



## Effects of forest plantation types on leaf traits of *Ulmus pumila* and *Robinia pseudoacacia* on the Loess Plateau, China



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### ABSTRACT

Understanding the physiological response mechanisms of plant leaf traits to forest plantation types in semi-arid regions is of vital importance to better understanding the interplay between ecological process and plant resource-allocation strategies of different tree species. Experimental forest plantations were constructed on the Loess Plateau of China in order to study leaf morphological, physiological and stoichiometric traits among four forest plantation types of *Ulmus pumila* and *Robinia pseudoacacia*: a single-species *Ulmus pumila* plantation (SP-U), a single-species *Robinia pseudoacacia* plantation (SP-R) and three mixed plantation ratios of *U. pumila*-*R. pseudoacacia* (UR) [2:1 (2U1R), 1:1 (1U1R) and 1:2 (1U2R)]. Leaf morphological traits examined include: specific leaf area (SLA), leaf dry mass (LM), leaf area (LA) and leaf dry matter content (LDMC); physiological traits: net photosynthetic rate (Pn), transpiration rate (Tr), stomatal conductance (Gs) and instantaneous water use efficiency (WUE); and stoichiometric traits: leaf nitrogen content (LNC), leaf phosphorus content (LPC), leaf carbon content (LCC), N:P, C:N and C:P were examined for the four plantation types on the Loess Plateau of China. The results indicate SLA, Pn, Tr, Gs, LPC, LCC, C:N and C:P of *R. pseudoacacia* and *U. pumila* varied significantly among the four plantation types (SP, 2U1R, 1U1R and 1U2R). However, LA, LM, LDMC, WUE, LNC and LPC differed little among forest plantation types. The relationships between leaf morphological and physiological traits, in particular SLA revealed a significantly negative correlation with LDMC, but a positive correlation with Pn, Tr and Gs. With regard to the leaf morphological and stoichiometric traits in the study area, SLA was positively correlated with LNC and LPC, but negatively correlated with LCC. As a nitrogen fixation species, *R. pseudoacacia* always showed higher SLA, Pn, Tr, Gs, LNC and LPC while *U. pumila* showed higher LDMC, WUE, LCC, C:N, C:P and N:P. This may reflect different environmental adaption strategies between the two tree species. Compared with *R. pseudoacacia*, *U. pumila* responded to the arid habitats by increasing leaf thickness and thus reducing water loss, showing potential physiological plasticity in adapting to dry environments. Regarding the four forest plantation types, the mixed plantation displayed increased plant leaf nutrient content and photosynthetic rate when compared to the SP treatment, especially the mixed 1U2R treatment. Based on the results herein, the mixed plantation of *R. pseudoacacia* and *U. pumila* could effectively improve leaf nutrient contents and photosynthetic capacity of both tree species, with the optimal planting ratio studied here being the 1U2R treatment of *R. pseudoacacia* and *U. pumila* among the four forest plantation types on the Loess Plateau of China.

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### 1. Introduction

The study of patterns and variations in plant traits along environmental and resource gradients is fundamental to understand

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both ecological (Silvertown, 2004; Westoby and Wright, 2006; Wu et al., 2015) and evolutionary processes (Ackerly et al., 2000). Ecophysiological theory predicts, in order to maintain fitness and improve adaptiveness, leaf traits need to exhibit plasticity in response to environmental demands (Zdravko, 2011). Past research activities have focused on plant functional traits, because these traits are considered to reflect the adaptations to environmental change and trade-offs among different functions within a plant, and thus can better link environmental drivers and plant responses to

ecosystem structure and functioning (Díaz et al., 1998; Reich et al., 2003; Wright et al., 2004; Lavorel et al., 2007). Especially at the community scale, plant traits are strongly correlated with soil resources, plant nutrients and water use efficiency (Cornwell and Ackerly, 2010), thus they have been widely used in explaining community assemblage processes among different forest types (Villegger et al., 2008). In recent years, many studies attempted to predict plant responses in terrestrial ecosystems, such as forest ecosystems (Valera-Burgos et al., 2013; David et al., 2013; Bussotti et al., 2015); agro-forestry ecosystems (Okubo et al., 2012); and grassland ecosystems (Zheng et al., 2010). These studies have focused on using plant functional traits, especially for some easily and quickly measured leaf traits (“soft” traits), such as leaf size, leaf area, leaf dry mass, leaf dry matter content, and specific leaf area (Reich et al., 1998a, 2007). In a diverse range of plant communities, these ‘soft’ traits are found to be closely related to plant functions because they are highly correlated with “harder” traits, such as relative growth rate, photosynthetic capacity, leaf nutrient concentration, and leaf turnover rate, which further reflect the fundamental trade-offs between fast growth and nutrient storage (Grime, 2001; Westoby et al., 2002; Wright et al., 2004) in plant functioning. SLA, the ratio of leaf area to leaf dry mass, is an important leaf trait that integrates plant investment into growth and storage and has been widely used to predict growth strategy (Poorter and Jong, 1999). SLA, measures the amount of leaf area available for light capture per unit of biomass of investment. Leaf N and P concentrations are a proxy for the leaf’s photosynthetic capacity and is therefore strongly positively correlated with photosynthetic rate (Reich et al., 1999). The relationship between SLA and both leaf N and P concentrations is well known for forest ecosystem (Reich et al., 1997). SLA captures the fundamental trade-off between resource acquisition and conservation in plants; therefore species with a high SLA typically have high leaf N and P, and consequently exhibit a higher photosynthetic capacity (Westoby et al., 2002). Leaf N and P are also positively related to stomatal conductance and relative growth rates (Reich et al., 1992; Westoby et al., 2002).

Although many studies on leaf traits exist for different forest species (Poorter and Bongers, 2006; Poorter, 2009; Coste et al., 2010; Wu et al., 2012; Russell et al., 2014), less is known about the mixed planting of tree species, especially on the Loess Plateau (China). There have been ecophysiological studies on common trees species (i.e., *Populus* L., *Pinus tabulaeformis*, *Hippophae rhamnoides* L. and *Platycladus orientalis* (Linn.) Franco) (Liu et al., 2012). Therefore, more research on plant “integration function” studies at different organizational levels is needed on the Loess Plateau, which will likely improve our understanding regarding mechanistic links between plant functional traits and ecosystem properties (Violle et al., 2007).

