Variation in structural and physiological leaf traits of eight species in karst desertification area of China

L.-Y. WEI*,***,+, D.-J. ZENG**, S.-H. LV**, J.-L. ZHANG**, J.-F. JIAO**, Y.-M. YOU**, and X.-K. LI**

*Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, 723 Xinke Rd. Tianhe District, Guangzhou 510160, China***
*Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, Guilin, Guangxi 541006, P.R. China*****
*Graduate School of Chinese Academy of Sciences, Beijing 100049, China****

Abstract

Leaf traits have long been recognized as influential factors in the acquisition and processing of resources by plants. However, there is less knowledge of between-species variations in seasonal changes in leaf traits and trait interrelationships. Therefore, we examined variations in leaf area (LA), dry biomass (DM), specific leaf area (SLA), and leaf gas-exchange parameters in one non-native and seven native tree species under field environmental conditions, in a karst area in China subjected to desertification. Measurements were taken three times during the growing season. The results show that the seven native trees had higher LA, DM, and water-use efficiency (WUE) than the non-native *Cinnamomum camphora*. In contrast, all the native tree species except *Ligustrum lucidum* had lower photosynthetic rates (P_N) than the non-native species. In all species, the relationship between LA and DM was less variable than the relationship between SLA and LA. However, leaves of the non-native *C. camphora* and native species *Sterculia lanceolata, Cleidiocarpon cavalerei* and *Cyclobalanopsis glauca* were highly sensitive to seasonal conditions, leaves of *Sapindus mukorossi* and *Ligustrum lucidum* were less sensitive to seasonal changes, and leaves of *Syzygium cumini* and *Cephalomappa sinensis* were insensitive. An understanding of leaf traits will aid the selection of suitable species for land restoration.

Additional key words: desertification; dry biomass; karst area; leaf area; photosynthesis; specific leaf area.

Introduction

The karst areas in China are characterized by exposed rocks, poor and superficial soil, sparse vegetation (coverage < 10%, forest coverage < 1%), and they are frequently subjected to drought and grazing disturbance, leading to desertification (Lv *et al.* 2007). Thus, the karst environment in China is ecologically fragile and there is little remnant native vegetation. Moreover, desertification to rock is increasing at an alarming rate (10% annually). The loss and degradation of native vegetation not only creates vast stretches of land with no economic, social and aesthetic value, but also poses a number of ecological risks that threaten the local and even global environment (Nath 2004).

Rocky desertification in the karst area requires remediation. Agriculture may not be suitable or feasible at all sites, and afforestation or reforestation seem to be the only alternatives for sustainable productivity that can be achieved with modest effort (Nath 2004, Lv *et al.* 2006). Large-scale reclamation and eco-restoration programs have been demonstrated to be effective in relieving some ecological crises, and in realizing the integrated development of the local economy, society, and environment (Nath 2004, He *et al.* 2004).

Screening of suitable tree species for remediating these areas has attracted increasing attention. Compared with non-native species, endemic species have lower photosynthetic capacity, specific leaf area, and leaf nitrogen content (Gulías *et al.* 2003). Alcover *et al.* (1999) suggested that these leaf traits may be disadvantageous for native plant species in competition with non-native species. There have also been reports that introduced species can decrease litter and soil pH, and alter

---

Received 27 February 2009, *accepted* 14 October 2010.

+Corresponding author; phone: (86)-20-37252950, fax: (86)-20-37252615, e-mail: weilanyingccn@163.com

Abbreviations: DM – dry biomass; LA – leaf area; P_N – photosynthetic rate per unit leaf area; SLA – leaf area per unit dry mass; WUE – instantaneous water-use efficiency; WUE_i – intrinsic water-use efficiency.

