

Assessing Adaptability of Planted Trees Using Leaf Traits: A Case Study with *Robinia pseudoacacia* L. in the Loess Plateau, China

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Abstract: Leaf trait patterns and their variations with climate are interpreted as an adaptive adjustment to environment. This study assessed the adaptability of planted black locust (*Robinia pseudoacacia* L.) based on the analysis of leaf traits and the comparison of its leaf traits with inter-specific ones existing in the same area. We measured some water and N use related leaf traits: leaf dry mass per unit area (*LMA*) and N, P and K concentrations based on both leaf area (N_{area} , P_{area} and K_{area}) and leaf mass (N_{mass} , P_{mass} and K_{mass}) of *R. pseudoacacia* at 31 sites along a water stress gradient in North Shaanxi Province, China. The results show that leaves of *R. pseudoacacia* have high N_{mass} and low *LMA* in the study area. High N_{mass} and low *LMA* are usually representative of luxurious resource use, and will advance plant resource competitiveness in high-resource conditions. As a whole, *LMA*-nutrient relationships of *R. pseudoacacia* display patterns that are fairly similar to the inter-specific relationships in both direction and intensity. The tendency for *LMA* and N_{area} to increase with decreasing water availability and the positive correlation between *LMA* and N_{area} reflect the trend for *R. pseudoacacia* to enhance water use efficiency (WUE) at the expense of down-regulated photosynthetic N use efficiency (PNUE) and high construction cost in dry conditions. However, the positive relationship between *LMA* and N_{area} in high mean annual precipitation (MAP) area is either unremarkable or reversed with decreasing water availability. This implies a lower photosynthetic capacity and a higher construction cost for high-*LMA* leaves. The inter-specific relationship between *LMA* and N_{area} is positive and does not change with water availability. This difference between inter-species and intra-species may be due to more diversified anatomies and more specialised structures for inter-species than intra-species. The failure of *R. pseudoacacia* adaption to dry conditions reflected by *LMA*- N_{area} relationship may be partially responsible for the emergence of rampike and dwarf forms found frequently in dry conditions. Incorporating intrinsic characteristics of planted trees into vegetation restoration project will be instructive and meaningful for species selection.

Keywords: water stress; planted tree; leaf trait; *Robinia pseudoacacia* L.; tradeoff; Loess Plateau

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1 Introduction

Plantation has been used extensively in the ecosystem restoration in arid and semiarid areas. Over the past several decades, the suitability of plantation in water shortage area has received considerable attention (Bellot *et al.*, 2004; Maestre and Cortina, 2004; Van Dijk and Keenan, 2007; Padilla, 2009). One of the most concerned

focuses is on the adaptability of planted trees.

Several previous studies have elaborated the adaptability of planted trees from several aspects, e.g., water use strategy (Almeida *et al.*, 2007; Querejeta *et al.*, 2008), photosynthetic physiology, growth (Oki and Kanae, 2006; Peichl and Arain, 2006), survival rate (Padilla *et al.*, 2009) and regeneration (Arrieta and Suarez, 2006). In arid and semiarid areas, water avail-

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ability is a major constraint to the planted trees. A few of studies have shown that the regeneration and growth of planted woody species, especially exotic ones, were constrained by water availability in these artificial ecosystems (Arrieta and Suarez, 2006; Oki and Kanae, 2006; Dye and Versfeld, 2007). According to the study by Padilla *et al.* (2009), the survival rate of some frequently used species in restoration projects hardly reached 55%. Yet the majority of the studies were based on control comparative (Querejeta *et al.*, 2008) or in situ spot experiments (Dye, 1996). With regard to the enormous differences between in situ and controlled experiments, incorporating environmental variation (especially water gradient) on large-scale into the research of the adaptability of planted trees (Oleksyn *et al.*, 2003) is indispensable to illuminate the actual adaptability of planted trees, however, related studies are sparse currently.

Representative and easily measured traits are preconditions for the research on large-scale. Leaf traits are closely correlated with the structure and function of ecosystems (Reich *et al.*, 1992; Poorter and Bongers, 2006; Fortunel *et al.*, 2009) and are sensitive to environmental variation. Over the past two decades, the leaf trait patterns and how they vary with climate have been studied intensively (Reich *et al.*, 1992; 1999; Wright *et al.*, 2005). Leaf trait patterns and their variations with climate reflect chemical, structural and physiological regulations of plants under varying environment and are interpreted as specific resource use and growth strategies corresponding to certain environment (Reich *et al.*, 1997; Diaz *et al.*, 2004; Wright *et al.*, 2004a, Wright *et al.*, 2005; Shipley *et al.*, 2006). Although only a modest portion of variation in leaf traits among species can be explained by variation in climate, striking and significant trends have been detected (Reich and Oleksyn, 2004; Wright *et al.*, 2004b; Westoby and Wright 2006; He *et al.*, 2010). Furthermore, some key leaf traits can be measured easily and economically (Cornelissen, 2003). The measurements of leaf traits, especially traits related to water use strategies, can provide much insight into the underlying mechanisms of species adaptation under water stress and will be instructive and meaningful for further vegetative reconstruction (Hatton *et al.*, 1998).

LMA and nutrient concentrations are important indicators of plant resource capture and usage strategies, and are fundamental for the growth and regeneration of

species (Westoby, 1998; Wilson *et al.*, 1999; Vendramini *et al.*, 2002; Hallik *et al.*, 2009; He *et al.*, 2009; Poorter *et al.*, 2009). *LMA* and N concentration per unit area (N_{area}) represent the economics of water and N in photosynthesis and are predominant for the water use strategy of plants with decreasing water availability (Centritto *et al.*, 2002; Bacelar *et al.*, 2004; Cornwell *et al.*, 2007; Poorter *et al.*, 2009).

This study was designed to explore the adaptability of planted trees on the basis of leaf traits. Our objectives were 1) quantifying leaf traits of planted trees, comparing them with inter-specific leaf traits in the same area, and analyzing their ecological significance; 2) discerning leaf trait associations of planted trees with precipitation; and 3) exploring the adaptive significance of environmentally induced leaf traits variation.

2 Materials and Methods

2.1 Study area

The study area (35°09'36"–37°51'36"N, 108°06'36"–110°13'12"E) is located in North Shaanxi Province of the Loess Plateau (Fig. 1), one of the 'hot spots' of environmental degradation and a typical arid and semiarid area in China. Centuries of deforestation and overgrazing, which have been aggravated by the population increase in China, have resulted in degenerated ecosystems and desertification (Wang and Wu, 2005). Intensive restoration projects have been implemented in the study area since 1994 (Zhang *et al.*, 2000; Fu *et al.*, 2002; Li, 2004). Black locust (*Robinia pseudoacacia* L.), a N₂-fixing species, was widely planted in restoration projects due to its drought resistance, high survival rate, ability to improve soil and remarkable growth rate (Boring and Swank, 1984; Li *et al.*, 1996; Shan *et al.*, 2003), and it was selected as the target species in this study. In the south of the study area, *R. pseudoacacia* grew well; however, rampike and dwarf forms were commonly seen in the north of the study area.