The Loess Plateau in China is well known for its complex terrain, extreme drought conditions and severe soil erosion (Zhang et al., 2011; Wang et al., 2015a, 2015b). To control soil erosion and restore ecosystems, the Chinese government has instituted various erosion mitigation measures on the Loess Plateau, especially the conversion of cropland to forest or grassland (“Grain for Green” Programs (GGP)) (Zhang et al., 2015; Deng et al., 2016). In the study area, the cropland had already been abandoned, and the process of natural and artificial restoration was underway. As such, understanding the physiological characteristics and ecological adaptive strategies of different plant species or forest community types on the Loess Plateau will aid future recover and restoration in this currently damaged ecosystem. *Ulmus pumila* L. is a widespread commercial tree species that dominates the arid region throughout its natural distribution range in northern China (Chen and Xu, 2012). For the fast-growing and high quality, *U. pumila* is a well-adapted and extensively used tree species which is the primary afforestation tree species on the Loess Plateau (Chen and Xu, 2012). As a typical

nitrogen-fixing leguminous plant, many studies indicate *R. pseudoacacia* L. can effectively improve soil quality and plant nitrogen nutrient levels in mixed forests, thus enhancing soil and water conservation efforts by improving the stability of forest structures and reducing occurrence of soil surface runoff (Shangguan, 2007). In addition, because of its resilience, fast growth, high yield, extensive root system and nitrogen fixation capacity, *R. pseudoacacia* trees are planted widely on the Loess Plateau and the northern regions of China as a means to address the intertwined environmental problems and soil and water conservation (Zhou and Shangguan, 2005; Li et al., 2015, 2016). As a result, *U. pumila*-*R. pseudoacacia* mixed forests are one of the most widespread mixed forest plantation types on the Loess Plateau which has been playing an important role in improving the ecological environment of the arid regions in northern China.

In this study plant leaf morphological, physiological and stoichiometric traits of *U. pumila* and *R. pseudoacacia* were studied among the four plantation types (i.e. a single-species *Ulmus pumila* plantation (SP-U), a single-species *Robinia pseudoacacia* plantation (SP-R) and three mixed plantation ratios of *U. pumila* and *R. pseudoacacia* (UR) [2:1 (2U1R), 1:1 (1U1R) and 1:2 (1U2R)] in the field on the Loess Plateau. Plant leaf traits (i.e., leaf area (LA), leaf dry mass (LM), specific leaf area (SLA), leaf dry matter content (LDMC); net photosynthetic rate (Pn), transpiration rate (Tr), stomatal conductance (Gs) and instantaneous water use efficiency (WUE); and leaf N content (LNC), leaf P content (LPC), leaf C content (LCC), leaf nitrogen/phosphorus ratio N:P, leaf carbon/nitrogen ratio C:N, leaf carbon/phosphorus ratio C:P of both species present at the 15 experimental plots were systematically determined across the four plantation communities on the Loess Plateau to address the following research questions: (1) How do plant leaf traits of the two species vary with forest plantation types? (2) What are the possible physiological mechanisms underpinning the observed responses of leaf traits to the variation of different mixed ratios in the field? And (3) Which mixed ratios of *U. pumila*-*R. pseudoacacia* performed best within the mixed plantations?

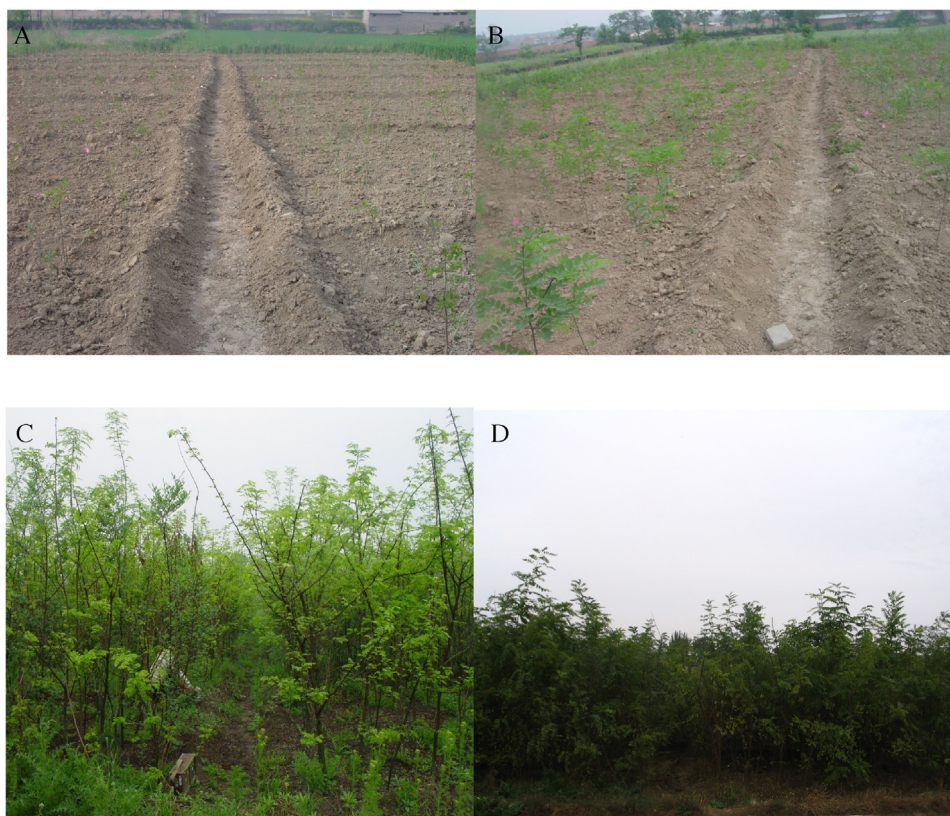
## 2. Materials and methods

### 2.1. Study area and experimental design

This study was carried out at Xibo village in the Yangling District, Shaanxi Province, China (34°18'N, 108°15'E, and 450 m above sea level). The topography at the experimental site was flat ground. It belongs to a warm temperate-humid and semi-humid climate zone. The mean annual temperature in the area was 12.9°C. The annual precipitation was 635 mm, with 70% occurring throughout the growing season (June–September). The average annual evaporation is approximately 1800 mm. The soil is Eum-Orthic Anthrosols. Topsoil organic matter content, total nitrogen, total phosphorus (0–30 cm) and pH are 18.3, 1.37, 0.81 g kg<sup>-1</sup> and 7.96, respectively.

The forests at the study area are dominated by *U. pumila* and *R. pseudoacacia* (broadleaf tree), which is a widely distributed community type on the Loess Plateau. *U. pumila* is a common deciduous tree, which is resistant to drought, salinity and low temperature. Its roots grow profusely through soil profiles, resulting in high wind-breaking and sand-fixing capacities. As a leguminous species, *R. pseudoacacia* is typically observed as a pioneer species and used as an associated species on afforesting barren hills.

