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PLANT FUNCTIONAL CLASSIFICATIONS BASED ON LEAF TRAITS IN A SUBTROPICAL KARST LANDSCAPE

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Abstract

Plant functional classifications has recently attracted much attention from ecologists. However, assessment on plant functional classifications in the special area of Karst were still absent in the literature. Therefore, in this study, plant functional types were classified into typical evergreen shrubs and deciduous shrubs according to their leaf traits in the subtropical Karst landscape of south-western China. The aforementioned leaf traits included leaf dry weight (DW), leaf dry matter content (LDMC), leaf area (LA), leaf thickness (LT), specific leaf area (SLA), and leaf tissue density (LTD) for 16 kinds of evergreen shrubs and 10 kinds of deciduous shrubs. Results showed that DW and LT were the principle parameters for evergreen shrubs, while DW, LT, and LA were the principle parameters for deciduous shrubs in Karst. Interestingly, it both can be classified into two types either in evergreen shrubs or in deciduous shrubs. They could be termed as shade-tolerant type (with higher DW and LT in evergreen shrubs or higher DW, LT, and LA in deciduous shrubs) and heliophilic type. These results were beneficial to understanding the vegetation formation in Karst and were expected to provide some help for vegetation restoration strategies in this unique degraded ecosystem.

Key words: Evergreen shrubs; Deciduous shrubs; Plant functional types; Karst.

Abbreviations: FW, Fresh weight; DW, Dry weight; LA, Leaf area; LDMC, Leaf dry matter content; LT, Leaf thickness; SLA, Specific leaf area; LTD, Leaf tissue density; LMA, Leaf mass per area.

Introduction

It is a big challenge to understand the ecological and physiological characteristics of huge amounts of plants. While, there is a way to classify species with common characteristics. Plant functional classifications has recently attracted much attention from ecologists (Lourens *et al*., 2006; Domingues *et al*., 2007; Duru *et al*., 2009). Plant functional traits were described by some measurable parameters for the ecological strategy of a species (Cadotte *et al*., 2011; Dwyer & Mason, 2018), and were affected by environmental factors (Wright *et al*., 2005; Mcgill *et al*., 2006), to some extent, reflecting the functional characteristics of a ecosystem and plants' acclimation to the ecosystem (Violle *et al*., 2007; Guittar *et al*., 2016). Plant functional classifications based on plant functional traits will help to understand and simplify the response mechanism of multitudinous species to an ecosystem.

The plants' foliar habit (i.e., evergreen or deciduous) has been considered as an important functional trait for classifying species into different plant functional types (Chaturvedi *et al*., 2011), which is an effective way to distinguish functional types with different ecological effects (Powers & Tiffin, 2010). Leaf traits indicated the plants' acclimation to various environmental conditions (Wang *et al*., 2017; Wang *et al*., 2019), as a primary feature of plants' ecological strategies (Riva *et al*., 2018). Compared with evergreen plants, deciduous plants had higher specific leaf area (SLA), higher leaf nitrogen content, and higher photosynthetic capacity (Kloeke *et al*., 2012). Evergreen plants' leaves, however, would compensate for increased consumption and low carbon net gains through continuous growing season (Wright *et al*., 2004; Hedin, 2007; Ogaya & Peñuelas, 2007). Previous study reported that the replacement rate of deciduous plants' leaves was faster relative to evergreen ones, regardless of less consumption in leaves (Athokpam *et al*., 2014). Studies on leaf traits and plant functional classifications can provide a feasible approach for quantitative and predictive ecology (Mcgill *et al*., 2006; Westoby & Wright, 2006).

It is an unique subtropical Karst landscape in Southwest, China, where vegetation restoration currently has become a concerned issue, due to its severe forest degradation. Specially, shrub species performed a significant growth advantage, and also played an important role in promoting the nutrition cycle and photosynthetic productivity in the ecosystem. The objectives of this study were, therefore, to analyze the principal component of leaf traits in typical evergreen shrubs and deciduous shrubs in isolation in the subtropical Karst landscape, and then to classify types for evergreen shrubs and deciduous shrubs separately. These results were expected to provide a theoretical basis for vegetation restoration strategies in this unique subtropical Karst.

Materials and Methods

Study sites: The study area was located in Guilin, Southwest, China (109°36′-111°29′E, 24°15′- 26°23′N), where was a mountainous and hilly area with a degraded vegetation Karst landscape (Su *et al*., 2017). The elevation was from 100 to 500 m. Annual average temperature was 18.9°C. The average temperature in January was 7.8°C, and the average temperature in July was 28°C. Annual average sunshine hours was 1670 h. Annual Frost-free period was 300 d. Annual average rainfall was 1949.5 mm, and annual average evaporation was 1490-1905 mm.

Plant species and sample collection: We identified common species of 16 kinds of evergreen shrubs and 10 kinds of deciduous shrubs, as list in (Table 1). 30 individuals per species were selected and tagged. Four fully expanded, non-senescent leaves from four branches per individual were sampled. 30 individuals within a species were collected on the same day within an hour, and all leaves from all species were collected during a 4-day period. Samples were transported to laboratory and stored in a freezer (4°C) for further determination.

Table 1. Species information in this study.

