Bot. Bull. Acad. Sin. (2005) **46:** 127-134

Specific leaf area and leaf dry matter content of plants growing in sand dunes

Yulin LI[1,*], Douglas A. JOHNSON[2], Yongzhong SU[1], Jianyuan CUI[1], and Tonghui ZHANG[1]

[1]*Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, 260 Donggang West Road, Lanzhou, 730000, P.R. China*

[2]*USDA-ARS Forage and Range Research Laboratory, Utah State University, Logan, Utah 84322-6300, USA*

(Received June 29, 2004; Accepted December 16, 2004)

Abstract. We investigated the variations in specific leaf area (SLA) and leaf dry matter content (LDMC) of 20 species (10 annuals and 10 perennials) that have different distributional patterns in the Kerqin Sandy Land in northern China. The main purpose of our study was to determine if SLA and/or LDMC could be used as indicators of plant resource-use strategy in sand dune environments. The selected species were mainly distributed in three types of sand dunes: mobile sand dune, semi-fixed sand dune, and fixed sand dune. The three differed in their soil nutrient content and vegetation productivity. Both SLA and LDMC varied substantially among species in the different dunes. Maximum SLA (28.2 m^2 kg^{-1}) was observed in the annual grass *Setaria viridis* in a fixed sand dune, and the lowest SLA (8.6 m^2 kg^{-1}) was found in the perennial grass *Pennisetum centrasiatum* in a semi-fixed sand dune. LDMC varied from 0.10 g g^{-1} for the annual forb *Chenopodium glaucum* in a fixed sand dune to 0.41 g g^{-1} for the perennial grass *Phragmitis australis* in a fixed sand dune. For species common to two or three sites, their SLA and LDMC were significantly different between sites ($P<0.05$), except for two species for SLA and six species for LDMC. SLA and LDMC were negatively correlated both in the three types of sand dunes and for each functional type (annual versus perennial species). However, SLA and LDMC were significantly correlated only for the species in fixed sand dune, perennial species as well as all species. The results of our study showed that the SLA of annual plant species was generally higher than that of perennial species and that LDMC was significantly different between annual compared to perennial plants ($P<0.05$).

Key words: Annuals; Leaf dry matter content; Perennials; Sand dune; Specific leaf area.

Introduction

Specific leaf area (SLA, leaf area per unit dry mass) and leaf dry matter content (LDMC, the ratio of leaf dry mass to fresh mass) are important traits in plant ecology because they are associated with many critical aspects of plant growth and survival (Garnier et al., 2001b; Shipley and Vu, 2002). Recent studies in controlled environments have demonstrated the important roles that these two traits play in explaining variation in potential relative growth rate (Poorter and Van der Werf, 1998) and ecological behavior in plants (Garnier et al., 2001a). According to a recent review (Poorter and de Jong, 1999), both SLA and LDMC are involved in the trade-off between rapid biomass production (high SLA, low LDMC species) and efficient conservation of nutrients (low SLA, high LDMC species). Because SLA and LDMC are indicator traits of resource-use strategies, it is important to evaluate these traits for different plant species in various environments (Westoby, 1998; Weiher et al., 1999).

Many studies have evaluated SLA and LDMC under both controlled and natural conditions involving various nutrient and water gradients (Cunningham et al., 1999; Garnier et al., 2001a), vegetation types (Poorter and de Jong, 1999), plant functional types (Garnier et al., 1997), and leaf types (Vendramini et al., 2002). However, to our knowledge, few studies concerning these traits have been conducted on plants growing in sand dunes. Plants growing in sand dunes exhibit various morphological and ecophysiological characteristics (Liu et al., 1996). In the Kerqin Sandy Land of northern China, sand dunes can be classified into mobile sand dune, semi-fixed sand dune, and fixed sand dune according to the criteria proposed by Zhu et al. (1989). These sand dunes are widely distributed and alternate with gently undulating interdune lowlands to produce distinct differences in spatial heterogeneity of soil resources, which in turn leads to differences in species distribution, plant growth, and biomass production (Su and Zhao, 2003). These processes further amplify the differences among different types of sand dunes.

The main objective of the present study was to determine if SLA and LDMC differ in three types of sand dunes that occur in Kerqin Sandy Land of northern China, and evaluate whether SLA and/or LDMC could be used as indicators of plant resource-use strategy in these environments. In addition, we hoped to determine if annual and perennial plants differed in SLA and LDMC in the three types of sand dunes.