In mid-March 2007, 1-year-old *U. pumila* and *R. pseudoacacia* seedlings were planted below 30 cm soil layer in the field. The experimental treatments were composed of three management systems single-species *U. pumila* plantation (SP-U), single-species *R. pseudoacacia* plantation (SP-R) and *U. pumila*-*R. pseudoacacia* mixed plantation (UR). The study area was 470 m<sup>2</sup> and each test



**Fig. 1.** Experimental design of the study area (Yangling District, Shaanxi Province, China).

Four plantation types (SP, 2U1R, 1U1R and 1U2R) in 15 experimental plots at different stages, (A) early growth stage-middle in March 2007; (B) middle growth stage in May 2007; (C and D) late growth stage in July 2008.

plot size was  $7\text{ m} \times 3\text{ m}$  for both single-species plantations (SP) and mixed plantations (UR). A total of 105 plant samples (including *U. pumila* or *R. pseudoacacia* seedlings) were selectively grown in each test plot, and the row spacing, strain spacing were both 0.5 m (Fig. 1). The single-species plantation types included either all *U. pumila* seedlings or *R. pseudoacacia* seedlings, the mixed plantation types were managed with three different ratios for 2:1 (2U1R), 1:1 (1U1R) and 1:2 (1U2R). For the 2U1R treatment, 70 *U. pumila* and 35 *R. pseudoacacia* seedlings were planted; in the 1U1R treatment, 53 *U. pumila* and 52 *R. pseudoacacia* seedlings were planted; and in the 1U2R treatment, 35 *U. pumila* and 70 *R. pseudoacacia* seedlings were planted. For the three mixed plantation ratios test plots, the seedlings of *U. pumila* and *R. pseudoacacia* were all planted with alternate arrangement according to the different mixed ratios. The test plot was established randomly in the field and mixed by strains in each plot. In the experiment, each plantation type was repeated three times and thus resulted in a total of 15 experimental plots. To protect the test plots from margin effects, protection lines were used around the entire study area. Field sampling and measurements were carried out at the experimental site.

## 2.2. Field leaf trait measurements and lab analyses

On July 10–11th of 2008, five individuals of each *U. pumila* and *R. pseudoacacia* at each plot were selected, then six to eight fully and expanded leaves were picked as a sample and totally 30 to 40 leaves from each species were measured in each plot.

Leaf area was determined by scanning the leaves with a flatbed scanner and analyzing the images using an area measurement software by Motic (Motic images advanced 3.0). After the leaf area and leaf saturated fresh mass were measured, all leaf samples were

oven-dried at  $70^\circ\text{C}$  for 24 h to constant mass and weighed for their dry mass. The leaf area and specific leaf area reported for each individual represents the average obtained from the six to eight leaves per individual tree collected at each canopy position. The SLA and LDMC were calculated for each leaf as the ratio between leaf area and leaf dry mass, and between leaf dry mass and leaf saturated fresh mass, respectively.

After SLA measurements the same leaves were ground to provide pooled nitrogen, phosphorus and carbon samples for each canopy position and each individual tree. The leaf samples were grounded to 100-mesh and leaf N content was analyzed using a Kjeltec analyzer (Kjeltec 2300 Analyzer Unit, Foss, Sweden). The leaf N content was expressed on a mass basis ( $N_{\text{mass}}$ , %). Total leaf P concentrations were measured by a molybdate/stannous chloride method (Kuo, 1996) after  $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2\text{-HF}$  digestion (Bowman, 1988) quantified by reference to a national standard material with a known P concentration (TU1901 UV spectrophotometer, China) (reference code GBW08513; General Administration of Quality Supervision, People's Republic of China). The leaf C content was analyzed via a  $\text{K}_2\text{Cr}_2\text{O}_7\text{-H}_2\text{SO}_4$  solution digestion with the oil-bath heating. All the chemical determinations were repeated three times with the same samples on a mass basis. Mass ratios of C:N, C:P and N:P were used here to facilitate comparisons with terrestrial ecology literature (Sterner and Elser, 2002; Güsewell, 2004).

## 2.3. Photosynthetic gas exchange measurements

The photosynthetic gas exchange parameters of the two tree species were measured with a Li-6400 Portable Photosynthetic System (Li-6400, Li-Cor, USA) between 9:00 and 11:30 on 10–11 July. The gas entry was connected to a gas pole 3 m above



ground. Net photosynthetic rate ( $P_n$   $\mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), transpiration rate ( $Tr$   $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ), and stomatal conductance ( $G_s$   $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) were measured at a  $\text{CO}_2$  concentration of  $360 \mu\text{mol mol}^{-1}$  and the cuvette temperature was approximately the atmosphere temperature, and their  $P_n$  were recorded 2 min after photosynthesis became stable. Instantaneous water use efficiency ( $\text{WUE} \mu\text{molCO}_2 \text{ m}^{-2} \text{ H}_2\text{O}$ ) was determined by  $P_n/Tr$ .

#### 2.4. Statistical analysis

The effects of forest plantation types on plant leaf traits for each species present were tested by One-way ANOVAs, and LSD multiple range tests were used for multiple comparisons of plant traits among treatments. The Pearson correlation analysis was used to test the relationships between plant leaf morphological traits (LA, LM, SLA and LDMC), physiological traits ( $P_n$ ,  $Tr$ ,  $G_s$  and WUE) and stoichiometric traits (LNC, LPC, LCC, N:P, C:N, C:P). Data were standardized before the analysis. All statistical analyses were performed using SPSS 17.0 software (SPSS Inc., USA).

### 3. Results

#### 3.1. Variations of leaf morphological traits among the four forest plantation types

Regarding the four treatments, the average values of LA, SLA, LM and LDMC in *U. pumila* and *R. pseudoacacia* were  $11.46 \text{ cm}^2$ ,  $213.83 \text{ cm}^2 \text{ g}^{-1}$ ,  $0.07 \text{ g}$ ,  $0.36 \text{ g g}^{-1}$  and  $12.92 \text{ cm}^2$ ,  $192.73 \text{ cm}^2 \text{ g}^{-1}$ ,  $0.06 \text{ g}$ ,  $0.31 \text{ g g}^{-1}$ , respectively (Table 1), and the variability (coefficient of variation-CV) of LA, SLA, LM and LDMC were less than 0.2. These variability coefficients displayed weak correlation, indicating the values of LA, SLA, LDMC and LM in *U. pumila* and *R. pseudoacacia* were relatively stable regardless of the four forest plantation types.

For both *U. pumila* and *R. pseudoacacia*, the effects of forest plantation types on leaf morphological traits, i.e., LA, LM and LDMC were not significant ( $P > 0.05$ ), except for SLA (Fig. 2C). LA of *U. pumila* and *R. pseudoacacia* did not show significant changes among forest plantation types (Fig. 2A). However, LA of *R. pseudoacacia* was higher in the mixed plantations than in the single-species plantation, and LA of *U. pumila* was the lowest in the 1U2R mixed plantation type. Comparatively, LA of *R. pseudoacacia* was higher than *U. pumila* (Fig. 2A).