No.	Foliar habit	Name of species	Sampled individuals
1.	Evergreen	*Ligustrum tenuipes*	30
2.		*Serissa serissoides*	30
3.		*Tarenna depauperata*	30
4.		*Pittosporum planilobum*	30
5.		*Ilex bioritsensis*	30
6.		*Secamone sinica*	30
7.		*Rhamnus kwangsiensis*	30
8.		*Pyracantha fortuneana*	30
9.		*Loropetalum chinense*	30
10.		*Wikstroemia indica*	30
11.		*Elaeagnus glabra*	30
12.		*Myrsine seguinii*	30
13.		*Salacia sessiliflora*	30
14.		*Ficus tinctoria* subsp. *gibbosa*	30
15.		*Sageretia rugosa*	30
16.		*Decaspermum esquirolii*	30
17.	Deciduous	*Rhamnus leptophylla*	30
18.		*Rhamnus lamprophylla*	30
19.		*Alchornea trewioides*	30
20.		*Spiraea cantoniensis*	30
21.		*Paliurus ramosissimus*	30
22.		*Mallotus repandus*	30
23.		*Ficus erecta*	30
24.		*Grewia biloba* var. *parviflora*	30
25.		*Flueggea suffruticosa*	30
26.		*Lagerstroemia indica*	30

Leaf traits: Leaf area (LA) was assessed by a CI-203 Portable Laser Area Meter (CID Inc., Camas, WA, USA). For determination of leaf dry matter content (LDMC), leaves were stored in a moist dark surrounding at 5°C for 12 h and weighed to get the leaf saturated fresh weight. Then, the leaves were oven-dried at 80°C for 48 h and weighed to get the dry weight (DW). Leaf dry matter content (LDMC) (g/g FW) = the leaf dry weight (g)/the leaf saturated fresh weight (g). Specific leaf area (SLA) (cm^2/g DW) = LA (cm^2)/DW (g). Leaf thickness (LT) (mm) was measured as the average of the thicknesses at 0.25 cm both sides away from the main vein in the leaf with a Vernier caliper. Leaf tissue density (LTD) (kg/m^3) = (SLA × LT)$\times 10^{-4}$.

Statistical analysis

The significances of differences in leaf traits parameters among species were analyzed using a one-way ANOVA and the Mann-Whitney U test for evergreen shrub and deciduous shrub, respectively. Post-hoc differences were determined using Fisher's least significant difference (LSD, P = 0.05). For all analyses alpha = 0.05. Lowercase on the bar was for evergreen shrub and uppercase on the bar was for deciduous shrub in Figs. 1-3. The correlations between leaf trait parameters were analyzed using Pearson Correlation analysis, and the principal factors of the leaf traits were determined using Principal Component analysis. To classify plant functional type, Hierarchical cluster were analyzed by the method of Between-groups linkage using Squared Euclidean distance based on leaf traits. These aforementioned analyses were all conducted using SPSS 21.0 software. Figures were drawn using the Sigmaplot 12.5 software program.

Results

Leaf traits: As shown in Figure 1A, the average DW values of 0.178±0.02 g and 0.134±0.01 g for 16 evergreen shrub species and 10 deciduous shrub species were detected in the Karst landscape in Southwest, China. DW values of *Serissa serissoides* and *Rhamnus leptophylla* were the lowest, and the highest was observed on *Rhamnus kwangsiensis* and *Alchornea trewioides* for evergreen shrub species and deciduous shrub species, respectively. The average LDMC values of 0.438±0.01 and 0.317 ±0.01 were observed for evergreen shrub species and deciduous shrub species, respectively (Fig. 1B). LDMC of *Serissa serissoides* and *Ficus erecta* were the lowest, whereas those of *Sageretia rugosa* and *Grewia biloba* var. *parviflora* were the highest in evergreen shrub species and deciduous shrub species, respectively. The average LA values for evergreen shrub species and deciduous shrub species were 12.585 ± 1.00 cm^2 and 21.351 ± 1.01 cm^2, respectively (Fig. 2A). LA of *Ligustrum tenuipes* and *Lagerstroemia indica* were the lowest in the evergreen shrub species and deciduous shrub species, respectively, whereas those of *Salacia sessiliflora* and *Alchornea trewioides* were significantly higher than others in evergreen shrub species and deciduous shrub species, respectively. The average LT values of 0.344 ± 0.01 mm and 0.269 ± 0.01 mm were found for evergreen shrub species and deciduous shrub species, respectively (Fig. 2B). The LT of *Serissa serissoides* was the lowest in the evergreen shrub species, and the lowest LT was observed on *Rhamnus leptophylla* and *Rhamnus lamprophylla* in deciduous shrub species. Contrastly, the highest LT was detected on *Secamone sinica* and *Mallotus repandus* in evergreen shrub species and deciduous shrub species, respectively. The average SLA values of 99.274 ± 10.95 cm^2/g and 193.363 ± 23.83 cm^2/g were observed for evergreen shrub species and deciduous shrub species respectively (Fig. 3A). SLA of *Pittosporum planilobum* and *Lagerstroemia indica* were the lowest, whereas those of *Serissa serissoides* and *Ficus erecta* were the highest in evergreen shrub species and deciduous shrub species, respectively. The average LTD values were 372.949 ± 31.15 kg/m^3 and 231.476 ± 26.39 kg/m^3 for evergreen shrub species and deciduous shrub species, respectively (Fig. 3B). LTD values of *Serissa serissoides* and *Greviabiloba* var.*parviflora* were the lowest, whereas those of *Pittosporum planilobum* and *Rhamnus lamprophylla* were the highest in evergreen shrub species and deciduous shrub species, respectively. Mann-Whitney U test in two independent samples showed that the LDMC, LT and LTD in evergreen shrub were significantly higher than those in deciduous shrub (p<0.000), however, the LA and SLA in evergreen shrub were significantly lower than those in deciduous shrub (p=0.021 and p<0.000, separately). No significant difference was observed on DW between evergreen shrub and deciduous shrub (p=0.554).

