p < 0.05$)



Among six soil factors in these three forest ages, Pearson's correlations showed that only seven pairwise correlations were significantly related (Table 2). Available N and TP content had a respectively high correlation with other factors. However, soil water content had no significant correlation with the other five factors.

3.3 The influences of soil factors and forest age on leaf variables

There were no significant correlations between leaf C, N, and P concentrations and soil TP ($p > 0.05$; Table 3). Leaf C concentration had significantly positive relationships with SOC, TN, and available N, but a negative relationship with soil water content ($p < 0.05$). Leaf P concentration had significantly negative relationships with soil available N and available P ($p < 0.05$). Leaf N only had a significantly negative relationship with soil available P ($p < 0.05$).

As seen in Fig. 4, there were no significant correlations between soil TP and available P with leaf stoichiometry ($p > 0.05$; Fig. 4c, d). SOC, TN, and available N had significantly positive correlations with C:N and C:P ratios ($p < 0.05$; Fig. 4a, b, e). Soil water content had a significantly negative correlation with leaf C:P ratios ($p < 0.05$; Fig. 4f).

The interaction between forest age and soil factors did not markedly influence any leaf variables except significant interaction effects between forest age and soil water content on leaf

C concentration and leaf C:N ratio, and between forest age and soil N:P ratio on leaf N concentration (Table 4).

4 Discussion

As the basic substrate for most plants across the globe, soil is the main nutrient source for plants (Rodríguez Rodríguez et al. 2005) and affects plant distribution, productivity, and stability (Condit et al. 2013). It has been well documented that *L. leucocephala* in dry-hot valley ecosystems, lacking water and growing in loosened soil, should preferentially supply comparatively higher quantities of organic compounds to the roots for absorbing more nutrients and water from soil, inducing a large amount of fine root growth (Guo et al. 2014). However, whether the response of *L. leucocephala* leaves to extreme environment can occur in a similar way to root growth has received little attention. Compared with the four types of forest ecosystems (485.49 g kg⁻¹ C concentration) in China (Wang et al. 2011), we found that *L. leucocephala* forests had comparatively lower leaf C concentration (394.01 g kg⁻¹), suggesting that *L. leucocephala* may supply lower quantities of organic compounds to leaves. This result may prove the hypothesis of Guo et al. (2014). In water shortage regions, where soil water availability appears to be one of the main factors that control plant distribution, it could be used as an indicator of the predominance of plant communities with

Table 2 Pearson’s correlation between soil attributes analyzed to be compared to the leaf nutrient concentrations in different ages of *L. leucocephala* forests

Index	SOC	TN	TP	Available nitrogen	Available phosphorus	Soil water content
SOC	1					
TN	0.857(+)**	1				
TP	0.377(+)**	0.275(+)**	1			
Available nitrogen	0.589(+)**	0.668(+)**	0.253(+)**	1		
Available phosphorus	0.034	0.073	0.028	0.222(+)*	1	
Soil water content	0.001	0.009	0.016	0.000	0.123	1

Data in the table are Pearson’s *r*. Plus (+) sign means positive correlation

*Significant correlation ($p < 0.05$)

**Extremely significant correlation ($p < 0.01$)

a conservative resource use strategy (Pérez-Ramos et al. 2012). Although soil water content did not have significant correlations with soil nutrient content in our study, it had significantly negative correlations with leaf C concentration and C:P ratio (Fig. 4), suggesting that high C concentration with fast growth rate in *L. leucocephala* may cause soil desiccation under water shortage conditions (Kang et al. 1999). Leaf N and P concentrations had no significant correlation with soil N and P concentrations, indicating that total soil nutrients do not appear to be control factors for nutrient accumulation in leaves. This result is consistent with other studies demonstrating non-significant impacts of soil N and P content on leaf N and P concentrations (Marler and Lawrence 2015; Miatto et al. 2016). We found that leaf C concentration was positively related to available soil nutrients, but leaf N and P concentrations were negatively related to available P (Table 3). This may be due to the decrease of available P in soil caused by rapid growth of *L. leucocephala*. Therefore, improving the amount of available mineral nutrients in soil or nutrient absorption capacity of plants may be a strategy to enhance plant growth or adaptability (Niinemets and Kull 2003).