The meteorological data used in this study were obtained from 7-year averaged temperature and precipitation records (2000–2006) at 174 well-distributed meteorological stations in and around the Loess Plateau, China. The mean annual temperature (MAT) and mean annual precipitation (MAP) was interpolated in ARCGIS (ESRI, Redlands, CA, USA) based on latitude, longitude and altitude. Both MAP and MAT increased from the north to the south of the study area (Fig. 1).

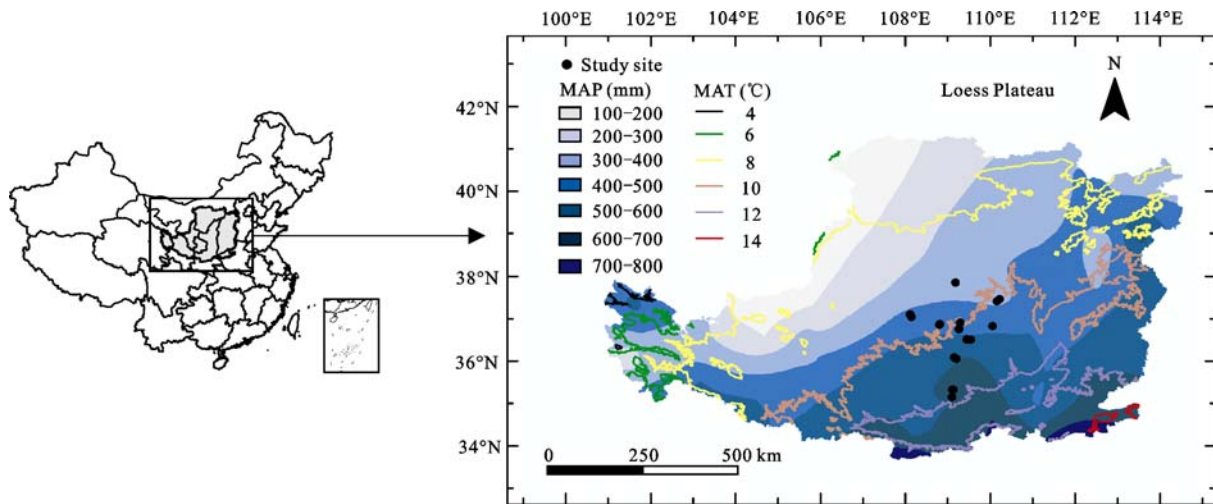


Fig. 1 Location of study sites and variation of mean annual temperature (MAT) and mean annual precipitation (MAP) of the Loess Plateau

The most widely distributed soil type is loessial soil, with sandy and purple soil scattered at the southern and northern margins of the study area. These three soil types have developed from loess parent material which typically has high permeability. The vegetation type changes from temperate forest-steppe in the southern portion of the study area to temperate steppe in the north (Wu, 1980). Indigenous vegetation is seldom found due to intensive human activities. Woody plants have been planted in the study area. The most common species are the *R. pseudoacacia*, *Pinus tabulaeformis* Carr. and *Caragana korshinskii* Kom.

2.2 Site selection and leaf sampling

Along a naturally occurring water stress gradient, *R. pseudoacacia* plantations with stand age ranging from 5 years to 45 years were selected. Stand age was determined by interviewing the natives. At last, 31 sites with a size of 10 m × 10 m were selected in the study area (Fig. 1).

In every site, five trees within 25th–75th percentiles of diameter at breast height (DBH) were randomly selected. For each tree, about 60 fully expanded, sun-lit and intact leaflets were collected from the outer canopy. Leaves from different trees were kept separate. Each sample from one tree was divided into two equal parts. Sampling was performed between late-July and mid-August 2008.

2.3 Measurement of leaf traits

One part of leaf sample was immersed in distilled water

for six to eight hours in a portable refrigerator to obtain a constant fresh weight, and it was dried with filter paper. Water-saturated fresh weights were then determined with an analytical balance (AL104, Mettler Toledo Co., Switzerland). Next, leaves were scanned with a scanner (Microtek, Scanmaker S460, China), and a pixel-counting method was used to determine the leaf area in ARC/INFO 8.1 (Environmental Systems Research Institute, Redlands, CA, USA). Then, samples were put on non-hygroscopic plastic plates and oven-dried at 60°C for at least 24 h to constant weight. After that, leaf dry mass was determined with an analytical balance. *LMA* was calculated through dividing the leaf dry mass by one-sided leaf area.

For the nutrient concentration measurements, the other part of the sample was placed in a paper bag and dried in the sun. Next, the leaf samples were oven-dried at 60°C for at least 24 h to constant weight. Dried samples were ground with a plant-sample mill and sieved through 0.15-mm grids for chemical analysis, which were performed at the State Key Laboratory of Urban and Regional Ecology in the Research Center for Eco-Environmental Science, Chinese Academy of Science. Total N concentration per unit mass (N_{mass}) was determined from 15 mg of homogeneously ground material using an elemental analyser (VarioEL III; Elementar Analysensysteme GmbH, Hanau, Germany). For determinations of P and K concentrations per unit mass (P_{mass} and K_{mass}), 0.3 g sieved sample was digested with $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2$ in two steps (Step one: 0–180°C about 10–20 min; step two: 180–360°C about 2.5 h) (Thomas

et al., 1967), and the digestion solution was diluted to 50 ml with deionised water. Duplicate digestion was conducted for each sample. The P and K concentrations in the digestion solution were quantified by inductively coupled plasma optical emission spectrometry (ICP-OES; Teledyne Lemman Labs Prodigy, Hudson, USA) (Ikem *et al.*, 2002). Lines of emission were: P 178.28 nm; K 766.49 nm. Standard solutions were made up: P (KH_2PO_4 , from 0.5 $\mu\text{g}/\text{mL}$ to 8 $\mu\text{g}/\text{mL}$), K (KCl, from 1 $\mu\text{g}/\text{mL}$ to 20 $\mu\text{g}/\text{mL}$). P and K concentrations of the digestion solution were derived from standard curves generated on the basis of standard solutions. The final concentration was calculated by concentration of the digestion solution and sample weight. Standard reference material of plant GBW07605 (GSV-4, Chinese tea leaves) was measured simultaneously for quality control. N, P and K concentrations per unit area (N_{area} , P_{area} and K_{area}) were calculated according to the conversion equation between area based and mass based element concentrations: $N_{\text{area}} = LMA \times N_{\text{mass}}$.