Correlation analysis: As shown in Table 2, DW indicated highly significantly positive with LA and LT for both evergreen shrubs and deciduous shrubs. Although no significant correlation was observed between DW and SLA for deciduous shrubs, it was extremely significantly negative for evergreen shrubs. For both evergreen shrubs and deciduous shrubs, extremely significantly negative correlations were found between LDMC and SLA, whereas no considerable correlation was detected between LDMC and LA. Differently, highly significantly positive correlation was found between LDMC and LTD for evergreen shrubs. For deciduous shrubs, highly significantly positive correlation was observed between LDMC and LT.

Principal component analysis: As shown in Table 3, for evergreen shrub species, the coefficients' absolute values of variables x_1 (DW) and x_5 (SLA) were greater among the first principal component (y_1), indicating that the first principal component was represented by SLA and DW. Moreover, SLA was calculated by DW and LA. SLA had a significant correlation with DW and no significant correlation with LA in evergreen shrub species (Table 2). Therefore, the first principal component was comprehensive factors primarily reflecting DW. The second principal component (y_2) was mainly represented by x_6 (LTD), which was assessed by DW, LA and LT. Since LTD had a significant correlation with DW and no significant correlations with LA and LT in evergreen shrub species (Table 2), the second principal component was also comprehensive factors reflecting DW. The third principal component (y_3) was mainly represented by x_4 (LT). From the aforementioned, the leaf characteristics for evergreen shrub species primarily depended on DW and LT.

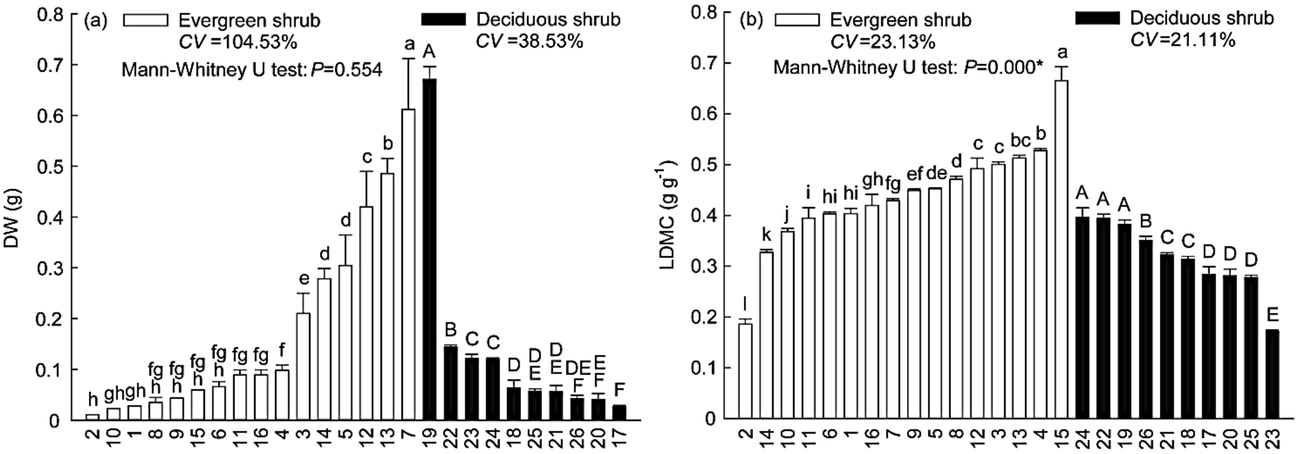

Fig. 1. Dry weight (DW) and leaf dry matter content (LDMC) in evergreen shrub species and deciduous shrub species in the subtropical Karst landscape. The error bars indicate the standard deviation from 30 replicates. Values not sharing a common letter on the bar in evergreen shrub species or in deciduous shrub species are significantly different (p<0.05). The 1, 2, 3, 16 on the x-coordinate represent evergreen shrub species, *Ligustrum tenuipes*, *Serissa serissoides*, *Tarenna depauperata*, *Pittosporum planilobum*, *Ilex bioritsensis*, *Secamone sinica*, *Rhamnus kwangsiensis*, *Pyracantha fortuneana*, *Loropetalum chinense*, *Wikstroemia indica*, *Elaeagnus glabra*, *Myrsine seguinii*, *Salacia sessiliflora*, *Ficus tinctoria* subsp. *gibbosa*, *Sageretia rugosa*, *Decaspermum esquirolii*, respectively. The 17, 18, 19, 26 on the x-coordinate represent deciduous shrub species, *Rhamnus leptophylla*, *Rhamnus lamprophylla*, *Alchornea trewioides*, *Spiraea cantoniensis*, *Paliurus ramosissimus*, *Mallotus repandus*, *Ficus erecta*, *Grewia biloba* var. *parviflora*, *Flueggea suffruticosa*, *Lagerstroemia indica*, respectively.

