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Generality of leaf traits relationships of dominant species along the secondary succession in the Loess Plateau of China

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The study investigated the specific leaf area (SLA), leaf photosynthetic rates (P_n), leaf nitrogen contents (on mass and area bases, Nm and Na, respectively) and nitrogen use efficiencies (PNUE) of 18 dominant species of four secondary succession groups in the Loess Plateau. The leaf SLA, N_m, P_n and PNUE significantly differed among the different secondary succession groups ($P<0.05$), but the leaf N_a and leaf chlorophyll content (Chl) did not differ. SLA varied in a high → low → high pattern with the secondary succession, reaching the lowest point in the early forest community. The N_m and Chl showed a double peak curve with the secondary succession and peaked in the shrub community. Of all the species, the photosynthetic nitrogen use efficiencies were positively correlated with the SLA, but negatively correlated with the N_a. The SLA of all the species negatively correlated with the N_a, but weak positively correlated with the N_m. The above resource capture-, use- and growth-related traits probably clarified the mechanism of the secondary succession in the Loess Plateau.

Key words: Photosynthetic nitrogen use efficiency, specific leaf area, secondary succession, Loess Plateau.

INTRODUCTION

Plant community succession is an important aspect of vegetation ecology (Martínez et al., 2001). Besides the difference of community composition, the ecophysiological attributes and adaptation of early succession species are also different from the late succession species. Plant functional traits are biological characteristics of plant species that respond to dominant processes in an ecosystem (Lavorel et al., 1997), and thus using plant functional traits instead of plant species might be helpful to identify general processes of succession (Kahmen and Poschlod, 2004). Specific leaf area (SLA; the ratio of leaf area to dry mass), nitrogen content (on mass and area bases, N_m and N_a, respectively), photosynthetic rate (P_n) and photosynthetic nitrogen use efficiency (PNUE) are fundamental leaf traits which play key roles in plant functioning (Ackerly, 2004). Later succession species exhibit lower capacities to photosynthetically acclimate to high light conditions than faster-growing, earlier succession species (Bazzaz and Carlson, 1982). Furthermore, the photosynthetic rates of late succession groups decline with increased shade tolerance (Bazzaz, 1979). Many shade tolerant species have thin leaves, which result in their high SLA, although the negative relations between SLA and shade tolerance have also been reported (Reich et al., 2003). In the Loess Plateau, dominant species of herb and shrub comm.-unities have higher photosynthetic rates (P_n) than those

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Abbreviations: SLA, Specific leaf area; **P_n,** leaf photosynthetic rates; **PNUE,** photosynthetic nitrogen use efficiencies; **Chl,** leaf chlorophyll content; **Nm**, leaf nitrogen content per unit dry mass; **Na**, leaf nitrogen content per unit area.

of early forest communities and climax forest communities through the secondary succession (An and Shangguan, 2007). At low light intensities, late succession species are photosynthetically more efficient than early succession species. Early succession trees have values between early succession herbs and late succession trees.

Several studies have reported the relations among these fundamental traits and their large-scale patterns (Wright et al., 2004, 2005b; He et al., 2006; Wang, 2007; Lloyd et al., 2010). As an indicator of the dry-mass cost of producing new leaves, SLA is positively correlated with leaf nitrogen content in different species (Westoby et al., 2002; Wright et al., 2004). Species with higher SLA generally have higher N_m, photosynthetic capacities (A_{max}) and PNUE (Poorter and Evans, 1998). These patterns lead to the hypothesis that the response of A_{max} to leaf nitrogen variation is regulated by leaf structure, thicker and/or denser leaves having both lower A_{max} per unit leaf nitrogen and smaller change in A_{max} per unit nitrogen variation (Reich and Walters, 1994). Leaf nitrogen content is strongly correlated with photosynthetic capacity (Frak et al., 2002; Hikosaka, 2004; Takashima et al., 2004). This correlation provides a useful link between processes on short-term, leaf-level scales and long-term, plant- and stand-level scales, and has been used to estimate maximum CO_2 uptake over a broad range of species. Studies on a range of ecosystems have shown that deciduous species generally have higher nitrogen contents and P_n than evergreen species (Eamus and Cole, 1997; Reich et al., 1997). Quantifying the relationships among leaf traits of multiple species can provide the information about major dimensions of the differences among plant species (Westoby et al., 2002).