Acknowledgements: This work was supported by the National Science and Technology Support Project (2006BAC01A10), and the Action-plan for Western China Development of the Chinese Academy of Sciences (KZCX2-XB2-08-02).

the carbon, nutrient and water cycles, and soil biodiversity (Scholes and Nowicki 1998). In turn, this may lead to more extensive colonization and invasion of native ecosystems by the introduced species (Richardson *et al.* 2000). Thus, successful reforestation needs sound information on the ecology and growth responses of target plant species acclimated to relevant environmental factors, especially their ecological leaf traits (Zhang *et al.* 2006, Zheng and Shangguan 2007). Leaves play particularly important roles in carbon assimilation, water relations and energy balance (Ackerly *et al.* 2002, Vile *et al.* 2005). Leaf traits also have a functional influence on the survival and growth of plants, and thus the species richness and composition of plant communities (Thomas and Winner 2002, Gratani and Varone 2006).

In this study, we examined the variation in plants' leaf traits and trait inter-relationships during the vegetative season, and tested the hypothesis that leaf traits may differ between non-native and native tree species. We measured LA, DM, SLA, and leaf gas-exchange parameters of one non-native tree species, *Cinnamomum camphora* (Linn.) Presl, and seven native tree species that grow in the karst area of southwestern China: *Sapindus mukorossi* Gaertn., *Syzygium cumini hainanense* Chang et Miau, *Sterculia lanceolata* Caw., *Cleidiocarpon cavalerei* (Levl.) Airy Shaw, *Cyclobalanopsis glauca* (Thunb.) Derst, *Ligustrum lucidum* Ait. and *Cephalomappa sinensi* (Chun et How) Kosterm.

Materials and methods

Study site: The study site is located at Longhe Village, Pingguo County, Guangxi province, China (107°22′40″E-107°25′30″E, 23°22′30″N-23°24′00″N). The study area covers an area of about 89,000 km^2. The average annual temperature is 19.1–22°C. Annual rainfall is 1,500 mm, with most of the rainfall occurring from May to September, accounting for 65% of the total. The dry and wet seasons are clearly distinct in this area, because of the uneven distribution of rainfall. Tree saplings were planted in 2003 in a nursery covering an area of 0.6 ha.

Morphological and structural leaf trait measurement: A total of 15–20 fully expanded and intact sun leaves of each species were sampled on each of three occasions (October 2007, March 2008, and July 2008) to measure their LA, DM, and SLA. LA was measured with a *LI-3000A* Portable Leaf Area Meter (*Li-Cor Inc.*, Lincoln, USA). After LA and fresh mass had been determined, they were oven-dried at 80°C to constant mass for DM measurement. SLA was calculated as the ratio of LA to DM (Vile *et al.* 2005). Mean values ± SE of these variables for each species, on each sampling occasion, are presented where xx is the number of trees sampled of each species on each sampling occasion.

Leaf gas-exchange measurements were carried out using a *Li-6400* portable gas-exchange system (*Li-6400*, *LiCor*, Lincoln, USA) on 24–25 July, 2008. Net photosynthetic rate (P_N) and transpiration rate (E), stomatal conductance (g_s), and intercellular CO$_2$ concentration (C_i) were measured at a saturating irradiance of 1,200 μmol m^{-2} s^{-1} provided by a built-in red LED light source. The gas entry was connected *via* a pipe from 3 m above ground. The open pathway was turned on to adjust the airflow rate to 0.5 ml min^{-1}, and the cuvette temperature was set at approximately the air temperature on each sampling occasion. The gas-exchange parameters were recorded 2 min after photosynthesis had stabilized. The instantaneous WUE was determined from P_N/E (Peñuelas *et al.* 1998). WUE$_i$ was determined from P_N/g_s. The photosynthetic gas-exchange parameters were measured on fully expanded leaves of six saplings of each species.

Measurement conditions were as follows: irradiance 1,500 μmol m^{-2} s^{-1}; CO$_2$ concentration 400 μmol mol^{-1}; air humidity, 63%, and temperature 28°C.