Data of inter-specific leaf traits (only data for *LMA*, N_{area} and N_{mass} were available) were from the study of Zheng and Shangguan (2007), and the data of Ningshan County were eliminated for consistency of the study area. At last, 66 species were included (22 herb species, 31 shrub species and 13 tree species). The 13 tree species were *Acer truncatum* Bunge, *Betula platyphylla* Sukats. var. *japonica* Hara., *Diospyros kaki* L., *Pinus tabulaeformis* Carr., *Platycladus orientalis* Endl., *Populus davidiana* Dode, *Populus hopeiensis* Hu et Chow, *Populus simonii* Carr., *Quercus liaotungensis* Koidz., *R. pseudoacacia*, *Tilia mongolica* Maxim, *Ulmus propinqua* Koidz. and *Ulmus pumila* L.

It should be noted that in Zheng and Shangguan's study, the N concentrations were measured using the modified Kjeldahl method, in which the sample was pre-treated with salicylic acid and thiosulfate to incorporate nitrate and nitrite (Bremner and Mulvaney, 1982). Thus the N concentrations determined by the modified Kjeldahl method were identical to the total N concentrations. In this study, the N concentrations also represented total N concentrations. Therefore, the N concentrations are comparable between the two studies.

2.4 Statistical analyses

Main features of *R. pseudoacacia* leaf traits were described through min, max, mean, geometric mean, *etc.*

To compare *R. pseudoacacia* leaf traits to inter-specific ones, box plots (Sakka *et al.*, 2002) were used to show the median, mean, 5th, 10th, 25th, 75th, 90th and 95th percentiles of *R. pseudoacacia* leaf traits in our study and tree species and all species leaf traits in Zheng and Shangguan's study. *R. pseudoacacia* leaf traits in our study and tree species and all species leaf traits in Zheng and Shangguan's study were compared with one-way ANOVA.

When testing the relationships between pairs of leaf traits, \log_{10} transformed values were used in the correlation analysis so as to attain the approximate normality and homogeneity of residuals in view of the common allometric scaling laws among leaf traits (West *et al.*, 1997; Hidaka and Kitayama, 2009; Reich *et al.*, 2010).

To explore the shift of *R. pseudoacacia* *LMA*-nutrient relationships with water stress, a tentative piecewise regression was conducted along water gradient. In the piecewise regression process, all sites were divided into two groups along water gradient (31 sites were sorted based on MAP, the 2nd to 30th sites were assigned as the cutting site in sequence), and the sum of the residual variances of the two areas were calculated. The breakpoint was designated as the point at which the sum was minimised. Different but close breakpoints were obtained for the relationships between *LMA* and N, P and K concentrations. A common breakpoint was assigned subjectively to maintain consistency, and the 31 sites were divided into a north area (21 sites) and a south area (10 sites). In the north area, the 21 sites were further divided. Finally, the 31 sites were separated into three areas: area A (ten sites with MAP ranging from 578 mm to 618 mm), area B (11 sites with MAP ranging from 465 mm to 511 mm) and area C (ten sites with MAP ranging from 352 mm to 457 mm) (Table 1). Figure 2 showed the typical growth status of *R. pseudoacacia* in area A, B and C.

Standardized major axis (SMA) slope-fitting techniques were used to analyse the intra-specific leaf trait relationships in the study area and *LMA*-nutrient relationships in areas A, B and C. The SMA slopes and intercepts were tested using the (S) MATR package within the R programming environment (version 2.10.1) (Warton *et al.*, 2006). SMA slope-fitting techniques were also used to analyse the inter-specific relationships among leaf traits. The divisions were designated subjectively according to the *MAP*. Pearson correlations between the

Table 1 Geographical and climatic descriptions of 31 study sites

Site	Latitude (°N)	Longitude (°E)	Elevation (m)	Stand age (yr)	MAT (°C)	MAP (mm)
A ₁	35.33	109.13	1300	5	11.2	618
A ₂	35.34	109.12	1368	10	11.0	617
A ₃	35.33	109.12	1361	20	11.0	617
A ₄	35.33	109.12	1379	30	11.0	617
A ₅	35.33	109.12	1379	5	11.0	617
A ₆	35.16	109.10	1057	7	11.5	612
A ₇	36.07	109.21	1122	25	10.8	584
A ₈	36.07	109.18	1154	5	10.7	582
A ₉	36.07	109.18	1154	8	10.7	582
A ₁₀	36.09	109.15	1160	20	10.6	578
B ₁	36.51	109.54	1274	10	10.4	511
B ₂	36.51	109.53	1280	20	10.3	511
B ₃	36.52	109.54	1258	10	10.4	509
B ₄	36.52	109.53	1245	30	10.4	509
B ₅	36.52	109.53	1262	30	10.4	509
B ₆	36.52	109.53	1245	5	10.4	509
B ₇	36.75	109.25	1220	13	10.2	477
B ₈	36.77	109.27	1164	30	10.3	475
B ₉	36.84	110.06	916	8	10.6	467
B ₁₀	36.86	108.81	1361	10	9.7	465
B ₁₁	36.86	108.81	1363	30	9.7	465
C ₁	36.91	109.28	1197	27	10.0	457
C ₂	36.92	109.29	1205	5	10.0	456
C ₃	36.92	109.27	1329	10	10.2	456
C ₄	36.92	109.29	1146	15	10.2	456
C ₅	36.92	109.29	1203	9	10.2	456
C ₆	37.05	108.15	1383	35	9.3	432
C ₇	37.11	108.11	1586	8	9.2	420
C ₈	37.42	110.16	968	30	10.4	382
C ₉	37.47	110.22	1023	5	10.1	375
C ₁₀	37.86	109.18	1092	45	9.5	352