In the Loess Plateau, the ecosystems are affected by various forms of human activities for millennia. The impacts of human activities on the Loess Plateau were basically characterized in terms of continuous and widespread stresses, e.g., over-grazing and large-scaled monocultures (wheat and maize) (Wang, 2002). During the second half of the twentieth century, habitat fragmentation and environmental degradation on the Loess Plateau were accelerated due to the extensive monocultures grown for the increasing population (e.g. the population increased from 37 million to >100 million) (Liu, 1999; Jiang et al., 2003). In the Loess Plateau, the vegetation cover tends to turn low and sparse, and thus soil degra-dation ensues from extremely serious soil erosion. Therefore, more attention has been paid to the secondary succession in the Loess Plateau by Chinese scientists. A lot of studies focused on plant community sere and soil changes with the secondary succession in the Loess Plateau region (Li and Shao, 2003; Jia et al., 2005; Fan et al., 2006; Du et al., 2007). Plant functional traits responses can also provide an insight into the mechanisms of the secondary succession and thus it is necessary to identify plant functional traits of the early and late succession species in the Loess Plateau.

The study aimed at investigating the secondary succes-sion in the Loess Plateau by analyzing; 1) the variation of specific leaf areas, leaf nitrogen contents, leaf photosynthetic rates and nitrogen use efficiencies of 18 dominant species and 2) correlations between the traits through the secondary successional sere, especially those with respect to the photosynthesis–nitrogen relationship.

MATERIALS AND METHODS

Study area

The study was carried out in the Lianjiabian forest farm in the Loess Plateau, Heshui, Gansu, China (35.03° – 36.37°N, 108.10°–109.08°E, 1500 m above sea level). The mean annual temperature is 7.4°C and the mean annual precipitation is 587.6 mm of which 60 to 70% mainly distributes in June, July, August and September (Wang et al., 2005); the aridity index is 0.72, and the atmospheric relative humidity is 63 to 68%. The soil of the study site was classified as calcareous cinnamon soil originated from 50 to 100 m deep primary or secondary loess and the thickness of laterite is 80 to 100 m below (Zou et al., 2002; Wang et al., 2005). Because of the influences of geographical and climatic factors, the vegetations on sunny and shady hillsides of the forest farm significantly differ from each other. Generally, there are abundant shrubs and herbs and sparse or no woods on sunny ridges and mounds, and abundant semi-natural forests on shady hillsides and in valleys. The vertical distribution of forest vegetation was indistinctive because of its small height difference. It is evident that in the forest farm, the vegetations belong to the north warm temperate zone and the deciduous *Quercus liaotungensis* sub-zone according to the characteristics of their vegetation types, distributions and successions (Zou et al., 2002).

The study area was situated in the transitional zone between forest and semi-arid steppe zones and most of its forests were semi-natural woods gradually recovered from frequent damages by human activities. Most vegetations of the area were semi-natural woods that had gradually recovered on abandoned farmlands after 1866, and then large scale secondary forest landscape had formed and developed towards a climax forest community (*Q. liaotungensis* Koidz) during the recovery (Zou et al., 2002). In the forest farm, there is relatively integrated vegetation sere: herb community (*Bothriochloa ischaemum* (L.) Keng, *Artemisia giraldii* Pamp, *Artemisia sacrorum* Ledeb, *Spodiopogon sibiricus* Trin) → shrub community (*Sophora viciifolia* Hance, *Hippophae rhamnoides* (L.), *Ostryopsis davidiana* Decne) → early forest community (*Populus davidiana* Dode, *Betula platyphylla* Suk, *Platycladus orientalis* (L.) Franco) → climax forest community (*Q. liaotungensis* Koidz).