Results

Leaf structural traits: During the study period, the mean leaf size (LA) varied substantially, both within and among species, ranging from 10.2–18.8 cm^2 for *C. camphora* to 31.5–35.9 cm^2 for *C. sinensis* (Fig. 1*A*). LA [cm^2] did not show any significant differences among *S. mukorossi* (32.9 ± 1.5), *S. cumini* (38.0 ± 2.9), *C. glauca* (35.9 ± 14.4), *L. lucidum* (36.5 ± 1.7) and *C. sinensis* (33.6 ± 2.2). However, these species had greater LA than *C. camphora* (14.4 ± 4.3), *C. sinensis* (97.2 ± 148) and *C. cavalerei* (57.6 ± 9.1), on average over the three sampling periods. Of all tested species, *C. camphora* had the lowest LA; 15% lower than that for *S. lanceolata*. Leaf DM was lowest for *C. camphora* (0.11 ± 0.04); 19% lower than that of *C. cavalerei* (0.56 ± 0.02) (Fig. 1*B*). The SLA values were lowest for *L. lucidum* and *C. sinensis* (99.0 ± 10.7) (Fig. 1*C*), although these species had intermediate LA and DM values.

Leaf functional traits: Leaf gas-exchange parameters for all the species measured in July 2008 are shown in Table 1. *C. camphora* and *L. lucidum* had the highest P_N values (17.8 ± 2.8 and 16.6 ± 4.2, respectively), followed by *C. glauca* (13.5 ± 3.5), *S. cumini* (12.0 ± 2.7), *S. lanceolata* (10.6 ± 1.3), *S. mukorossi* (9.4 ± 2.1), *C. cavalerei* (9.4 ± 2.8) and *C. sinensis* (7.8 ± 2.3). Values for g_s, C_i, E, V$_{pdl}$, WUE and WUE$_i$ all varied among the eight

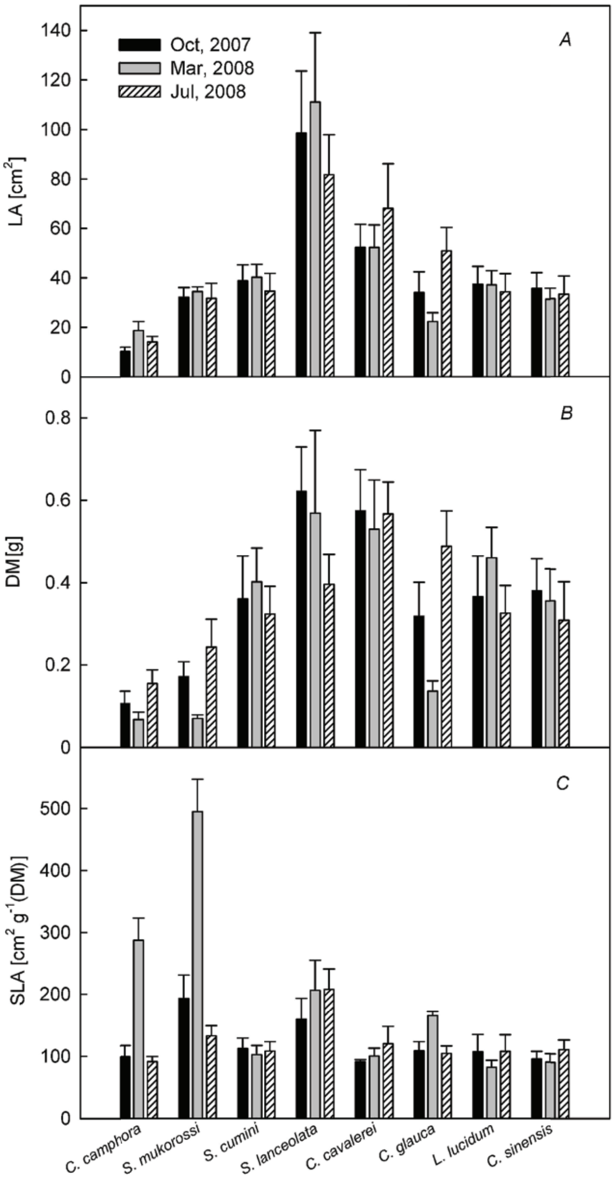

Fig. 1. Variations in leaf area (LA), dry biomass (DM), and specific leaf area (SLA) of eight species in karst desertification area.

species and differed from the patterns of P_N values. *C. camphora* had the highest P_N, g_s, and E values, but the lowest WUE and WUE$_i$ values. *C. sinensis* was characterized by the lowest P_N (7.8 ± 2.3), g_s (0.11 ± 0.04), and E (2.8 ± 0.8) values, but the highest WUE$_i$ (71.4 ± 10.1).