SLA of *R. pseudoacacia* increased significantly in the 1U1R and 1U2R mixed plantation types when compared to others, as well as displaying a higher SLA than *U. pumila* in the same mixed plantation type (Fig. 2C). SLA of *U. pumila* was significantly increased in the 1U2R mixed plantation type when compared to the SP treatment ( $P < 0.05$ ).

LM of *U. pumila* and *R. pseudoacacia* in the 1U2R mixed plantation type significantly reduced from SP treatment to the 1U2R treatment. For all treatments, LM of *U. pumila* in the SP treatment was the highest among the four forest plantation types and decreased from SP treatment to UR mixed treatments. LM of *R. pseudoacacia* and *U. pumila* in the 1U2R mixed plantation type were the lowest among the four forest plantation types (Fig. 2B). LDMC of *U. pumila* was a little higher than *R. pseudoacacia* though they all showed no statistical significance among the four forest plantation types (Fig. 2D) ( $P > 0.05$ ).

#### 3.2. Variations of leaf physiological traits among the four forest plantation types

Among the four forest plantation types, the range of variation of  $P_n$ ,  $Tr$ ,  $G_s$  and WUE of *U. pumila* and *R. pseudoacacia* were from 14.35 to  $18.54 \mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ,  $6.20$  to  $8.32 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ,  $0.19$  to

$0.37 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$  and  $2.08$  to  $2.68 \mu\text{molCO}_2 \text{ m}^{-2} \text{ H}_2\text{O}$ , respectively. Their variability coefficients also indicate weak variability (Table 1).

Leaf physiological traits of the two species were significantly affected by forest plantation types ( $P < 0.05$ ), except for WUE (Fig. 3D).  $P_n$ ,  $Tr$  and  $G_s$  of *R. pseudoacacia* significantly increased from SP treatment to UR mixed treatments, especially in the 1U2R plantation type (Fig. 3A,B and C). In addition,  $P_n$ ,  $Tr$  and  $G_s$  of *U. pumila* indicated no significant difference among the four forest plantation types. However, in the mixed plantation types,  $P_n$ ,  $Tr$  and  $G_s$  of *R. pseudoacacia* were higher than *U. pumila* in the 1U1R and 1U2R plantation types.

$P_n$ ,  $Tr$  and  $G_s$  of *R. pseudoacacia* were the highest in the 1U2R plantation type and declined in the others in the order of  $1U2R > 1U1R > 2U1R > SP$ . On average,  $P_n$ ,  $Tr$  and  $G_s$  of *R. pseudoacacia* in the 1U2R plantation type increased by 15.10%, 25.48% and 32.43%, respectively, compared to SP-R (Fig. 3A,B and C). In contrast, different forest plantation types had less effect on WUE of *U. pumila* and *R. pseudoacacia*, though WUE of *U. pumila* in mixed plantation types remained higher than SP-U and *R. pseudoacacia* in the UR mixed treatments (Fig. 3D). In most cases, compared with *U. pumila*, *R. pseudoacacia* showed much higher  $P_n$ ,  $Tr$ , and  $G_s$ , but lower WUE in the mixed plantation types.

#### 3.3. Variations of leaf stoichiometric traits among the four forest plantation types

The range of variation of LNC, LPC, LCC, N:P, C:N and C:P of *R. pseudoacacia* and *U. pumila* were from 3.07 to 3.74%, 0.16 to 0.26% and 34.50 to 65.74%, 14.15 to 20.43, 10.10 to 19.28 and 144.35 to 359.25 in the four forest plantation types, respectively. The variability coefficients of LNC, LPC and N:P indicate weak variability, while LCC, C:N and C:P of *R. pseudoacacia* displayed medium variability (Table 1).

The leaf stoichiometric traits of the two species differed significantly ( $P < 0.05$ ) among the four forest plantation types (Fig. 4). LNC of *R. pseudoacacia* and *U. pumila* did not show significant changes from SP treatment to 1U2R treatment. LPC of *U. pumila* in the 1U2R treatment was significantly higher than other plantation types while LPC of *R. pseudoacacia* showed no significance in the SP treatment and UR mixed treatments, though LPC of *R. pseudoacacia* were all higher than *U. pumila* (Fig. 4A and B). LCC of the two species showed substantial differences among the four forest plantation types. LCC of *R. pseudoacacia* and *U. pumila* showed significantly increase from SP treatment to UR mixed treatments, especially in the 1U2R treatment (Fig. 4C).

N:P and C:P of *U. pumila* were significantly higher than *R. pseudoacacia* (T-test) (Fig. 4D and F). For the four forest plantation types, C:N and C:P of *R. pseudoacacia* and *U. pumila* were all significantly higher in UR mixed treatments than in the SP treatment, especially in the 1U2R treatment (Fig. 4E and F).

#### 3.4. Relationships among plant leaf traits

The correlation analysis of the two species' leaf morphological traits showed a negative correlation with SLA and LDMC (0.439) (Table 2). SLA were positively correlated with  $P_n$  (0.772),  $Tr$  (0.655),  $G_s$  (0.749), LNC (0.783) and LPC (0.633), but negatively correlated with LCC (0.770). Leaf physiological traits of  $P_n$  were positively correlated with  $Tr$ ,  $G_s$ , LNC and LPC ( $P < 0.01$ ), and negatively correlated with N/P (0.701).  $Tr$  displayed a significant positive correlation with  $G_s$  ( $P < 0.01$ ) and LNC ( $P < 0.05$ ). LNC was positively correlated with LPC (0.867), and negatively correlated with LCC (0.480).

Across all plantation types, leaf physiological traits ( $P_n$ ,  $Tr$ ,  $G_s$  and WUE) of both tree species showed stronger relationships with

**Table 1**  
Statistical results for leaf morphological, physiological and stoichiometric traits of *U. pumila* and *R. pseudoacacia* among the four forest plantation types.