Sampling

The sampling and sample determination were conducted in early June of 2006. Different secondary succession groups were chosen to represent different temporal sequences and the research sites were chosen in the places that suffered minimal grazing and other human disturbances by visual vegetation examination. 18 species that represented the four secondary succession groups in the Loess Plateau (I, II, III and IV stands for herb community, shrub community, early forest community and climax forest community, respectively) were chosen: herb community (*Stipa bungeana* Trin, *B. ischaemum* (L.) Keng, *Carex lanceolata* Boott, *A. sacrorum* Ledeb, *Pulsatilla chinensis* (Bunge) Regel, *Potentilla chinensis* Ser); shrub community (*Sophora viciifolia* Hance, *H. rhamnoides* (L.), *O. davidiana* Decne, *Rubus palmatus* Thunb, *Rosa xanthina* Lindl, *Acer ginnala* Maxim, *Spiraea pubescens* Turcz, *Ziziphus*

jujuba var. spinosa); Early forest community (*Populus davidiana* Dode, *Betula platyphylla* Suk, *Platycladus orientalis* (L.) Franco); Climax forest community (*Q. liaotungensis* Koidz).

The chosen herbs and shrubs were mainly distributed on the sunny hillsides, while the chosen trees mainly distributed on the half-shady hillsides or half sunny hillsides. Mature and fully expanded leaves were sampled from the middle part of the herbs and from the middle canopy of shrubs and trees.

Plant traits

30 to 40 plants of each species were randomly chosen and divided into three samples, and each sample composed of 30 to 50 leaves from 10 to 12 plants of each species. The sample leaves were scanned with digital scanner and then their leaf surface areas were calculated on the basis of their scanned pictures with a digital image analysis software (Motic images advanced 3.0, China). After their scanning, all the sample leaves were carefully put into paper bags and then oven dried at 70°C; and the dry mass of the leaves were weighed for their SLA calculation (ratio of leaf area to leaf dry mass, $cm^2 \cdot g^{-1}$).

After their SLA measurement, the dried leaf samples were used for leaf nitrogen content determination. All the leaves from each sample of the same species were ground into a homogenous fine powder with a plant-sample mill (1093 Sample Mill, Foss, Sweden) and then their powders were sieved with a 2-mm mesh screen before they were weighed for nitrogen determination. Then, 200 mg powder of each sample was taken to determine the leaf nitrogen content by the modified Kjeldahl method. The 200 mg powder, 5 ml of concentrated sulphuric acid (H_2SO_4) and peroxide (H_2O_2) were put into a digestion tube. The mixture was heated at 365°C until it turned clear and then the clear solution was used for nitrogen determination with an autoanalyser (Kjeltec 2300 Analyzer Unit, Foss, Sweden). The leaf nitrogen content was measured as the average of three determinations of each sample and the nitrogen data were expressed on mass basis (N_m, $mg \cdot g^{-1}$) and area basis (N_a, the ratio of N_m to SLA, $g \cdot m^{-2}$). The PNUE was expressed as the ratio of P_n to N_m (Poorter and Evans, 1998).

Photosynthetic characteristics

The P_n of the mature and fully expanded leaves of the 18 dominant species were measured with a portable open gas exchange system (LI-6400, Li-Cor Inc., USA) between 9:00 to 11:30. For the P_n measurement, light was provided by LED (model 6400-02B; Li-Cor). The open pathway was turned on to adjust the airflow rate to 0.5 $ml \cdot min^{-1}$ and the cuvette temperature was set approximately at the air temperature on each sampling occasion. Six to eight mature and fully expanded leaves of each species were selected and placed inside the cuvette, and their P_n values were recorded 2 min after their photosynthesis became stable. After their P_n measurements, the leaf chlorophyll contents (Chl) of the sample leaves were determined with a portable chlorophyll meter (CM-1000, Spectrum, USA).

Data processing

The N_m, N_a, SLA, PNUE, P_n and Chl differences of the different species of the same secondary succession groups and the different secondary succession groups were statistically examined. The N_m, N_a, SLA, PNUE, P_n and Chl of the different species at the same secondary succession groups were compared by using one-way ANOVA, and their multiple comparisons were done by LSD test. The N_m, N_a, SLA, PNUE, P_n and Chl of the different secondary succession groups were statistically examined by following steps. First, the values of these parameters for each secondary succession group were obtained as the means of all the species in the group. Secondly, they were then compared by one-way ANOVA, and their multiple comparisons were done by LSD test. All these statistical analyses were carried out using SPSS software (SPSS Inc., Chicago, USA).