Relationships among leaf traits of the eight species: Considering all the species together, the SLA values were positively correlated with LA ones in October 2007 and July 2008, but weakly correlated with LA in March 2008 (Fig. 2*A,B,C*). SLA values were negatively correlated with DM in March 2008 (Fig. 2*E*), but SLA showed no significant correlation with DM in October 2007 and July 2008 (Fig. 2*D,F*). The relationships between LA and DM were positive and less variable, *i.e.* small leaves were usually associated with low DM (Fig. 2*G,H,I*).

Table 1. Average leaf photosynthetic parameters of the eight species (means ± SE). The same *superscript letters* in a column indicate no significant differences (P>0.05) according to LSD tests if variance is homogeneous, or else *Tamhane*'s *T2* tests. n = 6. Means ± SE are shown. P_N – photosynthetic rate per unit leaf area; g_s – stomatal conductance; C_i – intercellular CO_2 concentration; E – transpiration rate; V_{pdl} – vapor pressure deficit; WUE – instantaneous water-use efficiency; WUE$_i$ – intrinsic water-use efficiency.

Species	P_N [μmol m^{-2} s^{-1}]	g_s [mol m^{-2} s^{-1}]	C_i [μmol mol^{-1}]	E [mmol m^{-2} s^{-1}]	V_{pdl} [Pa]	WUE [mmol mol^{-1}]	WUE$_i$ [μmol mol^{-1}]
C. camphora	17.8 ± 2.8^a	0.48 ± 0.15^a	270.5 ± 13.2^b	7.1 ± 1.5^a	1.67 ± 0.19^a	2.5 ± 0.2^b	39.8 ± 10.2^c
S. mukorossi	9.4 ± 2.1^c	0.17 ± 0.01^c	259.2 ± 23.7^b	2.8 ± 0.2^b	1.66 ± 0.06^d	3.3 ± 0.7^a	56.6 ± 13.7^b
S. cumini	12.0 ± 2.7^{bc}	0.25 ± 0.09^{bc}	266.5 ± 14.7^b	3.5 ± 0.8^b	1.47 ± 0.19^{de}	3.5 ± 0.4^a	50.8 ± 11.5^{bc}
S. lanceolata	10.6 ± 1.3^{bc}	0.15 ± 0.03^c	233.5 ± 10.6^c	3.5 ± 0.4^b	2.29 ± 0.17^b	3.0 ± 0.1^{ab}	70.9 ± 6.9^a
C. cavalerei	9.4 ± 2.8^c	0.26 ± 0.08^{bc}	302.5 ± 18.8^a	3.6 ± 0.9^b	1.44 ± 0.09^{de}	2.7 ± 0.6^b	38.6 ± 11.7^c
C. glauca	13.5 ± 3.5^b	0.29 ± 0.10^b	267.4 ± 7.1^b	3.8 ± 0.9^b	1.44 ± 0.19^e	3.5 ± 0.3^a	48.9 ± 6.1^{bc}
L. lucidum	16.6 ± 4.2^{ab}	0.34 ± 0.11^b	252.5 ± 4.6^{bc}	5.9 ± 1.4^a	1.88 ± 0.18^c	2.8 ± 0.1^b	50.8 ± 5.6^{bc}
C. sinensis	7.8 ± 2.3^c	0.11 ± 0.04^c	232.4 ± 16.7^c	2.8 ± 0.8^b	2.50 ± 0.18^b	2.7 ± 0.2^b	71.4 ±1 0.1^a