Notes: MAT means annual mean temperature; MAP means mean annual precipitation

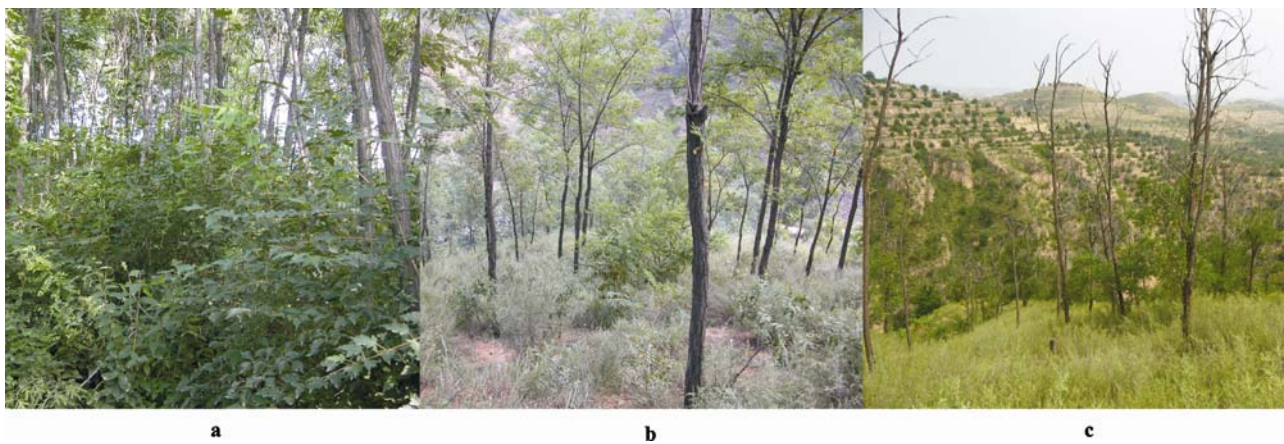


Fig. 2 Typical growth status of *R. pseudoacacia* in areas A (a), B (b) and C (c)

trait pairs and *p*-values were calculated with SPSS version 15.0 (SPSS Inc., Chicago, Illinois, USA).

3 Results

3.1 Intra- and inter-specific leaf trait variations

For *R. pseudoacacia*, different leaf traits exhibit different levels of variability. The leaf traits related to N and P change moderately (about threefold), and K_{area} varies the most (12.1-fold) (Table 2). Compared to the results from Zheng and Shangguan (2007), *LMA* of *R. pseudoacacia* is low in existing tree species in the study area (Fig. 3a). As an important N_2 -fixing species, *R. pseudoacacia* has a higher mean N_{mass} compared to means of tree species and pooled species of different life forms (Fig. 3b). However, N_{area} is similar to the means of tree species and pooled species (Fig. 3c), which results from a relatively low *LMA* for *R. pseudoacacia* (Fig. 3a).

3.2 Correlations among leaf traits

From Table 3, it can be seen that if considering pairwise, the N, P and K concentrations of leaves are positively

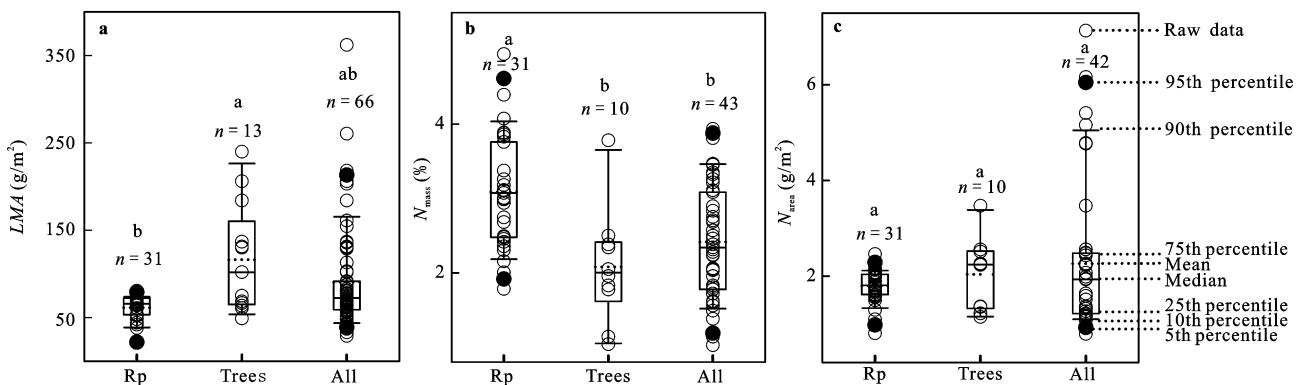
correlated at the 0.01 level on both mass and area bases. The mass-based nutrient concentrations are significantly negatively correlated with *LMA* (except for K_{mass} , $R = -0.037$, $p = 0.651$), while the area-based nutrient concentrations are significantly positively correlated with *LMA* at the 0.01 level. N and P concentrations, the most closely associated leaf traits, have correlation coefficients of 0.784 and 0.808, respectively, on mass and area bases ($p < 0.001$). P_{mass} and K_{mass} are more weakly correlated compared with the correlation between N_{mass} and P_{mass} . The relationship between N_{mass} and K_{mass} is even weaker, although the relationships involving K_{mass} are still highly significant (Table 3). The correlations among the concentrations of N, P and K are higher on an area basis than on a mass basis (Table 3). *LMA* is more highly correlated with N_{mass} than N_{area} . For P, there is a slight difference between the area- and mass-based concentrations. *LMA* is significant positively correlated with K_{area} , while no significant correlation is found between *LMA* and K_{mass} (Table 3).

As shown in Fig. 4, the relationships between *LMA* and nutrient concentrations seem to be incongruous in

Table 2 Summary statistics for leaf trait of *R. pseudoacacia*

Leaf trait	Min	Max	Max / Min	Mean ± S.D.	Geometric mean
<i>LMA</i> (g/m^2)	21.00	81.00	3.9	61.00 ± 15.00	59.00
N_{mass} (%)	1.78	4.94	2.8	3.09 ± 0.73	3.00
P_{mass} (%)	0.06	0.18	2.9	0.13 ± 0.03	0.13
K_{mass} (%)	0.24	1.19	4.9	0.66 ± 0.25	0.62
N_{area} (g/m^2)	0.81	2.46	3.1	1.80 ± 0.33	1.76
P_{area} (g/m^2)	0.03	0.12	3.5	0.08 ± 0.02	0.08
K_{area} (g/m^2)	0.05	0.64	12.1	0.40 ± 0.14	0.36

Notes: *LMA*: leaf dry mass per unit area; N_{area} , P_{area} and K_{area} : N, P and K concentrations per unit area; N_{mass} , P_{mass} and K_{mass} : N, P and K concentrations per unit mass; $n = 31$



LMA: leaf dry mass per unit area; N_{mass} : N concentration per unit mass; N_{area} : N concentration per unit area; Rp: leaf traits of *R. pseudoacacia* in our study; Trees: leaf traits of tree species in Zheng and Shangguan's study; All: leaf traits of all species in Zheng and Shangguan's study; *LMA*, N_{mass} and N_{area} with different lowercase letters are significantly different at the 0.05 level

Fig. 3 Box plots of intra- and inter-specific leaf traits

low-LMA and high-LMA sections. Further analysis is then conducted by SMA slope-fitting in the three areas along the water stress gradient.