*Corresponding author. E-mail: liyleml@263.net

Materials and Methods

Study Area

The study was conducted at the Naiman Desertification Research Station (N 42°58' and E 120°43', 345 m above mean sea level) of the Chinese Ecosystem Research Network (CERN) in eastern Inner Mongolia, China, which is located in the southwest portion of the Kerqin Sandy Land. This region has a continental, semi-arid monsoon climate. The landscape in this area is characterized by sand dunes that alternate with gently undulating interdunal lowlands that form farming lands and grasslands. Dunes in this region can be classified into mobile sand dunes, semi-fixed sand dunes and fixed sand dunes, according to the criteria of Zhu et al. (1989). Plant species common to mobile sand dunes include: *Agriophyllum squarrosum*, *Artemisia halodendron*, *Setaria viridis*, *Cynanchum thesioides* and *Salix gordejevii*, among which *A. squarrosum* is the dominant species. Species richness increases in semi-fixed sand dunes and fixed sand dunes, and species include: *Caragana microphylla*, *Salsola collona*, *Eragrostis pilosa* and *Artemisia scoparia* with *A. halodendron* a dominant species in both semi-fixed and fixed sand dunes.

The meteorological characteristics of the study area were summarized by Liu et al. (1996). Mean annual air temperature is 6.4°C, and the coldest and warmest monthly mean temperatures are 13.1°C recorded in January and 23.7 °C in July, respectively. Mean annual accumulated air temperature above 10°C ranges from 3000 to 3400°C, and the frost-free period is 137 to 150 days per year. Mean annual precipitation is 362 mm, nearly 70% of which falls from June through August. Mean annual pan evaporation is 2,000 mm. Prevailing wind directions are northwest in winter and spring, and southwest to south in summer and autumn with mean annual wind speed ranging from 3.4 to 4.1 m s^{-1}.

Sample Plots and Species Selection

Three sites were selected for our study including mobile sand dunes, semi-fixed sand dunes, and fixed sand dunes. At each site, three plots were established at three different locations with each plot covering an area of 1500-2500 m^2. Prior to plant sampling, a vegetation survey and soil analyses were performed in each plot. Five randomly selected soil samples were collected to a 15-cm depth from each plot using a soil auger and pooled to obtain a composite soil sample. These composite samples were air-dried and passed through a 2-mm sieve. Soil pH and electrical conductivity (EC) were measured in a soil-water suspension (1:1 and 1:5 soil to water ratio, respectively) (Multiline F/SET-3, Germany). Part of the air-dried and sieved samples was ground and passed through a 0.25-mm sieve for C and N analysis. Organic C was determined by the dichromate oxidation procedure of Walkley-Black (Nelson and Sommers, 1982), and total N was measured by the Kjeldahl procedure (UDK140 Automatic Steam Distilling Unit, Automatic Titroline 96, Italy). Five randomly sampled locations in each of the three plots were selected to measure aboveground vegetation biomass and cover using a 1-m^2 quadrat in each plot, giving a total of 15 sampling points for each site.

A total of 20 plant species (10 perennials and 10 annuals) were selected to study their SLA and LDMC. Five of the studied species were common to all three types of dunes, seven species were common to both semi-fixed sand dunes and fixed sand dunes, and eight species were found in only one of the three dune types. For selected species in each type of dune, a total of 15 individuals were selected, which included five individuals in each of three different plots.

SLA and LDMC Measurements

In August 2002, three fully expanded leaves with attached stems were collected from robust, well-established plants in unshaded habitats. Senescent or damaged leaves were avoided. Collected leaf-stem segments were immediately placed between wet papers, sealed in a plastic bag, and placed in a dark container with ice. After being transported to the lab (usually within 1 h after collection), leaf samples were placed in water in the dark at 5°C for 12 h after the stem or petiole was removed under water (Garnier et al., 2001b). This procedure ensured full leaf rehydration. Leaves were then dried with tissue paper to remove surface water and immediately weighed to determine their saturated fresh weight. Leaf area was then measured with an area meter (CI-400 Image Analysis Systems, USA). For species with very narrow or cylindrical leaves (e.g., *A. halodendron*), leaf length and leaf width were determined in the middle of the leaf with a digital vernier caliper. Leaf blade area was then calculated as half the total intercepted area, following the procedure of Chen and Black (1992). Samples were then oven-dried at 60°C for at least two days, and their dry weights were determined. Values of LDMC were calculated as the ratio between leaf dry mass and saturated fresh mass (g g^{-1}), and SLA was expressed as the ratio of leaf area to leaf dry mass (cm^2 g^{-1}).

Data Analysis

Differences in soil characteristics and vegetation productivities among the three types of sand dunes were tested with one-way ANOVA and LSD. To meet ANOVA assumptions, SLA and LDMC were transformed to their natural logarithms before analysis. Analyses were performed to test differences among sites, among species, and between annual and perennial species. Pearson's correlation analysis was used to test the relationship between SLA and LDMC in annual, perennial, all species, and different sand dune types. Hierarchical ANOVAs were performed with Minitab 13 for Windows, and other statistical analyses were conducted with SPSS 11.0 for Windows.