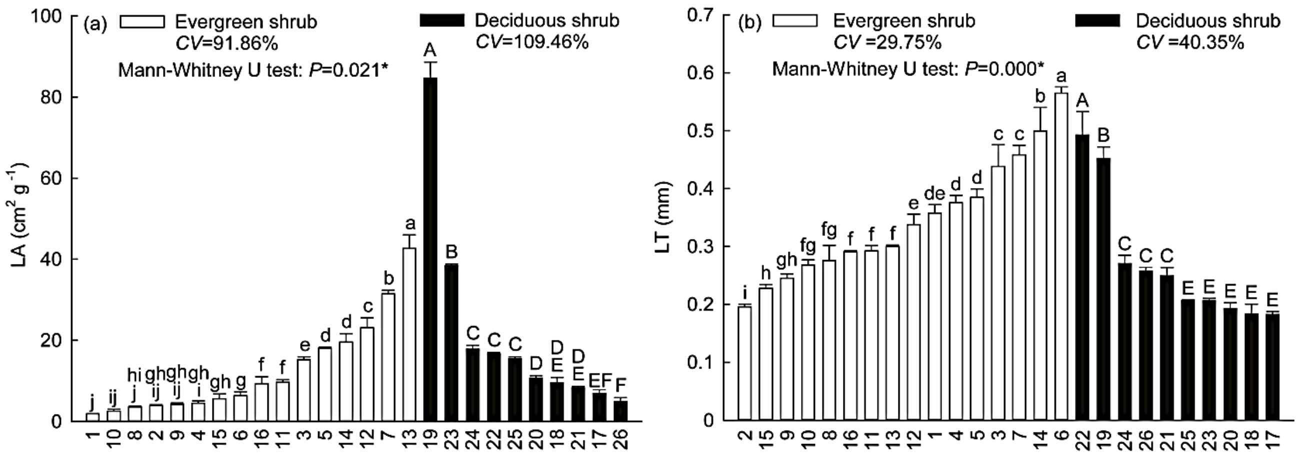

Fig. 2. Leaf area (LA) and leaf thickness (LT) in evergreen shrub species and deciduous shrub species in the subtropical Karst landscape. The error bars indicate the standard deviation from 30 replicates. Values not sharing a common letter on the bar in evergreen shrub species or in deciduous shrub species are significantly different (p<0.05). The meaning of numbers on the x-coordinate was referred in the caption of Fig. 1.

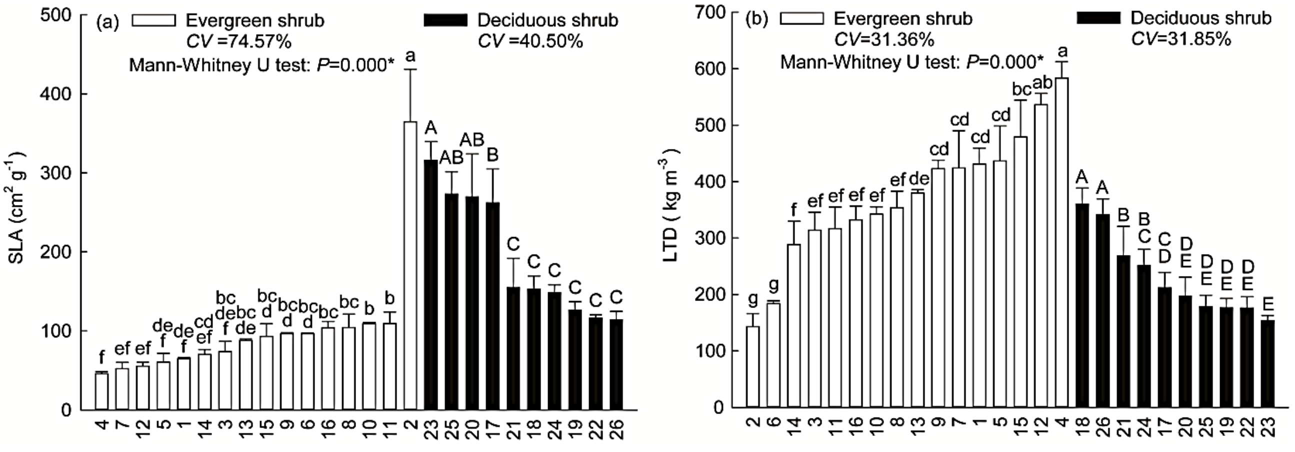

Fig. 3. Specific leaf area (SLA) and leaf tissue density (LTD) in evergreen shrub species and deciduous shrub species in the subtropical Karst landscape. The error bars indicate the standard deviation from 30 replicates. Values not sharing a common letter on the bar in evergreen shrub species or in deciduous shrub species are significantly different (p<0.05). The meaning of numbers on the x-coordinate was referred in the caption of Fig. 1.