Leaf traits	Species	n	Maximum value	Minimum value	Mean	SD	CV
LA (cm <sup>2</sup> )	<i>U. pumila</i>	12	12.04	11.01	11.46	0.46	0.04
	<i>R. pseudoacacia</i>	12	13.06	12.60	12.92	0.30	0.02
SLA (cm <sup>2</sup> ·g <sup>-1</sup> )	<i>U. pumila</i>	12	226.50	173.22	213.83	23.30	0.11
	<i>R. pseudoacacia</i>	12	242.52	177.73	192.73	32.39	0.17
LM (g)	<i>U. pumila</i>	12	0.074	0.055	0.07	0.01	0.14
	<i>R. pseudoacacia</i>	12	0.068	0.053	0.06	0.01	0.17
LDMC (g·g <sup>-1</sup> )	<i>U. pumila</i>	12	0.36	0.35	0.36	0.01	0.03
	<i>R. pseudoacacia</i>	12	0.31	0.30	0.31	0.01	0.03
Pn (μmolCO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	<i>U. pumila</i>	12	16.14	14.35	15.13	0.75	0.05
	<i>R. pseudoacacia</i>	12	18.54	15.74	17.13	1.33	0.08
Tr (mmol H <sub>2</sub> O m <sup>-2</sup> s <sup>-1</sup> )	<i>U. pumila</i>	12	7.17	6.41	6.79	0.32	0.05
	<i>R. pseudoacacia</i>	12	8.32	6.20	7.51	0.98	0.13
Gs (mol H <sub>2</sub> O m <sup>-2</sup> s <sup>-1</sup> )	<i>U. pumila</i>	12	0.25	0.19	0.23	0.03	0.13
	<i>R. pseudoacacia</i>	12	0.37	0.29	0.32	0.04	0.13
WUE (μmolCO <sub>2</sub> m <sup>-2</sup> H <sub>2</sub> O)	<i>U. pumila</i>	12	2.41	2.08	2.26	0.14	0.06
	<i>R. pseudoacacia</i>	12	2.68	2.23	2.39	0.20	0.08
LNC (%)	<i>U. pumila</i>	12	3.37	3.07	3.23	0.13	0.04
	<i>R. pseudoacacia</i>	12	3.74	3.38	3.51	0.16	0.05
LPC (%)	<i>U. pumila</i>	12	0.20	0.16	0.17	0.02	0.12
	<i>R. pseudoacacia</i>	12	0.26	0.23	0.23	0.01	0.04
LCC (%)	<i>U. pumila</i>	12	65.74	37.93	52.03	12.25	0.24
	<i>R. pseudoacacia</i>	12	60.06	34.50	48.82	11.68	0.24
N:P	<i>U. pumila</i>	12	20.43	16.88	18.82	1.72	0.09
	<i>R. pseudoacacia</i>	12	14.75	14.15	14.45	0.28	0.02
C:N	<i>U. pumila</i>	12	19.28	12.33	15.97	3.08	0.19
	<i>R. pseudoacacia</i>	12	16.24	10.10	13.88	2.90	0.21
C:P	<i>U. pumila</i>	12	359.25	220.52	300.02	59.14	0.20
	<i>R. pseudoacacia</i>	12	237.26	144.35	200.66	41.95	0.21

CV ≤ 0.2, weak variability.

0.2 < CV < 0.5, Medium variability.

CV ≥ 0.5, Strong variability, the same below.

**Table 2**  
Correlation analysis among leaf morphological, physiological and stoichiometric traits of *U. pumila* and *R. pseudoacacia* among the four forest plantation types.

Parameters	LA	SLA	LDMC	LM	Pn	Tr	Gs	WUE	LNC	LPC	LCC	N:P	C:N	C:P
LA	1.000	–	0.110	0.153	0.219	0.550	0.088	–0.672*	0.059	–0.131	0.379	0.220	0.511	0.503
SLA		1.000	–0.439	–	0.772*	0.655*	0.749*	–0.425	0.783*	0.633*	–0.770*	–0.493	–0.510	0.115
LDMC			1.000	–	–0.575	–0.655*	–0.432	0.414	–0.663*	–0.875**	0.504	0.850**	0.422	0.756*
LM				1.000	–0.502	–0.572	–0.128	–0.463	–0.530	–0.533	–0.452	0.408	–0.295	–0.011
Pn					1.000	0.896**	0.811**	–	0.872**	0.804**	–0.304	–0.701*	0.290	–0.192
Tr						1.000	0.801**	–	0.682*	0.570	0.473	–0.440	0.299	–0.079
Gs							1.000	–0.252	0.908*	0.846**	0.298	–0.428	0.046	–0.378
WUE								1.000	0.011	0.095	–0.085	–0.156	–0.071	–0.086
LNC									1.000	0.867**	–0.480	–	–	–0.221
LPC										1.000	–0.101	–	–0.150	–
LCC											1.000	0.080	–	–

“–” indicates that autocorrelation exists and no analysis is conducted.

\* Correlation is significant at the 0.01 level (2-tailed).

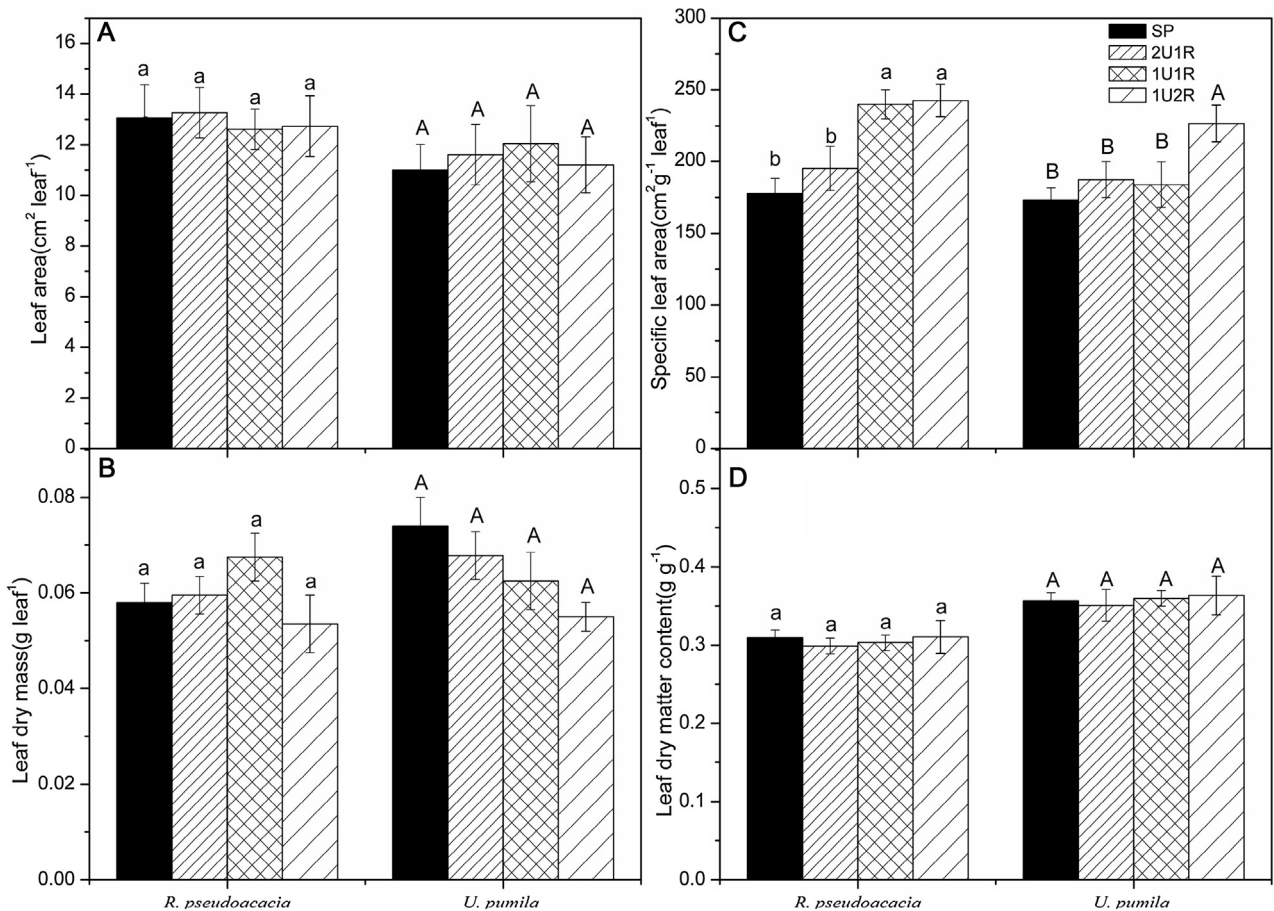
\*\* Correlation is significant at the 0.05 level (2-tailed).