Results

Site Characteristics

Soil chemical properties and vegetation productivity were used to characterize differences among the three types of sand dunes. Results from ANOVA showed that mean organic C, total N, EC, and C: N increased significantly

Table 1. Soil characteristics (0-15 cm depth) and vegetation productivity in three types of sand dunes (means ± SD)*.

Factor	Type of sand dune			F	P
	Mobile sand dune	Semi-fixed sand dune	Fixed sand dune		
Soil characteristics (n=3)					
Organic C (g kg^{-1})	0.32±0.05a	0.92±0.09b	2.80±0.06c	57.26	<0.001
Total N (g kg^{-1})	0.046±0.005a	0.106±0.01b	0.281±0.008c	55.94	<0.001
C/N ratio	7.03±0.39a	8.68±0.23b	9.96±0.47c	56.98	<0.001
pH (H_2O)	7.70±0.06	7.55±0.13	7.58±0.12	0.57	n.s
EC (μ s cm^{-1})	17±1.53a	34±2.16b	50±2.08c	58.06	<0.001
Vegetation productivity (n=15)					
Biomass (kg m^{-2})	0.11±0.08a	0.22±0.06b	0.37±0.09c	21.91	<0.001
Cover (%)	10±2.04a	52±4.28b	72±5.26c	26.63	<0.001

*Values in rows followed by a different letter indicate significant differences at P<0.05.

(P<0.001) from mobile sand dune to semi-fixed sand dune to fixed sand dune (Table 1). This same pattern was observed for above-ground biomass and vegetational cover. Soil pH did not vary among sand dune types.

Overview of SLA and LDMC for Plant Species in Dunes

Results of hierarchical ANOVA for SLA and LDMC are shown in Table 2. Mean SLA and LDMC differed substantially among species in different types of sand dunes (Tables 3 and 4). Maximum SLA was observed in the annual grass *S. viridis* (28.2 m^2 kg^{-1}) in a fixed sand dune, and the lowest SLA was exhibited in the perennial grass *P. centrasiatum* (8.6 m^2 kg^{-1}) in a semi-fixed sand dune. LDMC varied from 0.10 g g^{-1} for the annual forb *C. glaucum* in fixed sand dune to 0.41 g g^{-1} for the perennial grass *P. australis* on a fixed sand dune. The largest amount of variance for both SLA and LDMC was explained by the species factor, which explained more than 60% of the variance (Table 2). Functional type (annual versus perennial) explained more than 22% of the variance in SLA and LDMC with annual species having higher SLA (17.4 ± 5.2 m^2 kg^{-1}) and lower LDMC (0.21 ± 0.07 g g^{-1}) than perennial species (12.7 ± 4.1 m^2 kg^{-1} and 0.29 ± 0.08 g g^{-1}, respectively). Sites accounted for less of the variance than species and functional type, and their contributions were slightly higher for SLA than LDMC. Between-replicate variance was similar for both SLA and LDMC.

Variations of SLA and LDMC for Species Common to Three Sites

For species common to two or three sites, SLA and LDMC were compared to evaluate differences among types of sand dunes. SLA of most species common to two or three sites was significantly different among sites, except for *S. collona* and *S. gordejevii* (Table 3). In contrast, only six species common to more than two sites (*C. elongatum*, *C. thesioides*, *E. esula*, *I. chinensis*, *A. halodendron* and *P. centrasiatum*) showed significant differences in LDMC among sites (Table 4).

Table 2. Results of hierarchical ANOVAs for specific leaf area (SLA) and leaf dry matter content (LDMC). Results are the percentage of the total variance accounted for at each level.

Trait	Species	Site	Functional type*****	Replications
SLA	65	10	22	3
LDMC	60	6	30	4

*Functional type refers to annual versus perennial species.

Among five species common to three sites (*A. halodendron, C. thesioides*, *I. chinensis*, *S. viridis* and *S. gordjevii*), SLA was highest in fixed sand dunes (17.2 ± 7.4 m^2 kg^{-1}) and lowest in mobile sand dunes (14.7 ± 5.8 m^2 kg^{-1}) with an intermediate value (15.4 ± 6.2 m^2 kg^{-1}) in semi-fixed sand dunes. The mean LDMC of these five species showed a slight decrease from mobile sand dunes (0.27 ± 0.05 g g^{-1}) to semi-fixed sand dunes (0.26 ± 0.06 g g^{-1}) to fixed sand dunes (0.25 ± 0.08 g g^{-1}). For species that occur on two sites, a higher SLA was observed in fixed sand dunes (16.4 ± 4.4 m^2 kg^{-1}) than semi-fixed sand dunes (14.7 ± 4.1 m^2 kg^{-1}), but LDMC varied little between the two sites with 0.20 ± 0.08 g g^{-1} for semi-fixed sand dunes and 0.20 ± 0.07 g g^{-1} for fixed sand dunes.