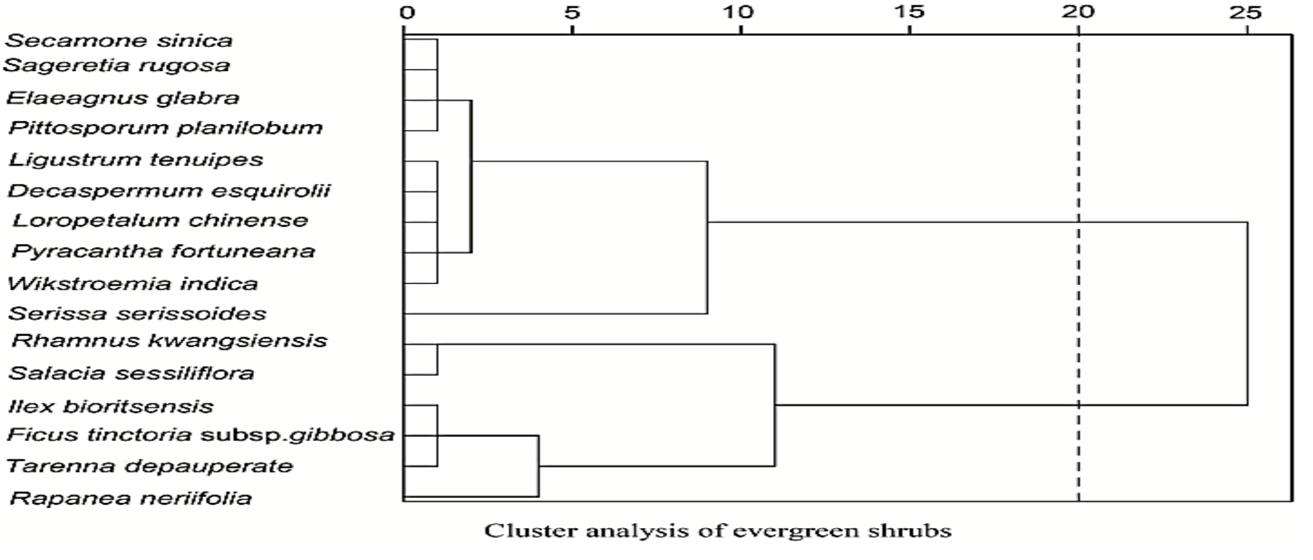

Fig. 4. Hierarchical cluster analyzed by Between-groups linkage method using Squared Euclidean distance for evergreen shrub species in the subtropical Karst landscape.

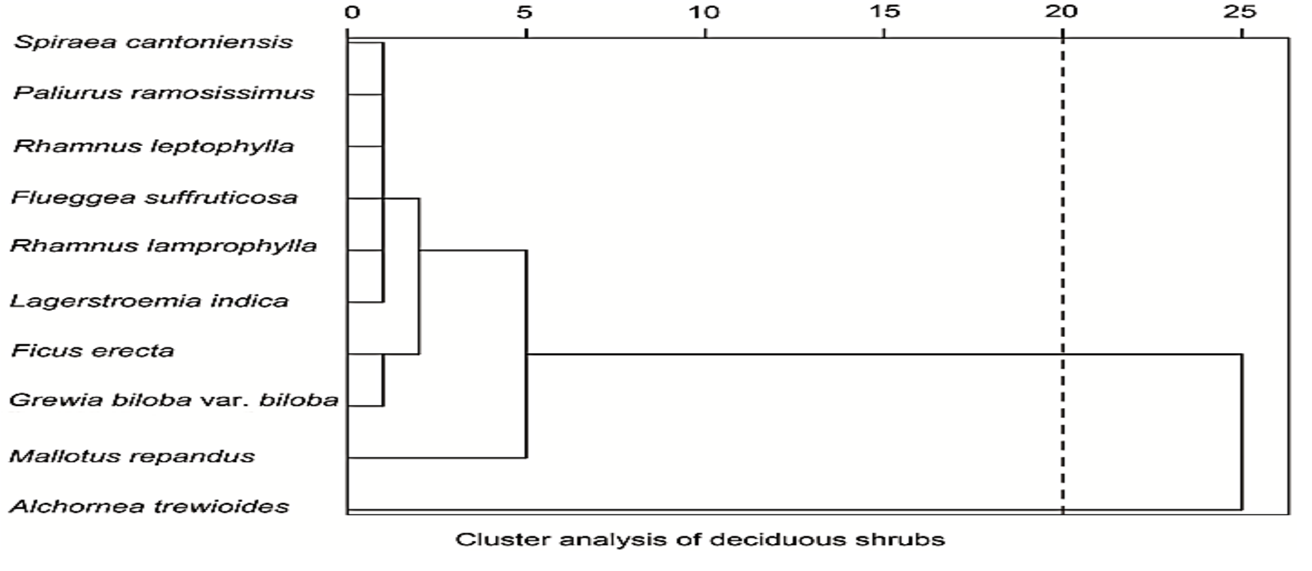

Fig. 5. Hierarchical cluster analyzed by Between-groups linkage method using Squared Euclidean distance for deciduous shrub species in the subtropical Karst landscape.

Table 2. Pearson correlation coefficients for leaf traits in evergreen shrub species and deciduous shrub species in the Karst Landscape.

Leaf Traits	DW		LDMC		LA		LT		SLA	
	Evergreen	Deciduous	Evergreen	Deciduous	Evergreen	Deciduous	Evergreen	Deciduous	Evergreen	Deciduous
LDMC	0.172^{NS}	0.355^{NS}								
LA	0.933^{**}	0.953^{**}	0.165^{NS}	0.101^{NS}						
LT	0.383^{**}	0.670^{**}	-0.031^{NS}	0.658^{**}	0.282^{NS}	0.544^{**}				
SLA	-0.378^{**}	-0.329^{NS}	-0.634^{**}	-0.835^{**}	-0.280^{NS}	-0.088^{NS}	-0.481^{**}	-0.603^{**}		
LTD	0.294^{*}	-0.310^{NS}	0.680^{**}	0.256^{NS}	0.134^{NS}	-0.456^{*}	-0.104^{NS}	-0.299^{NS}	-0.647^{**}	-0.547^{**}

*, $p< 0.05$; **, $p< 0.01$; NS, not significant; DW, dry weight; LDWC, leaf dry matter content; LA, leaf area; LT, leaf thickness; SLA, specific leaf area; LTD, leaf tissue density

Table 3. Principal component analysis for leaf traits in evergreen shrub species and deciduous shrub species in the Karst Landscape.