leaf stoichiometric traits (LNC, LPC, LCC, N:P, C:N and C:P) than leaf morphological traits (LA, SLA, LDMC and LM).

#### 4. Discussion

Plant traits link environmental factors, individuals, ecosystem structures and functions as plants respond and adapt to the environment (Meng et al., 2007). Some individual plant traits or trait combinations can influence species differences in performance, productivity and ecology (McGill et al., 2006; Violle et al., 2007; Kattge et al., 2011). Specific leaf area (SLA) and leaf dry matter content (LDMC) are important characteristics in plant ecology. These plant characteristics are associated with many critical aspects of plant growth and survival, and can be used as indicators of plant resource-allocation strategies (Diaz et al., 2004). Our results indicate SLA of *R. pseudoacacia* and *U. pumila* were increased in UR mixed treatments, especially in the 1U2R plantation type, while LDMC was less sensitive to planting ratios than SLA. Regarding

the results from correlation analyses between plant leaf traits, we found a significantly negative correlation between SLA and LDMC (the correlation coefficient was 0.439), indicating species of *U. pumila* exhibited low SLA and high LDMC, as well as a smaller leaf area and higher leaf dry mass in the mixed plantation types (Fig. 2). In our study area, *U. pumila* exhibited a hard, thick leaf cuticle during the time of measurement, while *R. pseudoacacia* exhibited soft, thin leaves. A hard, thick leaf cuticle likely prevents water loss from their leaf surface more effectively than does a soft, thin leaf structure. Many researchers have found leaf thickness to be a very valuable feature, efficiently enabling resource acquisition, water saving and CO<sub>2</sub> assimilation (Reich et al., 1998b; Cornelissen et al., 2003). In drought conditions, a reduction in SLA has often been observed (Marcelis et al., 1998; Casper et al., 2001; Marron et al., 2003; Laureano et al., 2008), as a decrease in leaf surface area would mean fewer avenues for water loss. Species with typically low SLA values are geared for the conservation of acquired resources, due to their large leaf dry mass and leaf dry matter content, high con-



**Fig. 2.** Effects of four forest plantation types on plant morphological traits of *U. pumila* and *R. pseudoacacia*. Vertical bars indicate standard errors of the mean (n = 24). Different letters in the same case represent significant differences among treatments (LSD test, P<0.05), with lowercases for *R. pseudoacacia* and capital letters for *U. pumila*, the same below.

centrations of cell walls and secondary metabolites, and high leaf and root longevity (Marron et al., 2003). These plant morphological traits have a close relationship with plant water use efficiency and the ability to acquire resources and are thus better adapted to drought environments. In general, plants growing in nutrient-poor environments and drought conditions produce small amounts of litter and conserve nutrients in long-lived and recalcitrant tissues, thus always form small area, thick leaves and exhibit the resulting low SLA values. In order to form tough leaves, plants need to allocate more biomass and nitrogen to form thick cell walls, thus resulting in reductions in mesophyll conductance and nitrogen allocation to photosynthetic apparatus (Cornelissen et al., 2003). So, compared with *U. pumila* in UR mixed treatments, single-species *U. pumila* adapt to the arid habitats by increasing their leaf thickness thereby reducing water loss on the Loess Plateau region. Our results also showed that LA and LDMC of *R. pseudoacacia* or *U. pumila* were generally unaffected by the four forest plantation types. In general, communities with a predominant conservative strategy exhibited high values of LDMC, positively associated to C concentration, C:N ratio and high water use efficiency (high  $\delta^{13}C$  values). On the contrary, communities with a predominantly resource-acquisition strategy display lower water-use efficiency (low  $\delta^{13}C$ ) and low LDMC (Poorter and Garnier 1999; Wright and Westoby, 2001). For the two species, results indicate that *U. pumila* had higher LDMC values when compared to *R. pseudoacacia* whether in the SP treatment or UR mixed treatments (Fig. 2D).

A tree's photosynthetic capacity directly affects their growth and development. The variation of photosynthetic capacity

between different trees reflects different nutrient utilization and storage strategies. In general, species with a high SLA also have high nitrogen concentrations, and were physiologically more active via higher rates of photosynthesis, respiration and stomatal conductance. A high SLA enables a tree to maximize light capture and forage opportunistically (Ackerly, 1997; Westoby and Wright, 2006). Among the four forest plantation types, Pn of *R. pseudoacacia* increased from the SP treatment to UR mixed treatments; Pn of *R. pseudoacacia* in the 1U2R, 1U1R and 2U1R treatments increased by 15.10%, 12.36% and 3.26% respectively when compared to SP-R (Fig. 3); Tr and Gs of *R. pseudoacacia* indicated the same variation. For the two species, Pn, Tr and Gs of *R. pseudoacacia* were significant higher than *U. pumila*, while WUE was lower than *U. pumila* in the mixed plantation types, especially in the 1U2R treatment. Lower SLA may improve mesophyll diffusion and stomatal density may decrease to improve water use efficiency (Ferris et al., 1996). This is likely part of an adaptive mechanism to reduce leaf area and thus transpiration rates (Craufurd et al., 1999). Since legumes are associated with N-fixing bacteria such as *Rhizobium* sp. capable of utilizing atmospheric N<sub>2</sub>, legumes always have higher photosynthetic rates and nitrogen contents than non-fixing plants (Wright et al., 2005; Zheng and Shangguan, 2007), our findings agree with this conclusion. Our study showed *R. pseudoacacia* had a higher photosynthetic rate, facilitating the capture of environmental resources and nutritional requirements and as such usually had higher growth rates and increased productivity on the Loess Plateau. Compared with *R. pseudoacacia*, *U. pumila* had a higher water use efficiency in UR mixed treatments than in