Comparisons of SLA and LDMC between Annuals and Perennials

Because SLA and LDMC are sensitive to environmental change (Wilson et al., 1999), SLA and LDMC of all species (nine annual species and ten perennial species) were compared in fixed sand dunes using a General linear model for unbalanced data with Minitab 13 for Windows. Results showed significant differences between perennial and annual plants for both SLA (F=5.896, P=0.027) and LDMC (F=9.182, P=0.008). Mean SLA for perennial plants was 13.3 ± 3.9 m^2 kg^{-1}, significantly lower than for annual plants (17.9 ± 4.0 m^2 kg^{-1}). Values of LDMC for perennial and annual plants were 0.31 ± 0.08 g g^{-1} and 0.20 ± 0.06 g g^{-1}, respectively.

Table 3. Specific leaf area (m^2 kg^{-1}) of species in three types of sand dunes (means ± SD)*.

Species	Family	Type of sand dune**			F	*P*
		MSD	SSD	FSD		
Annuals						
Agriophyllum squarrosum	Chenopodiaceae	17.8±1.0	–	–	–	–
Chenopodium acuminatum	Chenopodiaceae	–	17.2±1.0a	18.4±1.0b	10.9	0.003
Corisperum macrocarpum	Chenopodiaceae	–	13.6±0.8a	15.4±1.0b	25.5	<0.001
Cynanchum thesioides	Asclepiadaceae	17.9±0.8a	18.1±1.1a	21.0±1.1b	38.5	<0.001
Euphorbia esula	Euphorbiaceae	–	13.7±0.9a	15.5±0.7b	28.7	<0.001
Euphorbia humifusa	Euphorbiaceae	–	18.5±0.9	21.6±0.9	24.1	<0.001
Ixeris chinensis	Compositae	10.0±1.0a	12.2±0.8b	13.2±0.8c	43.3	<0.001
Salsola collona	Chenopodiaceae	–	10.6±0.9	10.4±1.1	0.32	0.579
Setaria viridis	Gramineae	24.4±1.3a	25.9±1.3b	28.2±1.2c	25.42	<0.001
Tribulus terrestris	Zygopgyllaceae	–	–	20.5±1.2	–	–
Means±SD		17.5±5.9	16.2±4.8	18.2±5.3		
Perennials						
Aneurolepidium dasystach	Gramineae	–	–	11.5±0.8	–	–
Astragalus adsurgens	Leguminosae	–	20.6±1.3a	22.3±1.1b	16.3	<0.001
Artemisia halodendron	Compositae	9.7±0.9a	9.9±0.7a	11.6±1.2b	30.7	<0.001
Lespedeza davurica	Leguminosae	–	–	12.0±1.1	–	–
Melissetus ruthencus	Leguminosae	–	–	13.1±0.6	–	–
Messerschmidia rosmarinifolia	Boraginaceae	–	–	19.3±1.2	–	–
Pennisetum centrasiatum	Gramineae	–	8.6±0.9a	10.6±0.8b	25.16	<0.001
Phragmitis australis	Gramineae	–	–	10.4 ±0.9	–	–
Potentilla chinensis	Rosaceae	–	–	10.4±1.0	–	–
Salix gordejevii	Salicaceae	11.1±0.8	10.5±1.0	10.9±1.1	2.06	0.14
Means±SD		10.4±1.0	12.4±5.5	13.2±4.1		

*Values in rows followed by a different letter indicate significant differences at P<0.05.

**MSD, SSD and FSD refer to mobile sand dune, semi-fixed sand dune and fixed sand dune, respectively.

Table 4. Leaf dry matter content (g g^{-1}) of species in three types of sand dunes (means ± SD)*.