RESULTS

The leaf SLA, N_m, P_n, PNUE significantly differed among the different secondary succession groups (Table1, Figures 1a to c and e), but the leaf N_a and Chl did not differ ($P>0.05$, Figures 1d and f). The leaf SLA, P_n and PNUE were higher in the herb community than in the other three succession groups, but the N_m, N_a and Chl were lower in the herb community than the other three succession groups. The N_m and Chl varied in a double peak curve along the secondary succession with the highest N_m appearing in the shrub community. It was therefore suggested that there were two symbiotic N-fixers (*S. viciifolia* Hance and *H. rhamnoides* (L.)) in the shrub community. The leaf N_m, N_a, SLA, P_n, PNUE and Chl significantly differed among the different species at the same secondary succession groups (Herb community, shrub community and early forest community) (Table1).

The SLA, P_n and PNUE differed in the different succession groups ($P<0.01$, Figure 1), the P_n and PNUE tended to vary similarly with the SLA along the secondary succession sequence. The SLA varied in a high → low → high pattern with the secondary succession, reaching the lowest point in the early forest community, and increasing in the climax forest community (Figure 1). The herb and shrub communities had higher SLA than the early forest community and climax forest community (Table 1), and evergreen woody species (*P. orientalis* (L.) Franco) had lower SLA than the others dominant species.

Of all the species, the PNUE were positively correlated with the SLA, but negatively correlated with the N_a (Figures 2c and d); the PNUE decreased as the N_a increased, but increased with the SLA increased. The SLA of all the species negatively correlated with the N_a, but weakly positively correlated with the N_m, with the N_m increasing and the N_a decreasing as the SLA increased. This was probably because there were two symbiotic N-fixers (*S. viciifolia* Hance and *H.rhamnoides* (L.)) in the shrub community.

DISCUSSION

Plant traits link environmental factors, individuals and ecosystem structures and functions as plants respond and adapt to the environment (Meng et al., 2007). Different plant species are more successful in some landscape parts than others, and this is because they have different quantitative traits such as SLA, leaf nitrogen concentration, rooting depth and leaf size. The SLA presented a high → low → high pattern of variation with the secondary succession, coming to the lowest in the

Table 1. Leaf photosynthetic rates, specific leaf areas, nitrogen contents and nitrogen use efficiencies of the species in the secondary succession groups in the Loess Plateau.