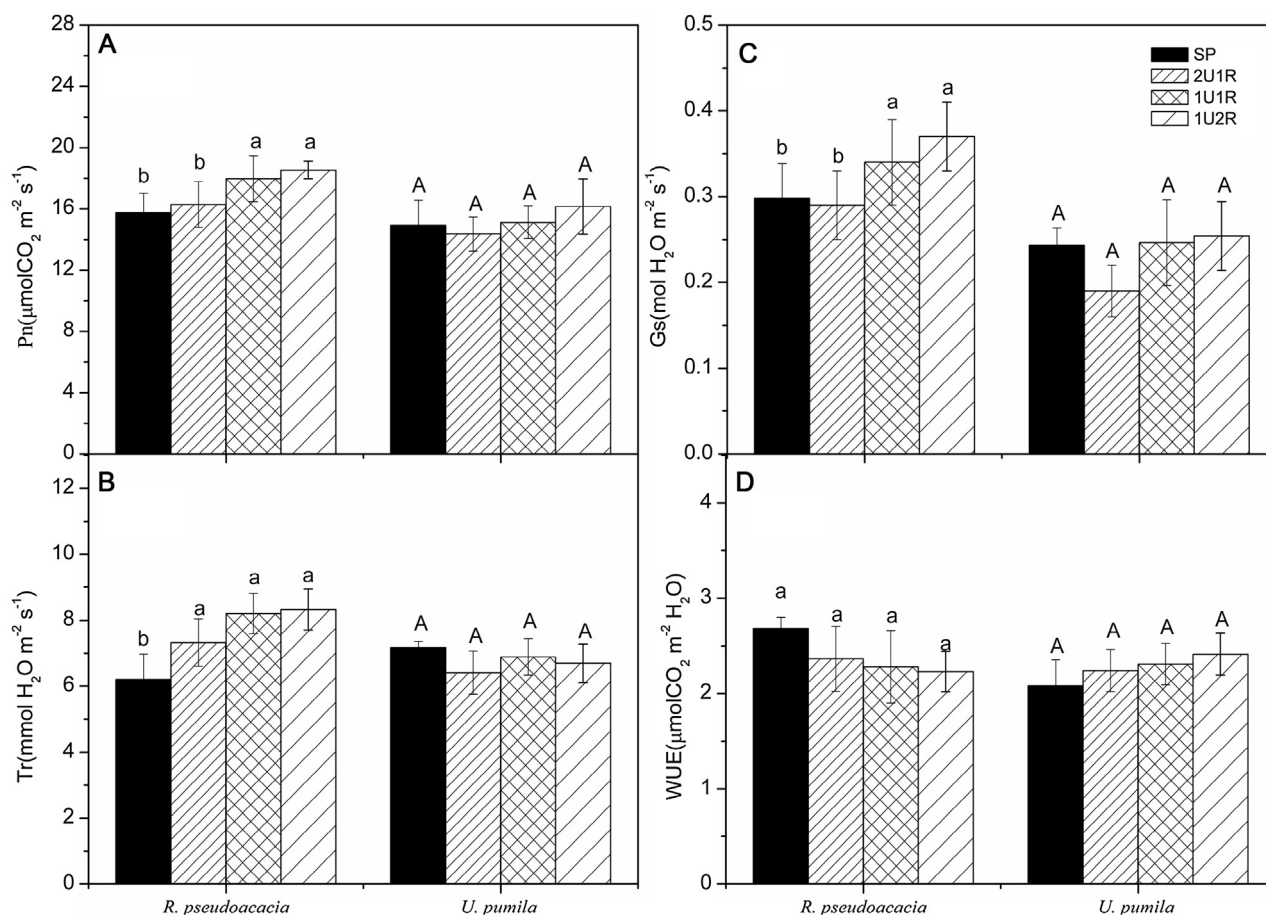


Fig. 3. Effects of four forest plantation types on plant physiological traits of *U. pumila* and *R. pseudoacacia*.

the SP treatment, especially in the 1U2R plantation type, indicating the water use efficiency of *U. pumila* can be improved by planting mixed plantations including *R. pseudoacacia* on the Loess Plateau region. Therefore, the adaptability of plant photosynthetic physiology to an environment, to a large extent, reflects plant survival and competitive ability in this area.

Nitrogen (N) is an essential plant macronutrient that influences plant growth and consequently biomass production as well as ontogenetic development, and thus has a significant impact on plant performance, plant physiology and resource allocation constraints (Kraiser et al., 2011; Alvarez et al., 2012), especially leaf nitrogen content which is strongly correlated with photosynthetic capacity (Hikosaka, 2004). Species exhibiting a high potential growth rate generally have high photosynthetic and respiration rate per unit mass, high nitrogen concentrations and other nutrients, a low leaf mass per unit area and higher leaf turnover rates, with slow-growing species showing the reverse (Grime, 1977; Lambers and Poorter, 1992; Reich et al., 1992, 1997; Wright et al., 2004). In our study, LNC was positively correlated with Pn and Tr ( $P < 0.05$ ). Many studies have reported the relationship between photosynthetic rate and leaf N content, most indicated Pn and LNC showed a positive correlation (Evans, 1989; Hikosaka, 2004), but others indicate Pn and LNC were negatively correlated in different species or exhibited no correlation at all (Warren and Adams, 2004), the relationship depends on the species and their environmental factors (Warren and Adams, 2004). For legume photosynthesis, McKey (1994) found the high photosynthetic rate and leaf N content were consistent and our findings support this conclusion. Leaf N, P and C content and the ratio of N:P, C:N and C:P likely reflect plant defense and adaptation strategies to the study area's adverse environment,

such as water stress (Sterner and Elser, 2002). The variations of C, N and P of *R. pseudoacacia* and *U. pumila* showed different defense and adaptation strategies among the four forest plantation types. In general, species with a high LNC and LPC are assumed to exhibit higher photosynthetic and growth rates along with strong resource competition abilities, while species with a high LCC indicate lower SLA, photosynthetic rates and comparatively slower growth rates with strong defense capabilities. Leaf N: P ratios may influence plant-herbivore interactions in food webs (Sterner and Elser, 2002), as well as indicate soil N or P limitations to plant growth and can be used as a plant growth indicator to determine limiting nutrients (Koerselman and Meuleman, 1996; Aerts and Chapin, 2000; Güsewell, 2004). Usually, plant growth rates are primarily restricted either by the N element if the N:P ratio was less than 14 or restricted by the P element if the N:P ratio was more than 16 (Koerselman and Meuleman, 1996). In our study area, the leaf N:P ratio of *R. pseudoacacia* was more than 16 and *U. pumila* was less than 14 (Fig. 4), it can be concluded that *R. pseudoacacia* was more susceptible to P limitations while *U. pumila* was more restricted by the N elements. This may be due to the substantial water and soil erosion which results in the loss of soil P. In organisms lacking major mineral storage of P (as in vacuoles or bones), the potential for rapid growth tends to be correlated with low biomass C:P and N:P ratios. This is believed to reflect increased allocation to P-rich ribosomal RNA, as rapid protein synthesis by ribosomes is required to support fast growth (Elser et al., 2000; Sterner and Elser, 2002; Sardans et al., 2006).