Species	Family	Type of sand dune**			F	*P*
		MSD	SSD	FSD		
Annuals						
Agriophyllum squarrosum	Chenopodiaceae	0.19±0.02	–	–	–	–
Chenopodium acuminatum	Chenopodiaceae		0.11±0.005	0.10±0.001	0.15	0.697
Corisperum elongatum	Chenopodiaceae		0.14±0.001a	0.11±0.0007b	29.1	<0.001
Cynanchum thesioides	Asclepiadaceae	0.27±0.018a	0.24±0.015b	0.22±0.013c	35.5	<0.001
Euphorbia esula	Euphorbiaceae		0.35±0.017a	0.32±0.016b	15.6	<0.001
Euphorbia humifusa	Euphorbiaceae		0.22±0.018	0.25±0.018	0.116	0.735
Ixeris chinensis	Compositae	0.27±0.019a	0.25±0.015b	0.22±0.01c	31.1	<0.001
Salsola collona	Chenopodiaceae		0.15±0.011a	0.16±0.021b	0.027	0.871
Setaria viridis	Gramineae	0.23±0.013	0.25±0.016	0.23±0.016	0.15	0.862
Tribulus terrestris	Zygopgyllaceae	–	–	0.19±0.012	–	–
Means±SD		0.24±0.038	0.21±0.077	0.20±0.069		
Perennials						
Aneurolepidium dasystach	Gramineae	–	–	0.34±0.021	–	–
Astragalus adsurgens	Leguminosae	–	0.24±0.006	0.24±0.01	0.47	0.499
Artemisia halodendron	Compositae	0.23±0.011a	0.21±0.009b	0.19±0.013c	17.8	<0.001
Lespedeza davurica	Leguminosae	–	–	0.38±0.015	–	–
Melissetus ruthencus	Leguminosae	–	–	0.34±0.011	–	–
Messerschmidia rosmarinifolia	Boraginaceae	–	–	0.21±0.014	–	–
Pennisetum centrasiatum	Gramineae	–	0.22±0.019a	0.20±0.017b	6.97	0.013
Phragmitis australis	Gramineae	–	–	0.41±0.009	–	–
Potentilla chinensis	Rosaceae	–	–	0.36±0.017	–	–
Salix gordejevii	Salicaceae	0.37±0.012	0.38±0.018	0.38±0.014	0.61	0.548
Means±SD		0.30±0.099	0.26±0.079	0.31±0.085		

*Values followed by a different letter in rows are significantly different at 0.05 levels.

**MSD, SSD and FSD refer to mobile sand dune, semi-fixed sand dune and fixed sand dune, respectively.

Relationship between SLA and LDMC

Relationships between SLA and LDMC were plotted separately for species found at each site (mobile sand dunes, semi-fixed sand dunes, and fixed sand dunes) and functional types (annuals, perennials, and all species) (Figure 1). Increased SLA was associated with decreased LDMC. Table 5 shows Pearson's correlation coefficients for SLA and LDMC for the three types of sand dunes and functional types. When the three sites were analyzed separately, significant negative associations were found between SLA and LDMC only in the fixed sand dunes (Table 5). When different functional types were considered separately, significant negative associations were found only for perennial species and all species combined. Although SLA and LDMC were negatively correlated for species in mobile sand dunes and semi-fixed sand dunes as well as annual species, these correlations were not statistically significant ($P>0.05$).

Discussion

Values of SLA in this study were in the low to middle range compared to those found in plants growing in other field and laboratory conditions (Garnier et al., 1997; Poorter and de Jong, 1999; Meziane and Shipley, 1999; Shipley and Vu, 2002; Ackerly et al., 2002; Shipley, 2002). It has been shown that SLA reflects previously captured resources and indicates that species with high SLA exhibit high productivity (Poorter and Van der Werf, 1998; Van der Werf et al., 1998; Wilson et al., 1999). Therefore, species with high SLA do better in resource-rich environments while species with low SLA do better in resource-poor environments