Species	SLA ($cm^2 \cdot g^{-1}$)	N_m ($mg \cdot g^{-1}$)	N_a ($g \cdot m^{-2}$)	Chl	P_n ($\mu mol \cdot m^2 \cdot s^{-1}$)	PNUE ($\mu mol \cdot mol^{-1} \cdot s^{-1}$)
Herb community						
Stipa bungeana Trin	172.6 ± 8.5^c	8.9 ± 0.01^f	0.515 ± 0.025^e	153.5 ± 3.8^c	21.01 ± 1.21^{ab}	573.21 ± 59.29^a
Bothriochloa ischaemum (L.) Keng	234.4 ± 4.5^a	13.4 ± 0.15^c	0.573 ± 0.011^d	174.3 ± 12.7^b	19.56 ± 0.99^b	478.26 ± 33.80^b
Carex lanceolata Boott	209.5 ± 1.7^b	11.8 ± 0.11^e	0.562 ± 0.009^d	215.8 ± 13.4^a	10.87 ± 0.98^c	271.11 ± 28.40^d
Artemisia sacrorum Ledeb	210.8 ± 0.2^b	18.3 ± 0.08^b	0.867 ± 0.004^c	217.0 ± 11.5^a	21.80 ± 1.43^a	352.14 ± 21.64^c
Pulsatilla chinensis (Bunge) Regel	107.7 ± 0.9^e	12.3 ± 0.06^d	1.144 ± 0.004^b	211.1 ± 10.7^a	19.97 ± 0.68^{ab}	244.33 ± 7.75^d
Potentilla chinensis Ser	150.8 ± 4.5^d	18.5 ± 0.08^a	1.230 ± 0.034^b	217.3 ± 12.9^a	19.55 ± 0.78^b	222.50 ± 2.88^d
Average	181.0 ± 46.7	13.9 ± 3.8	0.815 ± 0.315	198.2 ± 27.4	18.79 ± 3.98	356.92 ± 141.16
Significance	$P<0.01$	$P<0.01$	$P<0.01$	$P<0.01$	$P<0.01$	$P<0.01$
Shrub community						
Sophora viciifolia Hance	135.8 ± 1.8^f	30.3 ± 0.32^a	2.232 ± 0.011^a	365.3 ± 19.6^a	22.84 ± 1.50^a	143.25 ± 8.79^f
Hippophae rhamnoides (L.)	142.2 ± 2.0^e	26.9 ± 0.36^b	1.867 ± 0.026^b	303.2 ± 5.7^b	21.89 ± 1.50^a	164.20 ± 13.12^{ef}
Ostryopsis davidiana Decne	153.4 ± 2.5^c	14.4 ± 0.05^e	0.941 ± 0.013^d	266.7 ± 10.6^c	13.41 ± 1.29^c	199.70 ± 21.72^{dc}
Rubus palmatus Thunb	200.3 ± 1.1^a	15.7 ± 0.07^d	0.783 ± 0.001^e	267.1 ± 12.8^c	13.22 ± 0.93^c	236.43 ± 16.72^{ab}
Rosa xanthina Lindl.	149.7 ± 2.3^{dc}	14.1 ± 0.01^f	0.941 ± 0.015^d	237.5 ± 7.0^d	17.37 ± 1.49^b	258.39 ± 21.96^a
Acer ginnala Maxim	153.1 ± 2.3^c	10.0 ± 0.27^h	0.656 ± 0.015^f	169.3 ± 7.7^e	11.62 ± 0.63^c	248.16 ± 13.98^a
Spiraea pubescens Turcz	165.4 ± 4.5^b	13.1 ± 0.10^g	0.795 ± 0.016^e	243.4 ± 13.4^d	12.08 ± 0.25^c	212.86 ± 2.43^{bc}
Ziziphus jujuba var. spinosa	147.1 ± 3.4^d	24.5 ± 0.13^c	1.668 ± 0.029^c	212.8 ± 5.2^f	20.98 ± 2.43^a	175.88 ± 17.53^{de}
Average	155.9 ± 19.9	18.6 ± 7.5	1.235 ± 0.596	258.2 ± 58.8	16.68 ± 4.68	204.86 ± 41.61
Significance	$P<0.01$	$P<0.01$	$P<0.01$	$P<0.01$	$P<0.01$	$P<0.01$
Early forest community						
Populus davidiana Dode	152.5 ± 0.4^b	17.2 ± 0.23^a	1.128 ± 0.013^b	219.2 ± 10.3^b	12.19 ± 1.25^a	151.29 ± 16.02^b
Betula platyphylla Suk	176.1 ± 1.2^a	17.4 ± 0.12^a	0.985 ± 0.013^c	267.2 ± 11.9^a	13.40 ± 0.56^a	190.35 ± 5.68^a
Platycladus orientalis (L.) Franco	46.4 ± 0.3^c	7.5 ± 0.21^b	1.615 ± 0.041^a	178.7 ± 3.6^c	8.04 ± 0.32^b	69.71 ± 4.06^c
Average	125.0 ± 69.1	14.0 ± 5.7	1.243 ± 0.330	221.7 ± 44.3	11.21 ± 2.81	137.12 ± 61.56
Significance	$P<0.01$	$P<0.01$	$P<0.01$	$P<0.01$	$P<0.01$	$P<0.01$
Climax forest community						
Quercus liaotungensis Koidz	145.9 ± 0.6	16.9 ± 0.09	1.157 ± 0.007	272.7 ± 6.2	12.43 ± 0.67	150.48 ± 8.66
Significance (18 species)	$P<0.05$	$P<0.05$	NS	NS	$P<0.05$	$P<0.01$