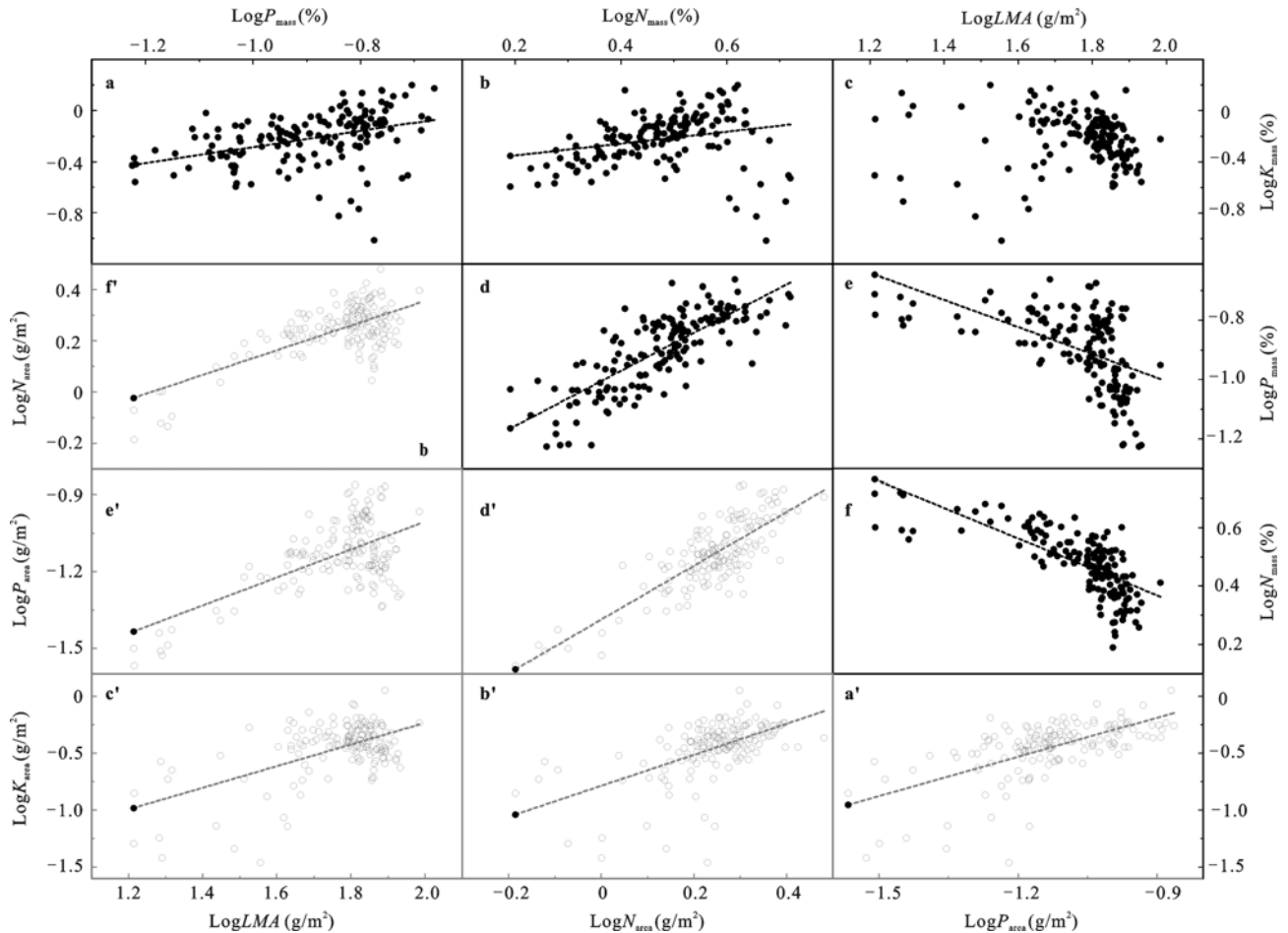
3.3 SMA slope-fitting of LMA-N, P and K concentrations in three areas

Overall, the leaves of *R. pseudoacacia* in the low pre-

Table 3 Bivariate relationships between leaf traits

	logLMA	logN _{area}	logP _{area}	logK _{area}
logLMA		0.963 (0.799, 1.127)	0.647 (0.508, 0.786)	0.338 (0.260, 0.416)
logN _{area}	0.681**		0.623 (0.551, 0.695)	0.242 (0.188, 0.297)
logP _{area}	0.593**	0.808**		0.345 (0.278, 0.412)
logK _{area}	0.567**	0.575**	0.63 ^{0**}	
	logLMA	logN _{mass}	logP _{mass}	logK _{mass}
logLMA		-0.966 (-1.118, -0.813)	-0.605 (-0.760, -0.449)	-0.026
logN _{mass}	-0.708**		0.662 (0.576, 0.742)	0.131 (0.051, 0.213)
logP _{mass}	-0.525**	0.784**		0.249 (0.160, 0.344)
logK _{mass}	-0.037	0.247**	0.400**	

Notes: Standardized major slopes (fitted with standardized major axis (SMA)) with 95% confidence intervals are given in the upper right section of the matrix if the relationships were significant at the 0.01 level (y-variable is in column n, x in row 1). Correlation coefficients (R) are given in the lower left section of the matrix. n = 155; * p < 0.05; ** p < 0.01. Refer to Table 2 for LMA, N_{mass}, P_{mass}, K_{mass}, N_{area}, P_{area} and K_{area}