According to the results of this study, for the two species, *R. pseudoacacia* had higher leaf N and P nutrient contents and photosynthetic capacity, showing *R. pseudoacacia* exhibited an optimized

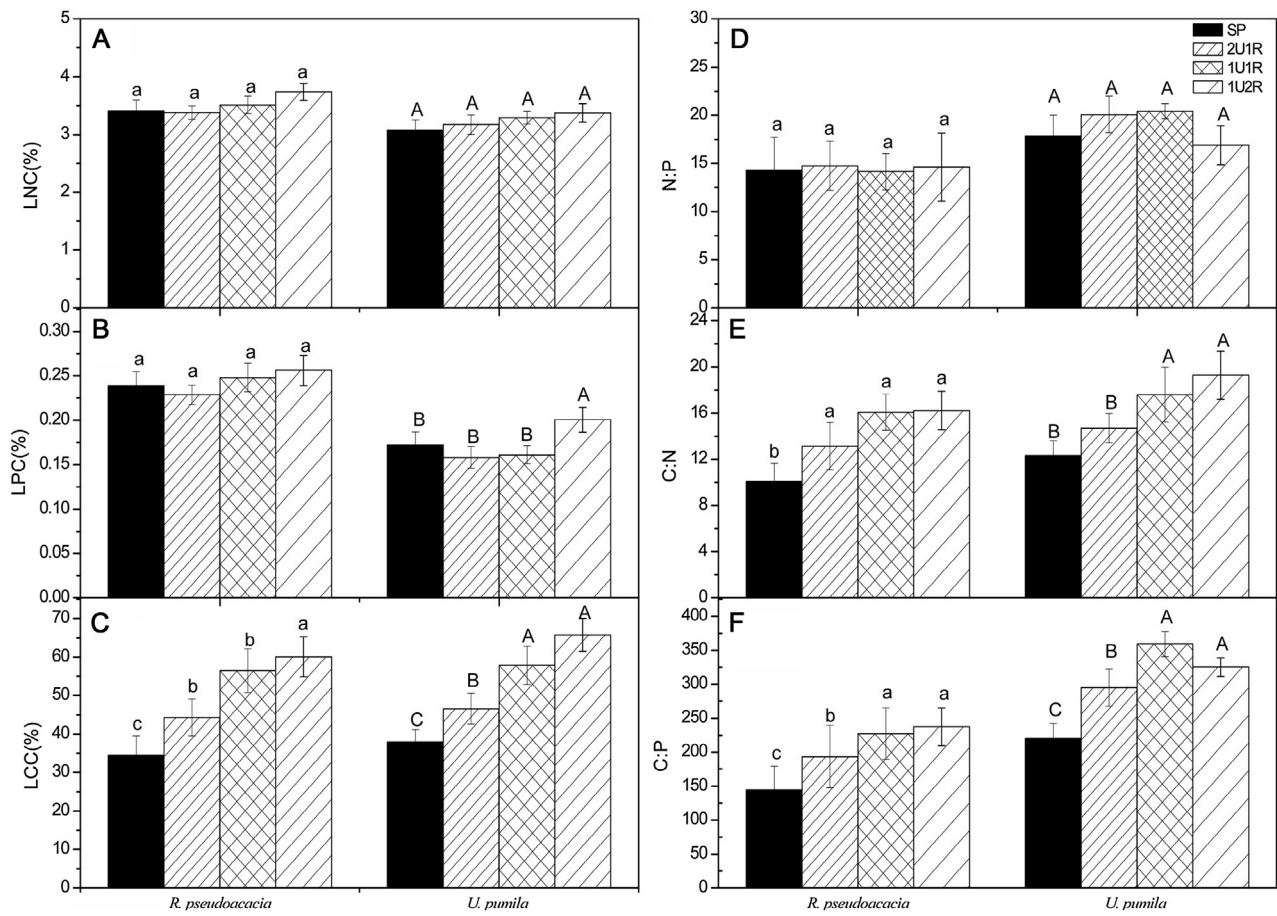


Fig. 4. Effects of four forest plantation types on leaf stoichiometric traits of *U. pumila* and *R. pseudoacacia*.

resource acquisition strategy rather than resource conservation. Compared to *R. pseudoacacia*, *U. pumila* exhibited more flexibility in adapting to droughty, barren and light adverse environments like the Loess Plateau of China, via the adoption of a conservative growth strategy. For the four forest plantation types, the UR mixed treatments exhibited advantages in leaf nutrient increases and photosynthetic capacity more than SP treatment; the 1U2R treatment was the optimum mixed plantation type. Thus, the differences in two species regarding plant leaf traits were greatly affected by the plantation ratio. Quantifying the relationships among leaf traits of multiple species can provide the information about major dimensions of the differences among plant species.

## 5. Conclusions

Different forest plantation types had significant effects on plant leaf morphological, physiological and stoichiometric traits. SLA of *R. pseudoacacia* and *U. pumila* increased in the mixed plantation types, especially in the 1U2R treatment when compared with single-species plantation, while the LDMC was less sensitive to variations in forest plantation types. The species *U. pumila* exhibited a comparatively low SLA and high LDMC, exemplified by a hard, thick leaf cuticle while *R. pseudoacacia* had soft, thin leaves in our study area. This indicates *U. pumila* adapt to the poor-nutrient and arid habitat by increasing leaf thickness and thus reducing water loss on the Loess Plateau region. As a leguminous species, *R. pseudoacacia* always had higher Pn, Tr and Gs, but lower WUE than *U. pumila* in UR mixed treatments, indicating the water use efficiency of *U. pumila* can be improved by planting mixed plantations with *R. pseudoacacia* on the Loess Plateau, especially when adopting the 1U2R

planting ratio. Our results also suggest nitrogen concentrations in UR mixed treatments can be effectively improved by *R. pseudoacacia* because of its strong nitrogen-fixing capacity. The species *R. pseudoacacia* had strong resource acquisition abilities as well as a high utilization efficiency, while *U. pumila* adopted the conservative strategy. For strong soil erosion conditions leading to soil P loss, the species of *R. pseudoacacia* was more susceptible to P limitations while *U. pumila* was more restricted by the N elements. In general, for the four forest plantation types, mixed plantations of *R. pseudoacacia* and *U. pumila* could effectively improve leaf nutrient contents and photosynthetic capacity of the two tree species, with an optimum mixed plantation ratio of *R. pseudoacacia* and *U. pumila* being the 1U2R treatment on the Loess Plateau of China.

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