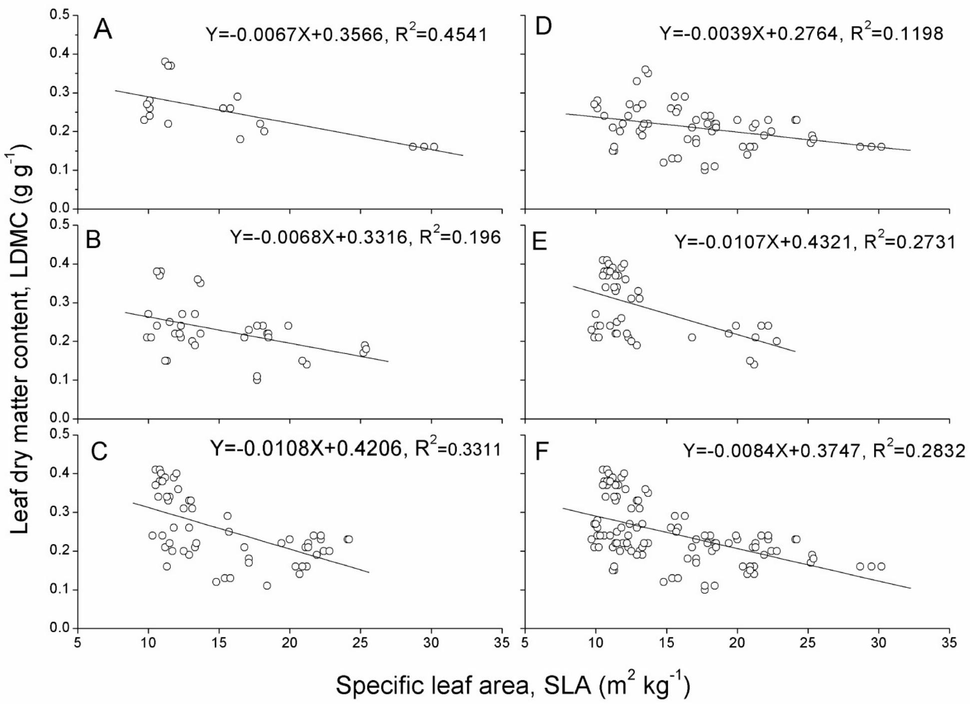

Figure 1. Relationship between specific leaf area (SLA) and leaf dry matter content (LDMC) for three types of sand dunes and functional types (A, Mobile sand dune; B, Semi-fixed sand dune; C, Fixed sand dune; D, Annual species; E, Perennial species; F, All species).

Table 5. Correlations between specific leaf area (SLA) and leaf dry matter content (LDMC) within different types of sand dunes and functional types.

	Sample number	Pearson's coefficients	Significance level (P)
Type of sand dune			
Mobile sand dune	18	-0.076	0.660
Semi-fixed sand dune	36	-0.360	0.142
Fixed sand dune	57	-0.436	0.001
Functional type			
Annual species	63	-0.085	0.357
Perennial species	48	-0.451	0.040
All species	37	-0.286	0.002

where retention of captured resources is a higher priority. As a result, most sand dune plants appear to exhibit low or middle SLA due to their adaptation to resource-poor environments. Negative correlations were observed between LDMC and SLA in our study (Figure 1).

Species that have a wide distribution typically exhibit broad adaptation to various environments (Migahid and Elhaak, 2001). In particular, leaf traits of plant species in nutrient-poor habitats differ significantly from those in nutrient-rich habitats. In the present study, SLA of all species common to more than two sites (species distributed in two or three sites) was significantly different between sites (Table 3 and 4). For species common to more than two sites, SLA from plants in fixed dunes (which have a relatively higher nutrient content than plants found in other dune types) were significantly higher than those in semi-fixed sand dunes or mobile sand dunes. The mean LDMC of all species common to more than two sites, however, did not differ among sites (Table 4). Differences in SLA suggested that soil fertility was highest in fixed sand dunes, intermediate in semi-fixed sand dunes, and lowest in mobile sand dunes, agreeing with data in Table 1. This trend was also supported by the results of the analysis of SLA between sites for a given species. The SLA of most species common to two or three sites was relatively higher than that from semi-fixed sand dunes or mobile sand dunes, except for *S. collona* and *S. gordejevii*. For LDMC, only six species (*C. elongatum, C. thesioides, E. esula, I. chinensis, A. halodendron* and *P. centrasiatum*) common to two or three sites showed significant differences among sites. SLA is usually higher (Cunningham et al., 1999; Poorter and de Jong, 1999) and LDMC lower (Cunningham et al., 1999) in fertile than infertile sites. Our results suggested that SLA is more sensitive than LDMC to variations in soil resources. A similar conclusion was reached by Ryser (1996), who found that interspecific ranking of LDMC was apparently unaffected by nutrient supply or competition. However, Wilson et al. (1999) compared SLA and LDMC in 769 species from central England and concluded that LDMC was a more preferred descriptor of plant resource use than SLA.

Plants may exhibit different phenotypes under different environments due to genotypic variation and/or phenotypic plasticity of genotypes. However, separating phenotypic from genotypic differences can be difficult. In the present study, the selected species were mainly distributed on several adjacent sand dunes. Furthermore, Zhao and Bai (2000) pointed out that species sources in different types of sand dunes in the study area were from interdune lowlands between sand dunes. As a result, plants sampled in the relatively small area used in our study are probably from the same population source. Therefore, most variation in SLA and LDMC is probably attributable to phenotypic plasticity.

In our study, the SLA of selected annual plant species was significantly higher than that of selected perennial species. This finding is consistent with results from laboratory experiments (Muller and Garnier, 1990; Garnier, 1992; Roumet et al., 1996) and a field study (Garnier et al., 1997). LDMC also differed significantly between annual and perennial plants in our study. What is behind this difference in SLA and LDMC between annual and perennial species? Several studies suggested that SLA may depend on leaf thickness and/or leaf tissue density (Witkowski and Lamont, 1991; Westoby, 1998; Wilson et al., 1999). Garnier and Laurent (1994) reported that differences in SLA between life-forms were related to differences in leaf density, but not leaf thickness under laboratory conditions. They also suggested that differences in anatomical features may contribute to differences in leaf density between annual and perennial species. Their main conclusions were that the higher leaf density in perennial species was related to a higher proportion of sclerenchyma and vascular tissues in the leaf. Differences in SLA and LDMC between annual and perennial species may also be related to other leaf traits such as leaf size (Shipley, 1995). Additional experiments are required to determine which factor plays the most important role in causing differences in SLA and LDMC between annual and perennial species.