The data are in the form of mean ± SD. SLA , specific leaf area; PNUE, photosynthetic nitrogen use efficiency, P_n, photosynthetic rate; Chl, leaf chlorophyll content; N_m, leaf nitrogen content per unit dry mass; N_a, leaf nitrogen content per unit area.
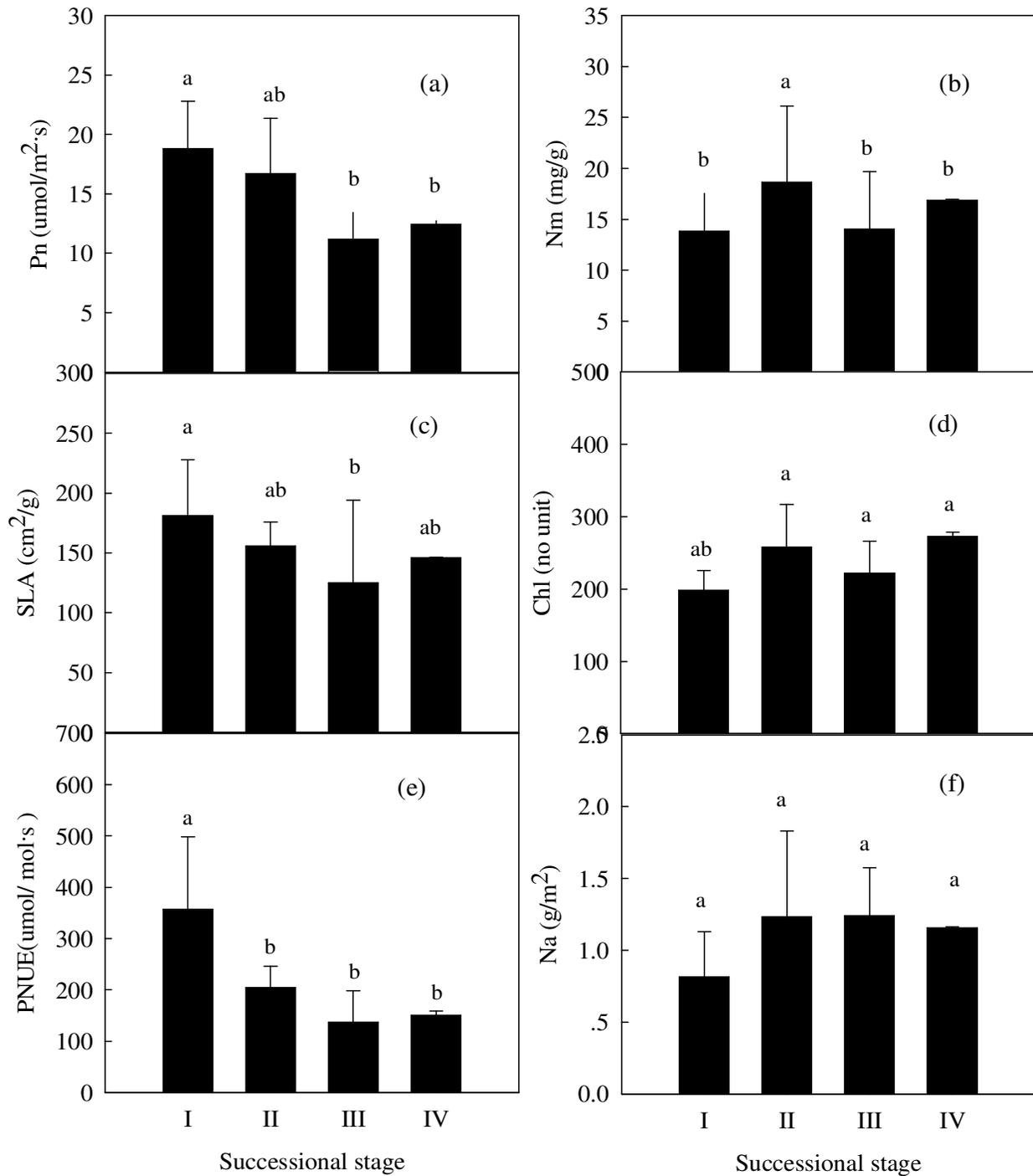
Figure 1. Leaf photosynthetic traits, nitrogen contents and specific leaf areas in the different secondary succession groups in the Loess Plateau. The data are in the form of mean ± SD. Bars with the different letters above them mean significant differences at $P<0.05$. In the horizontal axis; I, herb community (n = 6 species); II, shrub community (n = 8 species); III, early forest community (n = 3 species); IV, climax forest community (n = 1 species).