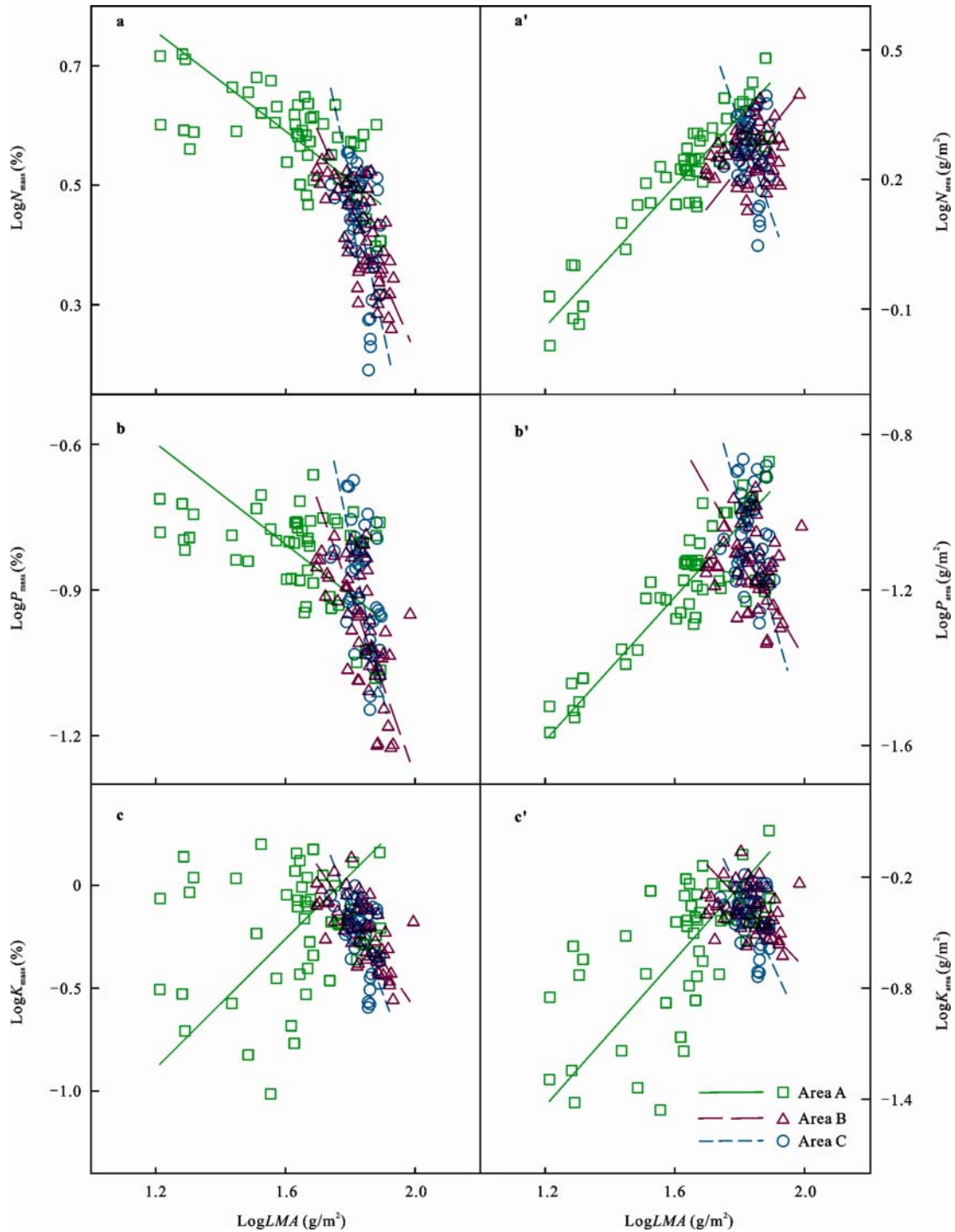
a–f in the upper right section show the relationship between LMA, N_{mass}, P_{mass} and K_{mass}; a'–b' in the lower left section show the relationship between LMA, N_{area}, P_{area} and K_{area}; data for individual slopes and correlation coefficients are given in Table 3; refer to Table 2 for LMA, N_{mass}, P_{mass}, K_{mass}, N_{area}, P_{area} and K_{area}

Fig. 4 Relationships between leaf traits of *R. pseudoacacia* fitted with SMA techniques

precipitation areas (area B and area C) tend to have lower mass-based and higher area-based nutrient concentrations than those in the high precipitation area (area A) (Fig. 5).

Regression slopes of the *LMA* and nutrient concentrations differ in the three areas (Fig. 5, Table 4). In area A,

N_{mass} and P_{mass} tend to decrease with increasing *LMA*; in contrast, K_{mass} tends to increase with increasing *LMA*, but the slope of *LMA*- K_{mass} is not significantly different from zero ($p = 0.999$). In areas B and C, N_{mass} , P_{mass} and K_{mass} decrease uniformly with increasing *LMA* (Fig. 5a–Fig. 5c). In area A, N_{area} , P_{area} and K_{area} increase uni-



Data for individual slopes and tests for slopes and intercepts are given in Table 4; refer to Table 2 for *LMA*, N_{mass} , P_{mass} , K_{mass} , N_{area} , P_{area} and K_{area}

Fig. 5 Relationships between *LMA* and nutrient concentrations

formly with increasing *LMA*. In areas B and C, this trend become obscure due to either insignificant correlations ($LMA-N_{\text{area}}$ and $LMA-P_{\text{area}}$) or a slope that is indistinguishable from zero ($LMA-K_{\text{area}}$) (Fig. 5a'–Fig. 5c'). *R. pseudoacacia* has stronger decreasing trends of the mass-based nutrient concentrations with increasing *LMA* in the low precipitation areas than in the high precipitation area. For the area-based nutrient concentrations, the high precipitation area has uniformly increasing trends with increasing *LMA*, while in the low precipitation areas these trends are not observed.

In contrast, the slopes of the inter-specific *LMA-N* are not different between low and high *MAP* areas on both the area and mass bases. A stronger decreasing trend for N_{mass} with *LMA* in the low precipitation areas is not found. N_{area} uniformly increases with increasing *LMA* in both the low and high *MAP* areas (Fig. 6, Table 5).

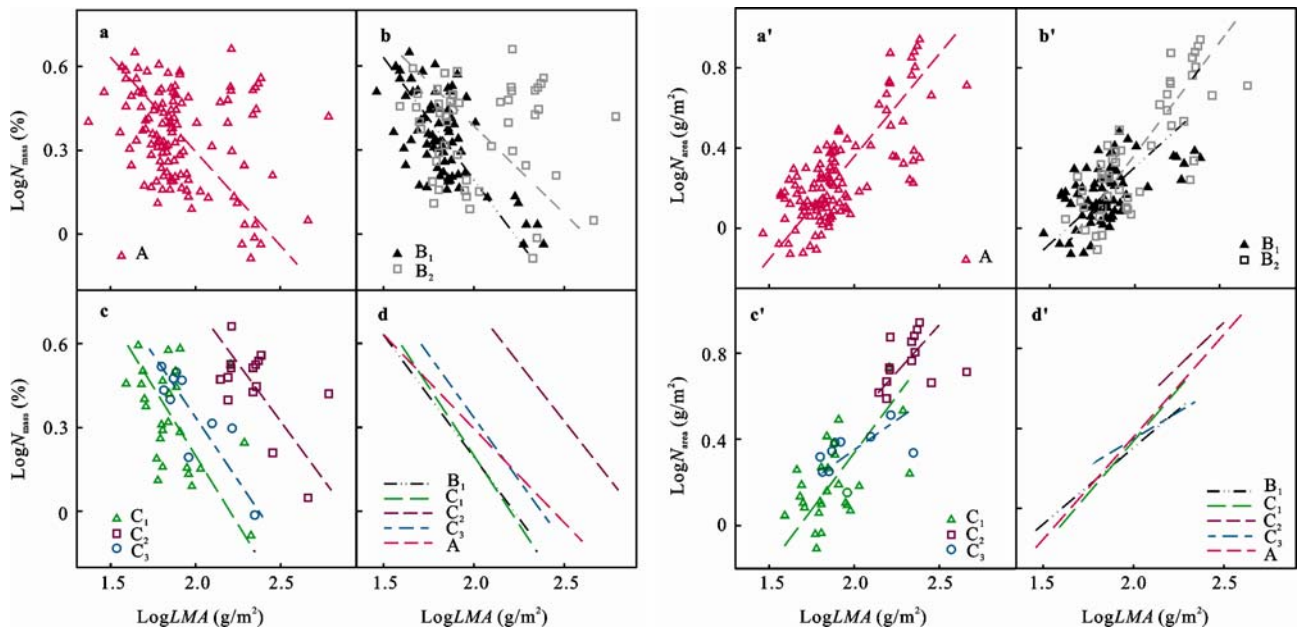
3.4 Plasticity of leaf traits in different areas