It has been proven that leaf stoichiometry was mainly influenced by N and P concentrations, reflecting the usage efficiency

of N, P, and C assimilative capacity (Wardle et al. 2004). Moreover, previous studies indicated that individual organisms growing rapidly have a special life history strategy to increase their growth rates with decreasing C:N and C:P (Elser et al. 1996; Makino et al. 2003). This strategy may also be working in our case, because *L. leucocephala* leaves’ C:N and C:P ratios were significantly lower than those of four types of forest ecosystems in China (Wang et al. 2011) and global forest systems (Megan et al. 2004) (Fig. 5), suggesting that *L. leucocephala* may have a comparatively fast growth rate, even when growing in a deteriorated environment. In addition, even though some researchers debate the suitability of the simple “N:P tool” on nutrient limitation detection, an N:P ratio is still used to simply and accurately predict nutrient limitation of the vegetation—an N:P ratio > 16 indicates P limitation, while an N:P ratio < 14 is indicative of N limitation (Koerselman and Meuleman 1996). Due to the strong ability of N fixation in *L. leucocephala* whose leaves had nearly 25% protein concentration (about 38.5 g kg⁻¹ N concentration) (Liu et al. 2010), N limitation is not a driving force for the growth of *L. leucocephala* according to the detecting tool of N:P ratio, because the average N:P ratio was 26.76, higher than 16. P concentration ability therefore limited the growth of *L. leucocephala* at our study site. This result is

Table 3 Regression analysis between leaf nutrient concentrations and soil attributes in different ages of *L. leucocephala* forests

	Index	SOC	TN	TP	Available nitrogen	Available phosphorus	Soil water content
Leaf C	<i>R</i> ²	0.231(+)	0.266(+)	0.044	0.279(+)	0.017	0.244(–)
	<i>p</i>	0.011	0.006	0.296	0.005	0.523	0.005
Leaf N	<i>R</i> ²	0.027	0.070	0.016	0.085	0.350(–)	0.007
	<i>p</i>	0.417	0.183	0.528	0.141	0.001	0.689
Leaf P	<i>R</i> ²	0.103	0.118	0.060	0.150(–)	0.305(–)	0.000
	<i>p</i>	0.102	0.079	0.217	0.046	0.003	0.955

Italic numbers represent a significant correlation at $p < 0.05$. Plus (+) sign means positive correlation; minus (–) sign means negative correlation