early forest community. This was probably because there were evergreen species (*P. orientalis* (L.) Franco) in the early forest community. The climax forest community has a higher SLA than the early forest community, and this is in accordance with the fact that the slow-growing species

have lower SLA than fast-growing species (Warren and Adams, 2004; Takashima et al., 2004). Herbs, grasses and deciduous trees tend to have higher SLA, and evergreen shrubs and trees tend to have lower SLA, but there is wide overlap between growth forms (Wright et al.,
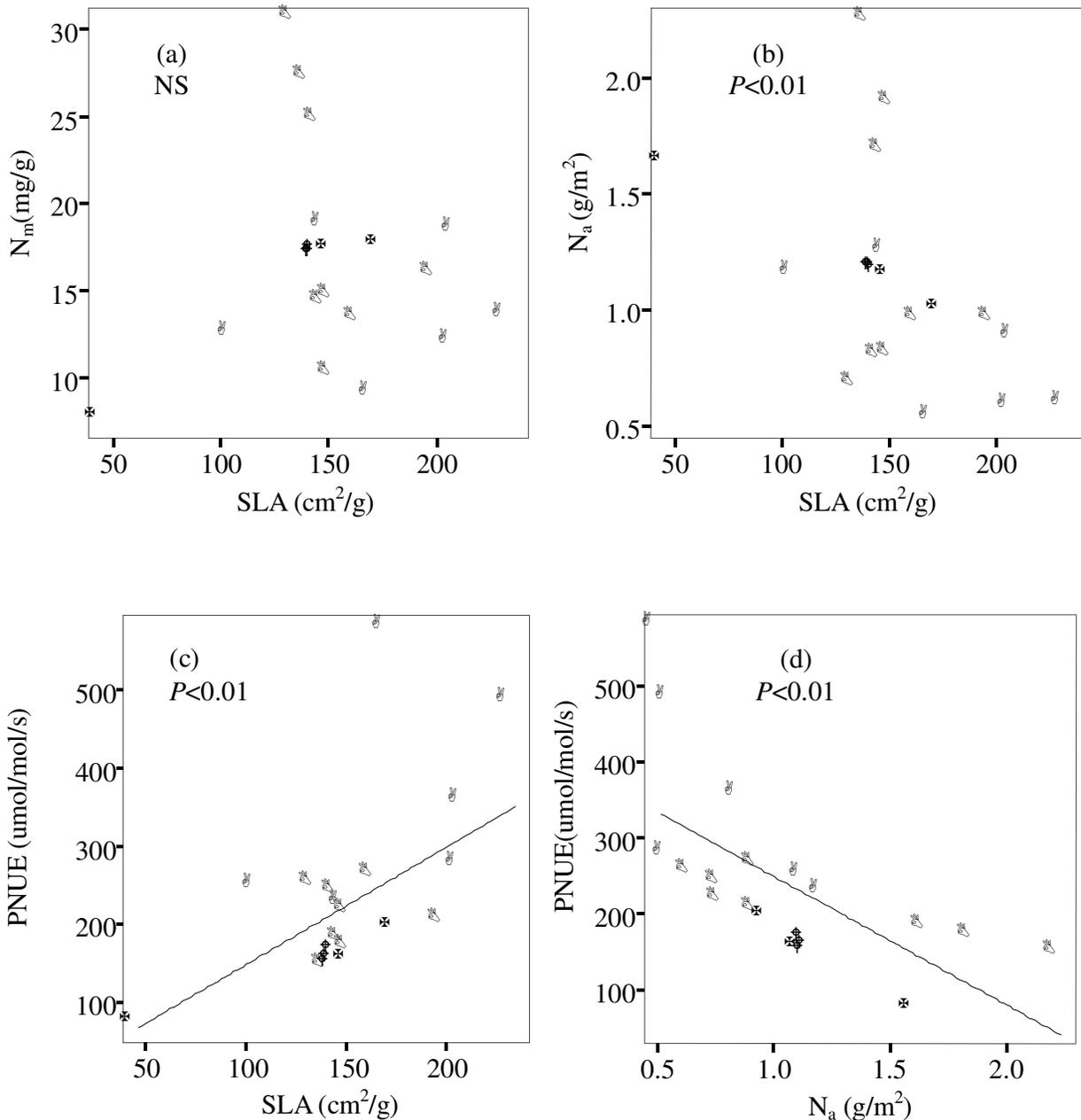
Figure 2. Relationships among the specific leaf areas, nitrogen contents (N_m and N_a) and photosynthetic nitrogen use efficiency of the dominant species. The different markers stand for different species. The open circle stands for the herb community, the open triangle stands for the shrub community, the solid triangle stands for the early forest community and the solid circle stands for the climax forest community.