As depicted in Table 6, the variations in the *LMA* and nutrient concentrations in area A are higher than those

Table 4 Data for intra-specific SMA slopes fitted for areas A, B and C in Fig. 5

	Area A (n = 50)	Area B (n = 60)	Area C (n = 45)
$LMA-N_{\text{mass}}$	-0.416 (-0.331, -0.522)a, 1.26 -0.62, $p < 0.001$	-1.234 (-1.016, -1.5)b, 2.69 -0.67, $p < 0.001$	-2.507 (-1.933, -3.251)c, 5.02 -0.52, $p < 0.001$
$LMA-P_{\text{mass}}$	-0.519 (-0.399, -0.675)a, 0.03 -0.40, $p = 0.004$	-1.888 (-1.548, -2.302)b, 2.49 -0.65, $p < 0.001$	-3.194 (-2.418, -4.22)c, 4.96 -0.40, $p < 0.007$
$LMA-K_{\text{mass}}$	1.572 (1.184, 2.086)a, -2.78 0.14, $p = 0.319$	-2.31 (-1.887, -2.827)b, 4.02 -0.63, $p < 0.001$	-4.16 (-3.206, -5.399)c, 7.38 -0.52, $p < 0.001$
$LMA-N_{\text{area}}$	0.813 (0.723, 0.914)aA, -1.12 0.92, $p < 0.001$	0.94 (0.728, 1.213)aB, -1.46 0.19, $p = 0.143$	-2.164 (-1.603, -2.922)b, 4.23 -0.14, $p = 0.364$
$LMA-P_{\text{area}}$	0.923 (0.795, 1.071)a, -2.70 0.857, $p < 0.001$	-1.453 (-1.124, -1.878)b, 1.53 -0.16, $p = 0.232$	-2.942 (-2.176, -3.978)c, 4.33 -0.09, $p = 0.543$
$LMA-K_{\text{area}}$	1.98 (1.58, 2.483)aA, -3.81 0.619, $p < 0.001$	-1.847 (-1.436, -2.377)aB, 3.01 -0.25, $p = 0.054$	-3.745 (-2.805, -4.999)b, 6.45 -0.31, $p = 0.042$

Notes: The data presented are SMA slopes, 95% confidence intervals, intercepts, Pearson correlations between the trait pairs and p -values. Slopes are significantly different at the 0.05 level with different lowercase letters in the same row. Different uppercase letters in the same row represent different SMA intercepts at the 0.05 level, but no difference is found between slopes



a–d show the inter-specific relationship between *LMA* and mass based N concentration (N_{mass}); a'–d' show inter-specific relationship between *LMA* and area based N concentration (N_{area}). Data from Zheng and Shangguan's study were separated stepwise according to *MAP*: A (635–441 mm)→B₁ (635–570 mm) and B₂ (505–441 mm); B₂→C₁ (505 mm), C₂ (451 mm) and C₃ (441 mm). Data for the individual slopes, tests for slopes and intercepts are given in Table 5

Fig. 6 Inter-specific relationships between *LMA* and N concentrations

Table 5 Data for inter-specific relationships between *LMA* and N concentrations in different areas in Fig. 6

Area	B ₁	C ₁	C ₂	C ₃
Number of samples	71	27	15	10
<i>MAP</i> (mm)	635–570	505	451	441
<i>LMA</i> - <i>N</i> _{mass}	-1.07aB, 2.26, -0.67, <i>p</i> < 0.001	-1.05aB, 2.25, -0.44, <i>p</i> = 0.022	-0.54aA, 1.70, -0.56, <i>p</i> = 0.031	-0.67aC, 1.67, -0.84, <i>p</i> = 0.002
<i>LMA</i> - <i>N</i> _{area}	1.14aA, -1.23, 0.53, <i>p</i> < 0.001	1.12aAB, -1.77, 0.54, <i>p</i> = 0.003	1.03aB, -1.25, 0.62, <i>p</i> = 0.14	0.86aA, -0.74, 0.45, <i>p</i> < 0.20

Notes: The data presented in *LMA*-*N*_{mass} and *LMA*-*N*_{area} rows are SMA slopes, intercepts, Pearson correlations between the trait pairs and *p*-values. Slopes in the same row with different lowercase letters are significantly different at the 0.05 level. Different uppercase letters in the same row represent different standardized major axis (SMA) intercepts at the 0.05 level, but no difference was found between slopes. Refer to Table 2 for *LMA*, *N*_{mass} and *N*_{area}

Table 6 Variations of climate and leaf traits in area A versus areas B and C

		<i>MAP</i> (mm)	<i>MAT</i> (°C)	<i>LMA</i> (g/m ²)	<i>N</i> _{mass} (%)	<i>P</i> _{mass} (%)	<i>K</i> _{mass} (%)	<i>N</i> _{area} (g/m ²)	<i>P</i> _{area} (g/m ²)	<i>K</i> _{area} (g/m ²)
Area A (<i>n</i> = 50)	Max	618	11.5	78	5.24	0.22	1.58	3.03	0.14	1.13
	Min	578	10.6	16	2.50	0.08	0.10	0.65	0.03	0.03
	Range (Max–Min)	40	0.9	62	2.74	0.13	1.49	2.37	0.11	1.09
Areas B and C (<i>n</i> = 105)	Max	511	10.4	97	3.59	0.21	1.36	2.49	0.14	0.86
	Min	352	9.2	50	1.55	0.06	0.25	1.11	0.05	0.18
	Range (Max–Min)	159	1.2	47	2.03	0.15	1.10	1.38	0.09	0.68

in areas B or C (except for *P*_{mass}), even though the variations in *MAP* and *MAT* in areas B and C are larger than those in area A.