A number of studies have been conducted to determine the relationship between SLA and LDMC (Wilson et al., 1999; Garnier et al., 2001b; Shipley and Vu, 2002). In general, increased SLA is associated with decreased LDMC. In a field study reported by Garnier et al. (2001b), the correlation between SLA and LDMC was -0.96. Our results were in general agreement with theirs although the correlation between SLA and LDMC was not significant for the mobile sand dunes, semi-fixed sand dunes, or annual species (Table 5). The relationship between SLA and LDMC in our study was inconsistent among sites where soil nutrient stress was a major limiting factor. This inconsistency may be due to plant plasticity in response to soil nutrients. However, when all species from the three types of sand dune sites were considered together, SLA and LDMC were significantly correlated. Garnier et al. (2001b) suggested that low SLA values are relatively independent of changes in LDMC, except when SLA values were higher than 10-15 m^2 kg^{-1}. In contrast, we found that SLA and LDMC of perennial species were significantly correlated when SLA values were significantly lower than that of annual species (Table 5).

In summary, variation in SLA and LDMC of plants among our three study sites suggested that LDMC is less sensitive to variations of soil resources in the three types of sand dunes. As a result, SLA appears to be a better indicator of plant resource-use strategy in sand dune environments. Nevertheless LDMC is still important in evaluating plant resource-use strategy in dune environments because it is easier to measure than SLA, especially for dune plants that have small, narrow leaves. Responses of SLA to variations in dune environments imply that environmental constraints have a direct effect on plant growth.

Acknowledgements. This research was supported by the national 973 Project "The Desertification Process and Its Prevention in North China" (G2000048704). Authors appreciated the constuctive suggestions of two anonymous referees .

Literature Cited

Ackerly, D., C. Knight, S. Weiss, K. Barton, and K. Starmer. 2002. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. Oecologia **130:** 449-457.

Chen, J.M. and T.A. Black. 1992. Defining leaf area index for non-flat leaves. Plant Cell Environ. **15:** 421-429.

Cunningham, S.A., B. Summerhayes, and M. Westoby. 1999. Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. Ecol. Monogr. **69:** 569-588.

Garnier, E. 1992. Growth analysis of congeneric annual and perennial grass species. J. Ecol. **80:** 665-675.

Garnier, E., P. Cordonnier, J.L. Guillerm, and L. Sonie. 1997. Specific leaf area and leaf nitrogen concentration in annual and perennial grass species growing in Mediterranean old-fields. Oecologia **111:** 490-498.

Garnier, E., A. Laurent, A. Bellmann, S. Debain, P. Berthelier, C. Ducout, and M.L. Navas. 2001a. Consistency of species ranking based on functional leaf traits. New Phytol. **152:** 69-83.

Garnier, E., B. Shipley, C. Roumet, and G. Laurent. 2001b. A standardized protocol for the determination of specific leaf area and leaf dry matter content. Funct. Ecol. **15:** 688-695.

Liu, X.M., H.L. Zhao, and A.F. Zhao. (eds.). 1996. Wind-Sandy Environment and Vegetation in the Korqin Sandy Land, China. Science Press, Beijing, China, 1-8 pp.

Meziane, D. and B. Shipley. 1999. Interacting determinants of specific leaf area in 22 herbaceous species: effects of irradiance and nutrient availability. Plant Cell Environ. **22:** 447-459.

Migahid, A. and A. Elhaak. 2001. Ecophysiological studies on some desert plant species native to the Mediterranean area in Egypt. J. Arid Environ. **48:** 191-203.

Muller, B. and E. Garnier. 1990. Components of relative growth rate and sensitivity to nitrogen availability in annual and perennial species of Bromus. Oecologia **8:** 513-518.

Nelson, D.W. and L.E. Sommers. 1982. Total carbon, organic carbon and organic matter. *In* A.L. Page, R.H. Miller, and D.R. Keeney (eds.), Methods of Soil Analysis, Part 2, Agronomy 9, second ed. ASA, Madison WI, pp. 539-577.

Poorter, H. and R. de Jong. 1999. A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. New Phytol. **143:** 163-176.

Poorter, H. and A. Van der Werf. 1998. Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. *In* H. Lambers, H. Poorter, and M.M.I. Van Vuuren (eds.), Inherent variation in plant growth. Physiological mechanisms and ecological consequences. Leiden, Netherlands, Backhuys Publishers, pp. 309-336.