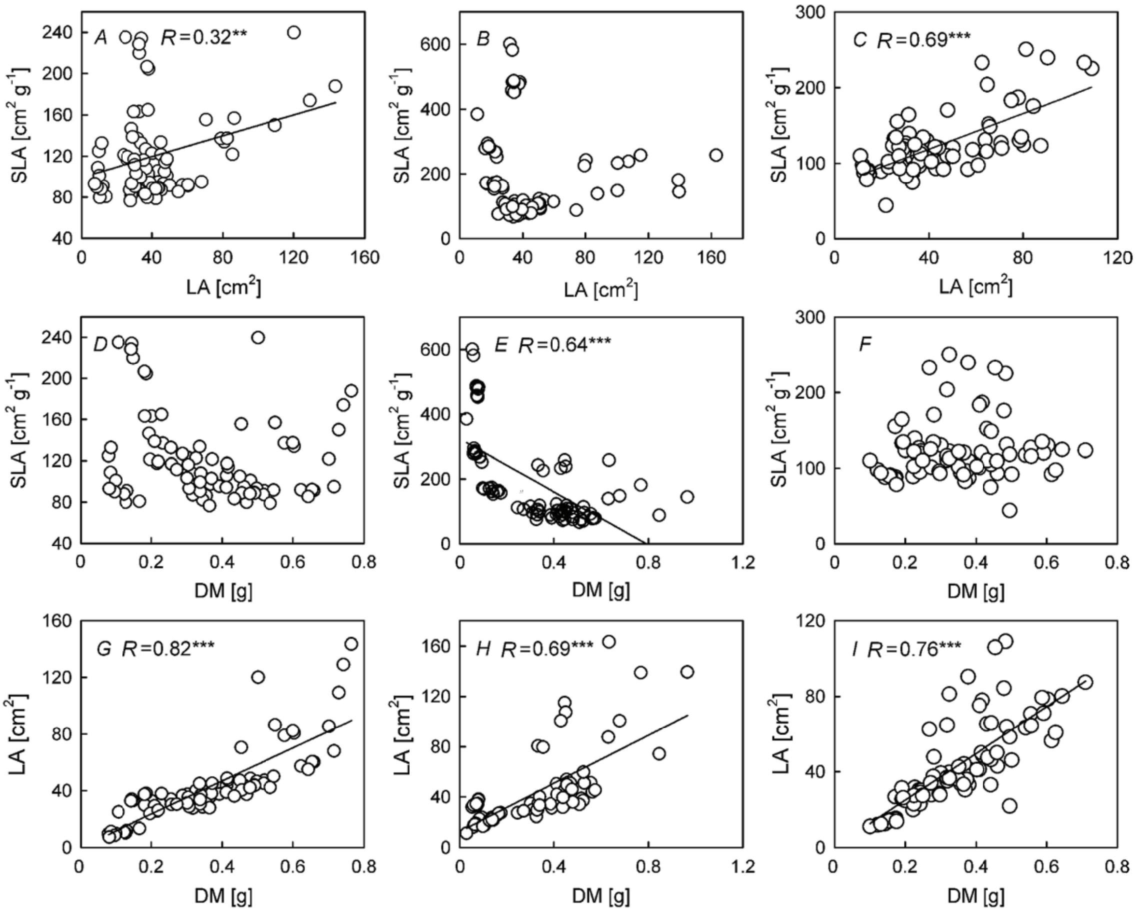

Fig. 2. The linear regression relationship among leaf traits of the eight species in karst desertification area (*A,D,G* : October 2007; *B,E,H*: March 2008; *C,F,I*: July 2008).

Discussion

The analysis of the measured leaf traits presented here indicates that the leaves of *C. camphora, S. lanceolata*, *C. cavalerei*, and *C. glauca* are more sensitive to changes in environmental conditions than those of the other species. *S. cumini* and *C. sinensis* appear to be less variable than other plants and thus less sensitive to seasonal changes. The native tree species had lower g_s and E than those of *C. camphora* Our results suggest that there are significant differences in WUE among the species, in accordance with our understanding of the functional role of the leaf traits. The differences in leaf traits also suggest that the tested species are variably adapted to the local environment (Zheng and Shangguan 2007). Species analysis indicated apparent shifts in mean trait values, which may represent a change in variance, with minimum or increasing maximum values across an environmental gradient (Ackerly *et al.* 2002). Since variations in, and inter-relationships among, leaf traits may reflect adaptations to climate, such information can be valuable for screening of suitable tree species for remediation and reforestation of the degraded karst areas (Lv *et al.* 2006). Further studies should focus on the detailed variation of leaf traits and resource interactions as affected by environment, in order to select the optimal tree species.