4 Discussion

Leaf trait variation is associated with internal regulation in both leaf morphological characteristics and biochemical composition. On the common biochemical, structural and physiological foundation, different species present similar trend of leaf trait variation despite of divergence in phylogenetic and acclimation (Wright *et al.*, 2004b; Westoby and Wright 2006; He *et al.*, 2010). Leaf trait values and their variations have a means of adaption to environment. The comparison of leaf traits and their variation of *R. pseudoacacia* to those of inter-specific on regional scale can give us some clues on the adaptability of planted *R. pseudoacacia*.

4.1 Leaf traits of *R. pseudoacacia* and their ecological implication

LMA, *N*_{area} and *N*_{mass} of *R. pseudoacacia* display considerable and divergent variations compared to those of other species. *R. pseudoacacia* has a higher *N*_{mass} than other species (Fig. 3b) and exhibits a wider range of *N*_{mass} than *LMA* and *N*_{area} (Fig. 3a, b, c), this was in accordance with the result about N₂-fixing species (Wright *et al.*, 2005). High *N*_{mass} and low *LMA*, usually accom-

pany with a high relative growth rate (Poorter *et al.*, 2009), represent a luxurious use of resources and are favorable in high-resource conditions. In low-resource conditions, lavish use of resources may be harmful for the survival of the plant.

4.2 Intra- and inter-specific *LMA*-nutrient associations

4.2.1 Similarities of intra- and inter-specific *LMA*-nutrient associations

Relationships between *LMA* and nutrient concentrations (Wright *et al.*, 2004b; He *et al.*, 2006; Poorter and Bongers, 2006; Salzer *et al.*, 2006) and between nutrient concentrations (Thompson *et al.*, 1997; Wright *et al.*, 2005) of *R. pseudoacacia* display the patterns that are fairly similar to the inter-specific relationships in both direction and intensity. These similar patterns of variation suggest that fundamental relationships among these key traits are applicable to all species on common biochemical, structural and physiological bases despite of divergence due to phylogeny and acclimation.

4.2.2 Tradeoff between photosynthetic N use efficiency and water use efficiency (WUE)

Among all of the resources required by plant, availability of N and water are vital limitations to photosynthesis in terrestrial ecosystems (Chapin *et al.*, 1987; Hungate *et al.*, 2003), and are particularly important for species in dry site, hence WUE and photosynthetic N use effi-

ciency (PNUE) are frequently used as measurements of species resources use strategies under water stress.

LMA and N_{area} have been shown to be the staunch indicators of tradeoffs between water and N (Niinemets, 2001). The tendency for LMA (Centritto *et al.*, 2002; Bacelar *et al.*, 2004) and N_{area} (Cornwell *et al.*, 2007) to increase with decreasing water availability is well known. High LMA in dry sites generally means thicker cell walls, smaller and more tightly packed cells and a lower portion of air spaces (Shields, 1950; Witkowski and Lamont, 1991; Poorter *et al.*, 2009), which collectively leads to increased leaf density. Given that high leaf density is accompanied with high leaf elastic modulus and low osmotic potential (Niinemets, 2001), hence increased leaf density is favorable to restricting water loss and will facilitate water uptake from drying soil. On the other hand, associated with morphological and biochemical changes, more N is partitioned to non-photosynthetic structures (e.g. lignin and cell-wall components). Therefore, PNUE in high- LMA leaves are down-regulated at a given N concentration (Onoda *et al.*, 2004; Alvarez-Clare and Kitajima 2007). High LMA and N_{area} in dry conditions reflect the tendency for plant to enhance WUE at the expense of down-regulated PNUE and high construction cost.

Overall, LMA of *R. pseudoacacia* increased with decreasing MAP ($n = 31$, $R = -0.57$, $p < 0.01$), and the leaves in areas B and C had higher LMA and N_{area} than those in area A ($p < 0.05$). Nevertheless, the positive relationship between LMA and N_{area} in area A was either unremarkable or reversed in areas B and C (Fig. 5a' and Table 4). This implies a lower photosynthetic capacity (Hikosaka, 2004) and a higher construction costs for high- LMA leaves. In contrast, inter-specific N_{area} increased with increasing LMA uniformly both in high and low precipitation areas (Fig. 6a'–d'). The emergence of a turning point in the LMA - N_{area} relationship for *R. pseudoacacia* perhaps indicates a failure of *R. pseudoacacia* adaption to dry conditions. This may be partially responsible for the emergence of rampike and dwarf forms found frequently in dry conditions. The inter-specific diversity in anatomy and specialised structures can compensate for this limitation of intra-specific variation. According to He *et al.* (2009), climate- and soil-induced species shift accounted mostly for the plant adaptation under a large environmental gradient.

4.3 Phenotypic plasticity and species shifts

Phenotypic variation triggered by the local environmental conditions reflects the adaptive adjustments of species to environmental stress (Dorn *et al.*, 2000; Reylea, 2002). Species that express high adaptive plasticity tend to be ecological generalists and frequently thrive over large environmental ranges (Sultan, 2000; Nicotra and Davidson, 2010). The plasticity of leaf traits related to water use strategies, e.g., higher LMA and N_{area} and lower relative growth rates in more xeric environments (Wright *et al.*, 2004a; Poorter *et al.*, 2009), are of primary importance for species under dry conditions. The reduced leaf traits variability in areas B and C indicated an inability to adjust under dry conditions and was detrimental to the survival of plant.

5 Conclusions

This paper assessed the regional adaptability of planted *R. pseudoacacia* using leaf traits in the Loess Plateau, China. *R. pseudoacacia* is an important fast growing species, and has been widely planted in the Loess Plateau. However, fast growth rate is backed up with plentiful resources. In the Loess Plateau, which is typical of water shortage, *R. pseudoacacia* tended to enhance WUE at the expense of down-regulated PNUE and high construction cost in dry conditions. But in severe water-shortage area, unremarkable or reversed positive relationship between LMA and N_{area} and the reduced leaf traits variability indicated an inability to adjust under dry conditions. This may explain the emergency of rampike and dwarf forms in severe water-shortage area. The inter-specific diversity in anatomy and specialised structures can compensate for this limitation of intra-specific variation effectively. Thus, future vegetation construction should take species' intrinsic characteristics into account.

Leaf traits present a simple and feasible method to assess the adaptability of planted trees on large-scale. Compared to large scale inter-specific leaf traits research, intra-specific leaf traits yet is seldom studied. Further researches on some other structural and physiological leaf traits are needed to get a comprehensive understanding of the relationships between intra-specific leaf trait variations and the adaptability of species. These observations will provide further support for species selection in vegetation restoration project.

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