Roumet, C., M.P. Bel, L. Sonié, F. Jardon, and J. Roy. 1996. Growth response of grasses to elevated CO_2: a physiological plurispecific analysis. New Phytol. **133:** 595-603.

Ryser, P. 1996. The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. Funct. Ecol. **10:** 717-723.

Shipley, B. 1995. Structured interspecific determinants of specific leaf area in 34 species of herbaceous angiosperms. Funct. Ecol. **9:** 312-319.

Shipley, B. 2002. Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: relationship with daily irradiance. Funct. Ecol. **16:** 682-689.

Shipley, B. and T-T. Vu. 2002. Dry matter content as a measure of dry matter concentration in plants and their parts. New Phytol. **153:** 359-364.

Su, Y. Z. and H.L. Zhao. 2003. Soil property and plant species in an age sequence of *Caragana micropylla* plantations in Horqin Sandy Land, north China. Ecol. Eng. **20:** 223-235.

Van der Werf A., R.M. Geerts, and F.H. Jacobs. 1998. The importance of relative growth rate and associated traits for competition between species during vegetation succession. *In* H. Lambers, H. Poorter, and M.M.I. Van Vuuren (eds.), Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences. Leiden, Netherlands, Backhuys Publishers, pp. 309-336.

Vendramini, F., S. Diaz, D. Gurvich, P. Wilson, K. Thompson, and J. Hodgson. 2002. Leaf traits as indicators of resource-use strategy in floras with succulent species. New Phytol. **154:** 147-157.

Weiher, E., A. van der Werf, K. Thompson, M. Roderick, E. Garnier, and O. Eriksson. 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. J. Veg. Sci. **10:** 609-620.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil **199:** 213-227.

Wilson, P., K. Thompson, and J. Hodgson. 1999. Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. New Phytol. **143:** 155-162.

Witkowski, F. and B. Lamont. 1991. Leaf specific mass confounds leaf density and thickness. Oecologia **88:** 486-493.

Zhao, W.Z. and S.M. Bai. 2000. Characteristics of seed bank at fenced grassland in Horqin sandy land. Chinese J. Desert Res. **21:** 204-208.

Zhu, Z.D., S. Liu and X.M. Di. 1989. Desertification and Its Rehabilitation in China. Science Press, Beijing, 43-48 pp.

沙丘生境主要植物比葉面積和葉乾物質含量的比較研究

李玉霖[1] Douglas A. JOHNSON[2] 蘇永中[1] 崔建垣[1] 張銅會[1]

[1] 中國科學院寒區旱區環境與工程研究所

[2]USDA-ARS Forage and Range Research Laboratory

Utah State University, Logan, Utah 84322-6300, USA

本文研究了生長在不同沙丘生境中（流動沙丘，半固定沙丘和固定沙丘）20個植物種（10 個一年生植物種和 10 個多年生植物種）的比葉面積（SLA）和葉乾物質含量（LDMC）的變化，並且分析了各個沙丘生境的土壤養分特徵。研究的主要目的是為了確定 SLA 及 LDMC 是否可以作為沙丘生境植物資源利用對策的指示指標。結果表明， 3 種沙丘生境的土地生產力及土壤養分之間存在顯著差異。各個植物種的平均 SLA 和 LDMC 在植物種之間差異顯著，在所研究的植物種中，固定沙丘上一年生草本狗尾草 *Setaria viridis* 的 SLA 最大（28.2 m^2 kg^{-1}），半固定沙丘上多年生禾草白草 *Pennisetum centrasiatum* 的 SLA 最小（8.6 m^2 kg^{-1}），LDMC 的變化範圍在 0.1（固定沙丘上的一年生雜草灰綠藜 *Chenopodium glaucum*）至 0.41（固定沙丘上的多年生草本蘆葦 *Phragmitis australis*）之間。多數在兩種或三種沙丘生境均有分佈的植物其 SLA 在不同沙丘生境之間差異顯著，但是僅有 6 個植物種的 LDMC 在不同沙丘生境之間表現出差異 ($p<0.05$)。SLA 和 LDMC 的相關分析發現，不同生境（流動沙丘，半固定沙丘和固定沙丘）或生活型（一年生和多年生）植物 SLA 和 LDMC 之間均呈負相關趨勢，但僅固定沙丘上植物多年生植物 SLA 和 LDMC 之間呈顯著負相關；就植物的生活型而言，一年生植物 SLA 和 LDMC 之間相關性不顯著。與許多研究結果類似，一年生植物的SLA顯著大於多年生植物的SLA，而且兩者之間 LDMC 存在顯著的差異 ($p<0.05$)。通過分析可以初步確定， SLA 可以作為沙丘環境植物資源利用對策的指示指標。

關鍵詞：一年生植物；葉乾物質含量；多年生植物；沙丘；比葉面積。