Principal components	Foliar habit	Eigenvector						Eigenvalue	Contribution rate
		DW (x_1)	LDMC (x_2)	LA(x_3)	LT (x_4)	SLA (x_5)	LD (x_6)		(%)
y_1	Evergreen	0.47	0.38	0.42	0.28	-0.48	0.39	2.86	47.62
	Deciduous	0.49	0.41	0.41	0.51	-0.39	-0.10	3.15	52.43
y_2	Evergreen	0.40	-0.45	0.44	0.36	0.22	-0.51	1.57	26.23
	Deciduous	0.26	-0.41	0.41	0.01	0.49	-0.59	2.10	35.00
y_3	Evergreen	0.30	0.04	0.39	-0.75	0.39	0.18	0.98	16.32

DW, dry weight; LDWC, leaf dry matter content; LA, leaf area; LT, leaf thickness; SLA, specific leaf area; LD, leaf density

Similarly, for deciduous shrub species, as x_1 (DW) and x_4 (LT) were greater among the first principal component, the first principal component was represented by DW and LT. The second principal component was represented by x_6 (LTD), which was calculated by DW, LA and LT. LTD showed a significant correlation with LA and no significant correlations with DW and LT in deciduous shrub species (Table 2). Therefore, the leaf characteristics for deciduous shrub species mainly depended on DW, LT and LA. Since the cumulative contribution rate for the first and second principal component was more than 85 %, the third principal component analysis was unnecessary for deciduous shrub species.

Functional type classification based on leaf traits: According to (Table 3), the principle components equation of leaf traits for evergreen shrub species was $y_1 = 0.47x_1 + 0.38x_2 + 0.42x_3 + 0.28\ x_4 - 0.48\ x_5 + 0.39\ x_6$, $y_2 = 0.40x_1 - 0.45x_2 + 0.44x_3 + 0.36x_4 + 0.22x_5 - 0.51x_6$, and $y_3 = 0.3x_1 + 0.04x_2 + 0.39x_3 - 0.75x_4 + 0.39x_5 + 0.18x_6$, thus the scores of the principle components (y_1, y_2, and y_3) for a given species were obtained. For the adaptive values (*F* value), $F = (2.86y_1 + 1.57y_2 + 0.98y_3) / (2.86 + 1.57 + 0.98)$, where the coefficients of y_1, y_2 and y_3 were eigenvalues of the principal components. Hierarchical cluster analysis was conducted on *F* values. 16 kinds of evergreen shrub species can be objectively divided into 2-15 types using the method of Between-groups linkage (Fig. 4). Thus, the 16 species were classified into two types due to their leaf characteristics. Type 1 (six species), including *Rhamnuskwangsiensis, Salacia sessiliflora, Rapanea neriifolia, Ilex bioritsensis, Ficus tinctoria* subsp. *gibbosa,* and *Tarenna depauperat,* was termed as a shade-tolerant type with higher DW and LT. Type 2 (ten species), including *Decaspermum esquirolii*, *Pittosporum planilobum*, *Pyracantha fortuneana*, *Secamone sinica*, *Loropetalum chinense*, *Sageretia rugosa*, *Elaeagnus glabra*, *Ligustrum tenuipes*, *Wikstroemia indica* and *Serissa serissoides,* was termed as a heliophyte type with less DW and LT. Similar to evergreen shrub species, 10 species were classified into two types considering the leaf characteristics of each deciduous shrub species (Fig. 5). Type 1 (only one species), *Alchornea trewioides,* was termed as a shade-tolerant type with higher DW, LT, and LA. Type 2 (nine species), including *Mallotus repandus*, *Ficus erecta*, *Grewia biloba* var. *parviflora*, *Flueggea suffruticosa*, *Spiraea cantoniensis*, *Paliurus ramosissimus*, *Rhamnus leptophylla*, *Lagerstroemia indica*, and *Rhamnus lamprophylla,* was termed as a heliophyte type with less DW, LT, and LA.

Discussion

Difference in leaf traits for evergreen shrubs and deciduous shrubs: When seasonal conditions are unfavorable, deciduous plants are defoliated to reduce the leaves consumption to resist to drought and severe cold environment (Kloeke *et al*., 2012). A significant advantage of evergreen plants is that they can continue photosynthesis under certain adverse environmental conditions, whereas deciduous plants can not. Plants that have defoliated may use other organs, like green stems, to produce carbohydrate with less input and maintain high water-use efficiency (Franco *et al*., 2005; Silva *et al*., 2015). In this study, LTD in evergreen shrub species was significantly higher than that in deciduous shrub species in Karst (Fig. 3B). Moreover, there was a significantly negative correlation between LDMC and SLA in both evergreen shrub species and deciduous shrub species (Table 2). As we know, SLA and LMA (leaf mass per area) were reciprocal. Therefore, the changes in LDMC were in the same direction with LMA, which was mainly reflecting the plants' ability to retain nutrient concentrations (Riva *et al*., 2018). Previous research showed that the larger the LMA, the larger the LTD (Niinemets, 2001), suggesting that plants invested more heavily per leaf area (Villar & Merino, 2001). Higher LTD in evergreen shrub species in this study indicated that the evergreen plants invested more in their leaves than deciduous plants.