2004; Wright et al., 2005a; Westoby and Wright, 2006).

The secondary succession plays a critical role in shaping the structures of natural communities (Crain et al., 2008). Light is agreed as a major factor in species replacement and particularly in forest succession (Bazzaz, 1979). Plants can acclimate to different light environments by several ways such as regulating leaf morphology and photosynthetic capacity (Warren and Adams, 2001; Walcroft et al., 2002). The leaf photosynthetic traits (P_n and PNUE) and N_m were found to differ greatly among the different secondary succession groups. The leaf photosynthetic capacities significantly varied and the P_n and PNUE presented a wide range of variation. Except for the P_n and PNUE of the species in the early forest community, the P_n and PNUE of the dominant species declined along the secondary succession, and the lowest P_n and PNUE occurred in the early forest community, which was probably attributed to the presence of evergreen

woody species (*P. orientalis* (L.)). The leaves of evergreen plants had thicker cell walls, weaker mesophyll conductance, and stronger resistance to CO_2 diffusion than those of herbaceous and deciduous plants (Hanba et al., 1999), so that herbaceous and deciduous species presented higher P_n and PNUE.

In addition, this study shows that the deciduous species generally had higher N_m and P_n than the evergreen species, which was consistent with previous study (Eamus and Cole, 1997; Reich et al., 1997). Deciduous species invested less in the production of non-photosynthetic leaf tissues and formed the leaves with higher SLA, compared with evergreen species (Franco et al., 2005). Species with higher nitrogen concentrations and faster gas exchange rates are associated with the higher SLA end of the leaf economic spectrum (Westoby and Wright, 2006). The N_m in shrub community significantly differed from those in the others succession groups (herb community, early forest community and climax forest community). Higher N_m in the shrub community than those in the other three succession groups were probably attributed to the presence of legumes (e.g. *H. rhamnoides* (L.) and *S. viciifolia* Hance). Due to the fact that legumes are associated with N-fixing bacteria such as *Rhizobium* sp. capable of utilizing atmospheric N_2, legumes have higher nitrogen contents than other plant groups.

PNUE is an important leaf trait that is correlated with other leaf traits, such as SLA and leaf life span, regardless of life-forms, phylogeny and biome. This study found that of all the species, the PNUE were positively correlated with the SLA, which was consistent with the report of Poorter and Evans (1998). The positive correlation between the PNUE and SLA may be due to the influence of the SLA on nitrogen allocation to photosynthesis (Feng et al., 2008). Nitrogen allocation and mesophyll conductance for CO_2 diffusion are important factors related to inter-specific difference in PNUE. In order to form tough leaves, plants need to allocate more biomass and nitrogen to form thick cell wall, thus resulting in reductions in mesophyll conductance and nitrogen allocation to photosynthetic apparatus. Some studies showed that low-PNUE species allocate lower proportions of nitrogen to their photosynthetic apparatus (Warren and Adams, 2000; Ripullone et al., 2003; Takashima et al., 2004). It therefore follows that nitrogen allocation to photosynthetic apparatus is a major factor for inter-specific PNUE differences.

Conclusion

This study demonstrated that PNUE was correlated with other leaf traits, such as SLA and leaf nitrogen content. The relation between PNUE and SLA was probably attributed to the influence of SLA on nitrogen allocation to photosynthetic apparatus. Ecologically important plant traits that may clarify the mechanism of different plant species are more successful at the different secondary succession stages in the Loess Plateau.

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