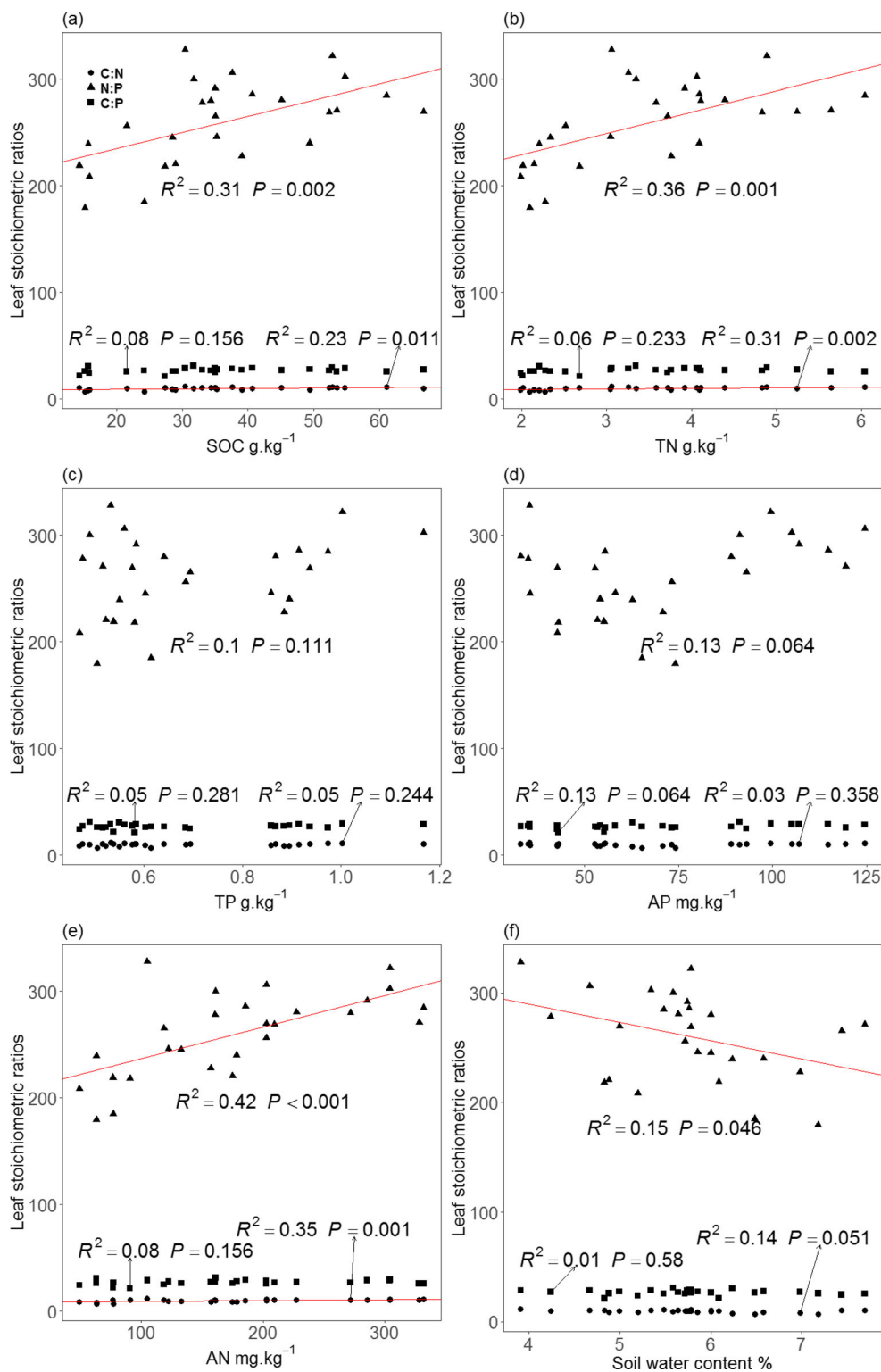


Fig. 4 Linear regression analysis between leaf stoichiometries and soil attributes including SOC, TN, TP, available nitrogen (AN), available phosphorus (AP), and soil water content in different ages of *L. leucocephala* forests

consistent with our previous investigations, which highlighted stronger P re-absorption compared to N re-absorption as an adaptive strategy of *L. leucocephala* in deteriorated environments (Deng et al. 2015). Therefore, we hypothesized that

L. leucocephala is subject to a trade-off between P concentration and soil nutrient gradient, so it alters P concentration ability across a nutrient limitation gradient (Bernard-Verdier et al. 2012).

Table 4 Analyses of covariance for the interactions between forest age and soil attributes on leaf nutrient concentrations and stoichiometric ratios

Source	Ages × SOC	Ages × TN	Ages × TP	Ages × SW	Ages × AN	Ages × AP	Ages × C:N	Ages × C:P	Ages × N:P
Leaf C	0.979	0.542	0.784	<i>0.019</i>	0.053	0.322	0.886	0.319	0.097
Leaf N	0.772	0.388	0.640	0.810	0.879	0.390	0.507	0.248	<i>0.040</i>
Leaf P	0.913	0.869	0.517	0.232	0.686	0.590	0.777	0.836	0.523
Leaf C:N	0.837	0.966	0.672	<i>0.020</i>	0.083	0.190	0.883	0.727	0.576
Leaf C:P	0.855	0.780	0.518	0.685	0.300	0.225	0.988	0.581	0.498
Leaf N:P	0.978	0.788	0.700	0.081	0.587	0.823	0.844	0.806	0.817

Italic numbers mean significant interaction effects at $p < 0.05$

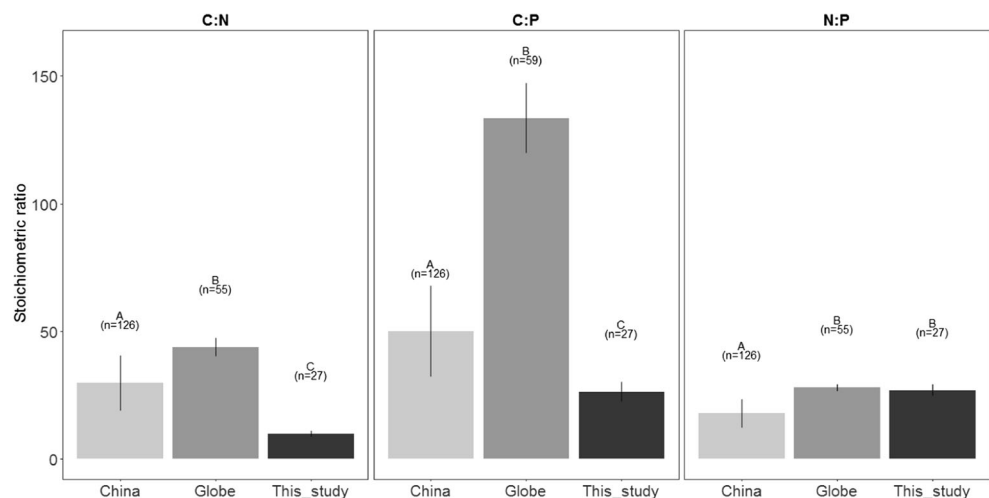
SW soil water content, AN available nitrogen, AP available phosphorus, C:N C:N ratio, C:P C:P ratio, N:P N:P ratio