The SLA in evergreen shrub species was significantly lower than that of deciduous shrub species in this study, which was consistent with previous researches that the evergreen plants performed lower SLA and higher LMA than deciduous plants (Ackerly *et al*., 2002; Wright *et al*., 2004; Kloeke *et al*., 2012). SLA represents the light-harvesting areas per dry matter invested by plant, which can inversely reflect the plant's water use efficiency and ability to obtain resources (Ellsworth & Reich, 1993; Blackman *et al*., 2014). In this study, the higher SLA in deciduous shrub indicated higher plant growth rate and lower nutrient use efficiency in Karst. The LA in deciduous shrub was significantly higher than evergreen shrub species in this study, which was directly related to plants' photosynthesis and transpiration, indicating that deciduous shrub had higher photosynthetic capacity and higher transpiration requirements (Eamus, 1999; Fu *et al*., 2012). Deciduous shrub species accumulated sufficient carbohydrates by continuously distributing photosynthetic product to plant growth position and storage organs, and resisted the adverse surroundings by defoliation (Kitajima, 1994; Poorter & Kitajima, 2007). By comparison, evergreen shrub species presented a lower photosynthetic capacity and more conservative in water use efficiency, with strong structural defenses (Wyka *et al*., 2016). No significant difference was observed on average DW between evergreen shrub species and deciduous shrub species in this study. It was probably due to high DW variation in evergreen shrub and deciduous shrub (Fig. 1A). Besides, in this study, results showed that leaves in evergreen shrub species were more thicker, higher leaf dry matter content, higher leaf tissue density, and lower specific leaf area, which were consistent with characteristic conservative strategies in leaf economics spectrum described by Wright *et al*., (2004), whereas leaves in deciduous shrub species were thinner, less leaf dry matter content, lower leaf density, and higher specific leaf area, which were suggested as representative acquisition strategies in leaf economics spectrum described by Lavorel & Grigulis (2012). Thus, the leaf traits in plants with two different foliar habits belonged to two different leaf economics spectrum, suggesting their divergent acclimation to the Karst environment.

Plant functional classifications based on leaf traits: In this study, DW and LA of the shade-tolerant type were 7.1 times and 4.9 times higher than those of the heliophyte type in evergreen shrub species, indicating that the shade-tolerant type in evergreen shrub species were outstanding in the ability to resist adverse environment (Fu *et al*., 2012) and capture sunlight (Lusk *et al*., 2008). The shade-tolerant type in evergreen shrub species were distributed in the lower layer of the community in Karst, with representative shade tolerance characteristics. In contrast, the heliophyte type in evergreen shrub species had low resistance to adverse environment, poor light harvesting ability (Montgomery, 2004), and were often distributed in the upper layer of the community, with considerable heliophilic characteristics. Similarly, DW and LA in the shade-tolerant type were higher than the heliophyte type by 8.9 times and 5.9 times in deciduous shrub species, indicating that the shade-tolerant type were outstanding in resisting adverse environment, such as water stress (Yin & Bauerle, 2017; Silva *et al*., 2018). Furthermore, the shade-tolerant type in deciduous shrub was usually distributed in bare ground or in pioneer shrub communities. Interestingly, only one species (*Alchornea trewioides*) for this type was found in Karst. Specifically, LA, DW, and LT in *Alchornea trewioides* were 3.4-16.5 times, 1.7-12.4 times, and 1.1-1.8 times higher than the other plant types, respectively. Thus, *Alchornea trewioides* performed strong resistance to external disturbance, and also showed the high capability for harvesting light in the Karst landscape.

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References

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(3): 449-457.

Athokpam, F.D., S.C. Garkoti and N. Borah. 2014. Periodicity of leaf growth and leaf dry mass changes in the evergreen and deciduous species of southern assam, india. *Ecol. Res*., 29(2): 153-165.

Blackman, C.J., S.M. Gleason, Y. Chang, A.M. Cook, C. Laws and M. Westoby. 2014. Leaf hydraulic vulnerability to drought is linked to site water availability across a broad range of species and climates. *Ann. Bot*., 114(3): 435-440.

Cadotte, M.W., K. Carscadden and N. Mirotchnick. 2011. Beyond species: Functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol*., 48(5): 1079-1087.

Chaturvedi, R.K., A.S. Raghubanshi and J.S. Singh. 2011. Plant functional traits with particular reference to tropical deciduous forests: a review. *J. Biosci*., 36(5): 963-981.

Domingues, T., A. Luiz and J.R. Ehleringer. 2007. Ecophysiological traits of plant functional groups in forest and pasture ecosystems from eastern amazctnia, brazil. *Plant. Ecol*., 193(1): 101-112.

Duru, M., R. Khaled, C. Ducourtieux, J.P. Theau, F. Quadros and P. Cruz. 2009. Do plant functional types based on leaf dry matter content allow characterizing native grass species and grasslands for herbage growth pattern? *Plant. Ecol*., 201(2): 421-433.

Dwyer, J.M. and R. Mason. 2018. Plant community responses to thinning in densely regenerating acacia harpophylla forest: Recruitment in woody regrowth after thinning. *Restor. Ecol*., 26(1): 97-105.

Eamus, D. 1999. Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. Trends. *Ecol. Evol*., 14(1): 11-16.

Ellsworth, D.S. and P.B. Reich. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia*., 96(2): 169-178.

Franco, A.C., M. Bustamante, L.S. Caldas, G. Goldstein, F.C. Meinzer, A.R. Kozovits, P. Rundel and V. Coradin. 2005. Leaf functional traits of neotropical savanna trees in relation to seasonal water deficit. *Trees*, 19(3): 326-335.

Fu, P., Y. Jiang, A. Wang, T. Brodribb, J. Zhang, S. Zhu and K. Cao. 2012. Stem hydraulic traits and leaf water-stress tolerance are co-ordinated with the leaf phenology of angiosperm trees in an asian tropical dry karst forest. *Ann. Bot*., 110(1): 189-199.