References

Ackerly, D., Knight, C., Weiss, S., Barton, K., Starmer, K.P.: 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, 2002.

Alcover, J.A., Perez-Obiol, R., Yll, E.-I., Bover, P.: The diet of Myotragus balearicus Bate 1909 (Artiodactyla: Caprinae), an extinct bovid from the Balearic Islands: evidence from coprolites. – Biol. J. Linn. Soc. **66**: 57-74, 1999.

Vile, D.E., Garnier, B. Shipley, G. Laurent, M.L., Navas, C. Roumet, S. Lavorel, S. Diaz, J.G., Hodgson, F. Lloret, G. F., Midgley, H. Poorter, M.C., Rutherford, P.J., Wilson, Wright. I.J.: Specific leaf area and dry matter content estimate thickness in laminar leaves. – Ann. Bot. **96**: 1129-1136, 2005.

Gratani, L., Varone, L.: Long-time variations in leaf mass and area of Mediterranean evergreen broad-leaf and narrow-leaf maquis species. – Photosynthetica **44**: 161-168, 2006.

Gulías, J., Flexas, J., Mus, M., Cifre, J., Lefi, E., Medrano, H: Relationship between maximum leaf photosynthesis, nitrogen content and specific leaf area in Balearic endemic and non-endemic Mediterranean species. – Ann. Bot. **92**: 215-222, 2003.

He, B.H., Hao, Y.Q., Li, X.G., Han, C.X., Chen, C.P., Zheng, G.C.: Community characteristics in Hongchiba area of Wuxi County during ecological restoration after controlled burning. – Chin. J. Appl. Ecol. **15**: 1105-1108, 2004. [In Chin.]

Lv, S.H., Li, X.K., Lu, S.H., Xiang, W.S., Qing, J.K., Ou, Z.L., Wang, X.Y.: The preliminary study on seedling and afforestation of native trees in karst region of Guangxi. – Guangxi Sci. **13**: 236-240, 2006. [In Chin.]

Lv, S.H., Lu, S.H., Xiang, W.S., Wang, X.Y., Qing, J.K.: Basic characters of soil seed bank and measures of vegetation restoration in rock desertification area in southwest of Guangxi. – J. Plant Resour. Environ. **16**: 6-11, 2007. [In Chin.]

Nath, S.: Ecosystem approach for rehabilitation of coal mine areas. – In: Sinha, I.N., Ghose, M.K. Singh, G. (ed.): Proc. Nat. Seminar on Environmental Engineering with Special Emphasis on Mining Environment. Pp.19-20. Calcutta 2004.

Peñuelas, J., Filella, I., Llusià, J., Siscart, D., Piñol J.: Comparative field study of spring and summer leaf gas exchange and photobiology of the mediterranean trees *Quercus ilex* and *Phillyrea latifolia*. – J. Exp. Bot **49**: 229-238, 1998.

Richardson, D.M., Pysek, P., Rejmanek, M., Barbour, M.G., Panetta, F.D., West, C.J.: Naturalization and invasion of alien plants; concepts and definitions. – Divers. Distrib. **6**: 93-107, 2000.

Scholes, M.C., Nowicki, T.E.: Effects of pines on soil properties and processes. – In: Richardson, D.M. (ed.): Ecology and Biogeography of Pinus. Pp. 341-353. Cambridge Univ. Press, Cambridge 1998.

Thomas, S.C., Winner, W.E.: Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. – Tree Physiol. **22**: 817-817, 2002.

Zhang, S.B., Hu, H., Xu, K., Li., Z.R.: Gas exchanges of three co-occurring species of Cypripedium in a scrubland in the Hengduan Mountains. – Photosynthetica **44**: 241-247, 2006.

Zheng, S.X., Shangguan, Z.P.: Spatial patterns of leaf nutrient traits of the plants in the Loess Plateau of China. – Trees-Struct. Funct. **21**: 357-370, 2007.