Forest age also had a significant effect on C, N, and P concentration ability of *L. leucocephala* leaves. This study showed that the older tree had comparatively higher N and P concentration ability (Fig. 2). Intraspecific variation in leaf nutrient concentrations was reported in other locations, where leaf nutrient and stoichiometry were indicators of plant nutrient use efficiency at different growth stages across nutrient gradients (Sternner and Elser 2002; Wu et al. 2010). In our study, different ages of *L. leucocephala* forests developed from bare land conditions similar to the beginning stages of community succession. We found that leaf N and P concentration ability increased and caused comparatively lower C:N and C:P ratios with forest age (Fig. 2), indicating that *L. leucocephala* adjusted its nutrient use efficiency to adapt to environment and growth. This result is consistent with the findings of Aerts and Chapin (1999), who suggest that species at an early stage with high C:N and C:P ratios have high competitive abilities in dry and nutrient-poor environments. In theory, plants tend to minimize nutrient use or loss and allocate less biomass to stems in infertile environments (Yan et al. 2016). Although the present study does not address the role of biomass allocation in determining nutrient use, it does reveal that leaf stoichiometry plays a critical role in soil available nutrient detection in nutrient-limited environments. Thus,

to improve the management and community structure of plantation, a trade-off between plant growth and minimization of nutrient use in infertile environments should be considered as a criterion when selecting species. Moreover, forest age combined with soil water content significantly affected leaf C concentration and leaf C:N, suggesting that the growth of *L. leucocephala* accompanying high C concentration ability may cause the decrease of soil water content. However, this statement should be tempered by the fact that we did not set up control experiments containing similar soil water content at different forest ages. Elucidating the interactions between soil water content and forest age requires additional research.

Though there are considerable debates about the negative effects of introduced plants, including biological invasion, landscape change, and lack of native species (Chung 2006), exotic plantations have been carried out to reduce erosion, protect soil, and improve rehabilitation in degraded lands across the globe (Le Houérou 2000). Due to their comparatively better adaptations to drought, high light intensity, nutrient deficiency, and other environmental stressors, they make for great success in land rehabilitation and productivity restoration (Hesp 1991; Le Houérou 1996). However, long-term utilization of introduced plants induces soil desiccation, loss of biodiversity, and increasing occurrences of plant diseases

Fig. 5 Mean values ± SE of stoichiometric ratios in China, globe, and this study. C:P ratio showed in the original value and SE divided by 10. Differences between locations were tested using a one-way ANOVA, and differences significant at $p < 0.05$ are indicated by uppercase letters



and insect pests, especially in arid lands (Wang et al. 2011). For example, monocultures of *L. leucocephala* destroyed the composition and structure of the original community in dry-hot valley ecosystem types (Chou and Kuo 1986). Considering the main limitation factors—soil nutrient gradient and forest age—affecting plant growth in local ecological conditions, land managers need to improve the nutrient usage efficiency of *L. leucocephala* and reduce soil desiccation by forest tending or thinning and biological substitution with ecologically adequate native plants, rather than keep its population dispersing throughout a dry-hot valley.

5 Conclusions

We studied how soil nutrients and water content affect leaf nutrients and stoichiometry at different ages of *Leucaena leucocephala* forests in dry-hot valley ecosystem types. Our result suggests that in areas with extreme climate conditions, available nutrients and soil water content, rather than total nutrient content, might be the main limitation to plant productivity and stability. Both available N and P had a significant relationship with leaf N and P concentration. Available N had a higher correlation with C:N:P stoichiometry of *L. leucocephala*. As another limitation factor, soil water content played an indispensable role in nutrient accumulation and ecologic environment of soil. Though some limitations exist, our study provides a reference to improve *L. leucocephala* community structure and soil rehabilitation in a deteriorated environment. Future research should extend this work by setting up control experiments containing similar soil condition at different forest ages.

Acknowledgements The authors thank H. J. Deng, G. S. Zhang, and the staff of Dongchuan debris flow observation research station for the help in collecting and analyzing the data.

Funding information This study was supported by the National Natural Science Foundation of China (41790434 and 41471010), the Outstanding Young Scientific Research Project of Fujian Agriculture and Forestry University (xjq201716), and the Scientific and Technological Innovation Foundation of Fujian Agriculture and Forestry University (CXZX2016058, CXZX2017111, and CXZX2017283).

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