Guittar, J., D. Goldberg, K. Klanderud, R. Telford and V. Vandvik. 2016. Can trait patterns along gradients predict plant community responses to climate change? *Ecol*., 97(10): 2791-2801.

Hedin, L.O. 2007. Biological scaling: Does the exception prove the rule? (reply). *Nature*, 445(7127): E11.

Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, 98(3-4): 419-428.

Kloeke, A., J.C. Douma, J.C. Ordoñez, P.B. Reich and P.M. Bodegom. 2012. Global quantification of contrasting leaf life span strategies for deciduous and evergreen species in response to environmental conditions. *Global. Ecol. Biogeogr*., 21(2): 224-235.

Lavorel, S. and K. Grigulis. 2012. How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *J. Ecol*., 100(1): 128-140.

Lourens, P., B. Laurent and B. Frans. 2006. Architecture of 54 moist-forest tree species: Traits, trade-offs, and functional groups. *Ecol*., 87(5): 1289-1301.

Lusk, C.H., P.B. Reich, R.A. Montgomery, D.D. Ackerly and J. Cavender-Bares. 2008. Why are evergreen leaves so contrary about shade? Trends. *Ecol. Evol*., 23(6): 299-303.

Mcgill, B.J., B.J. Enquist, E. Weiher and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends. Ecol. Evol*., 21(4): 178-185.

Montgomery, R. 2004. Relative importance of photosynthetic physiology and biomass allocation for tree seedling growth across a broad light gradient. *Tree. Physiol*., 24(2): 155-167.

Niinemets, Ü. 2001. Global-scale climatic controls of leaf dry mass per area, density, andthickness in trees and shrubs. *Ecol*., 82(2): 453-469.

Ogaya, R. and J. Peñuelas. 2007. Tree growth, mortality, and above-ground biomass accumulation in a holm oak forest under a five-year experimental field drought. *Plant Ecol*., 189(2): 291-299.

Poorter, L. and K. Kitajima. 2007. Carbohydrate storage and light requirements of tropical moist and dry forest tree species. *Ecol*., 88(4): 1000-1011.

Powers, J.S. and P.Tiffin. 2010. Plant functional type classifications in tropical dry forests in Costa Rica: Leaf habit versus taxonomic approaches. *Funct. Ecol*., 24(4): 927-936.

Riva, E., R. Villar, I.M. Pérez-Ramos, J.L. Quero, L. Matías, L. Poorter and T. Marañón. 2018. Relationships between leaf mass per area and nutrient concentrations in 98 mediterranean woody species are determined by phylogeny, habitat and leaf habit. *Trees*, 32(2): 497-510.

Silva, J., A. Souza, A. Caliman, E. Voigt and J. Lichston. 2018. Weak whole-plant trait coordination in a seasonally dry south american stressful environment. *Ecol. Evol*., 8(1): 4-12.

Silva, J., M. Espirito-Santo and H. Morais. 2015. Leaf traits and herbivory on deciduous and evergreen trees in a tropical dry forest. *Basic. Appl. Ecol*., 16(3): 210-219.

Su, Y., Q. Tang, F. Mo and Y. Xue. 2017. Karst tiankengs as refugia for indigenous tree flora amidst a degraded landscape in southwestern China. *Sci. Rep*., 7(1): 1-10.

Villar, R. and J. Merino. 2001. Comparison of leaf construction costs in woody species with differing leaf life-spans in contrasting ecosystems. *New. Phytol*., 151(1): 213-226.

Violle, C., M.L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel and E. Garnier. 2007. Let the concept of trait be functional! *Oikos*., 116(5): 882-892.

Wang, C., J. Zhou, K. Jiang and J. Liu. 2017. Differences in leaf functional traits and allelopathic effects on seed germination and growth of lactuca sativa between red and green leaves of rhus typhina. *S. Afr. J. Bot*., 111: 17-22.

Wang, H., Y. Chen, W. Hu, L.J. Snider and Z. Zhou. 2019. Short-term soil-waterlogging contributes to cotton cross tolerance to chronic elevated temperature by regulating ROS metabolism in the subtending leaf. *Plant. Physiol. Bioch*., 139: 333-341.

Westoby, M. and I.J. Wright. 2006. Land-plant ecology on the basis of functional traits. *Trends. Ecol. Evol*., 21(5): 261-268.

Wright, I.J., P.B. Reich, J. Cornelissen, D.S. Falster, P.K. Groom, K. Hikosaka, W. Lee, C.H. Lusk, L. Niinemets, J. Oleksyn, N. Osada, H. Poorter, D.I. Warton and M. Westoby. 2005. Modulation of leaf economic traits and trait relationships by climate. *Global. Ecol. Biogeogr*., 14(5): 411-421.

Wright, I.J., P.B. Reich, M.Westoby, D.D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. Cornelissen, M. Diemer, J. Flexas and R. Villar. 2004. The worldwide leaf economics spectrum. *Nature*, 428(6985): 821-827.

Wyka, T., P. Karolewski, R. Żytkowiak, P. Chmielarz and J. Oleksyn. 2016. Whole-plant allocation to storage and defense in juveniles of related evergreen and deciduous shrub species. *Tree Physiol*., 36(5): 536-547.

Yin, J. and T. Bauerle. 2017. A global analysis of plant recovery performance from water stress. *Oikos*., 126(10): 1377-1388.

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