

Characteristics of Leaf Epidermis of 22 Liliaeae (Liliaceae) under Different Altitudes in China

Genshen Yin, Shuangshuang Zhang, Wenlei Cheng, Minghua Dong, Ye Chen*

School of Agriculture & Life Sciences, Kunming University, Kunming, China

Email: *chenyefls@163.com

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Abstract

In this study, 22 leaf samples of 22 Liliaeae species were collected in six Province at 90 - 3740 m to study the variations of leaf characteristics with altitude change. The Qualitative character of leaf epidermis and two stomatal indexes, viz. stomatal area (SA), stomatal index (SI), were analyzed in laboratory. The results show that: 1) the shape of the leaf epidermis cells and the pattern of the anticlinal walls provide some useful taxonomic information to distinguish the genus, however, none of the stable traits are exclusive to a genus; 2) there are significant or even very significant linear correlations between the two indexes and altitude, of which SA exhibit a negative correlation with altitude ($r^2 = 0.294$, $p = 0.009$), while SI exhibit a positive correlation with altitude ($r^2 = -0.254$, $p = 0.017$). As a result, the pattern of leaf cells and anticlinal walls is influenced by genetic factors, while the stomatal area and stomatal index are influenced by environmental factors. Members of the tribe Liliaeae have a relatively stable elevation range, which is related to their long-term adaptation to the local environment in the structure of their leaf epidermis.

Keywords

Liliaeae, Leaf Epidermis, Stomatal Area, Stomatal Index, Altitudes

1. Introduction

Leaves are critical for plant growth and are directly exposed to the air environment. Stomata are the pores on the surface of leaves, flanked by guard cells, that regulate the gas exchange between the internal plant tissues and the atmosphere, especially water vapor and CO₂ [1] [2]. In addition, stomatal characteristics have been shown to correlate with the environmental factors in their habitat. Their quantitative properties, such as stomatal size and stomatal density, are sensitive to changes in environmental factors such as temperature, CO₂ concentration, precipitation and light [3]. Since there is a clear linear correlation between envi-

ronmental factors and altitude, significant statistical relationships between stomatal characteristics and altitude have been documented in many species [4] [5] [6]. However, when research interest is focused on higher levels of taxonomy, such as genera, tribe, families, etc., it is not clear whether changes in stomatal characteristics between species also vary linearly with altitude.

Tribe Lilieae [7] [8], belonging to the family Liliaceae, contains four genera: *Lilium* L. (including *Nomocharis* Franch.), *Fritillaria* L., *Notholirion* Wallich ex Boissier and *Cardiocrinum* (Endlicher) Lindley. This tribe is the species-abundant taxonomic group with about 91 species in China (61 species in *Lilium*, 24 species in *Fritillaria*, three species in *Notholirion*, and three species in *Cardiocrinum*) [9]. Many species of this tribe have been cultivated worldwide for ornamental, and some species are used as folk medicine [10] [11]. For example, the bulbs of *Fritillaria cirrhosa* D. Don, *F. unibracteata* Hsiao et K. C. Hsia, *F. przewalskii* Maxim., *F. delavayi* Franch. are widely used as a traditional Chinese medicine named “Chuan bei mu” for the treatment of cough and chest congestion; *Lilium lancifolium* Thunb., *L. brownii* F.E. Brown and *L. pumilum* DC. are known as “Bai he”, which are used to soothe the nerves [10]. Numerous species of *Lilium*, *Fritillaria*, and *Cardiocrinum*, are commonly cultivated as potted plants or cut flowers for their bright color and fragrance [11].

Members of the tribe Lilieae grow in vastly different habitats in China. For example, the altitudinal distribution of tribe Lilieae members ranges from 0 m (*L. tsingtauense* Gilg, near sea level, in Shandong, China) to 5100 m (*F. afusca* Tur-rill, live in moist and gravelly places, in Southern Xizang, China) [9]. This tribe therefore represents an excellent system to study the relationship between leaf epidermis and environmental factors.

In this study, 22 Liliaceae species were collected from different localities in six provinces of China to explore whether there is a detectable altitude correlation in the dynamics of leaf stomatal characteristics. The aim of the present work is to answer a fundamental question: is the leaf stomatal affected by the elevation factor at the tribe level? In addition, the leaf epidermis characteristics, which currently contains the entire Tribe Lilieae, are poorly studied, thus this data also contributes to the taxonomy at the tribe level.

2. Materials and Methods

2.1. Plant Material

A total of 22 taxa belonging to the tribe Lilieae were studied (Table 1). Materials have been collected at different localities in the field except *F. anhuiensis* S. C. Chen & S. F. Yin (cultivated material). Plant samples were made into herbarium specimens, from which leaf study material was obtained. The vouchers of all the collections were deposited in the herbarium of Kunming University.

2.2. Indoor Sample Treatment

For leaf epidermis examination, mature, fully expanded leaf samples were obtained

Table 1. Spatial distribution of tribe Liliae samples.

Taxa	Voucher	Locality	Altitude (m)
<i>Cardiocrinum cathayanum</i>	ygs1206006	Liuyang, Hunan	950
<i>C. giganteum</i> var. <i>yunnanense</i>	ygs1010002	Malipo, Yunnan	1650
<i>Fritillaria anhuiensis</i>	ygs1209005	Jinzhai, Anhui	750
<i>F. crassicaulis</i>	ygs1107012	Lijiang, Yunnan	3740
<i>F. tortifolia</i>	ygs1106017	Yumin, Xinjiang	1400
<i>L. apertum</i>	ygs1007019	Gongshan, Yunnan	3400
<i>Lilium bakerianum</i> var. <i>delavayi</i>	ygs1107021	Xianggelila Yunnan	2600
<i>L. brownii</i>	ygs1108023	Zhaotong, Yunnan	1810
<i>L. duchartrei</i>	ygs1207001	Xianggelila Yunnan	2600
<i>L. leucanthum</i>	ygs1008002	Yichang, Hubei	670
<i>L. meleagrinum</i>	ygs1008002	Gongshan, Yunnan	3710
<i>L. nanum</i>	ygs1107022	Deqing, Yunnan	4350
<i>L. pardanthinum</i>	ygs1207007	Xianggelila Yunnan	3350
<i>L. primulinum</i> var. <i>burmanicum</i>	ygs1010009	Malipo, Yunnan	1660
<i>L. primulinum</i> var. <i>ochraceum</i>	ygs1008007	Fugong, Yunnan	2720
<i>L. sealyi</i>	ygs1008008	Lushui, Yunnan	3110
<i>L. sulphureum</i>	ygs1009009	Jianshui, Yunnan	1360
<i>L. taliense</i>	ygs1207002	Xianggelila Yunnan	2600
<i>L. tsingtauense</i>	yyj1105001	Qingdao, Shandong	90
<i>L. wenshanense</i>	ygs1104006	Xichou, Yunnan	1160
<i>Notholirion bulbuliferum</i>	ygs1207005	Xianggelila Yunnan	3670
<i>N. campanulatum</i>	ygs1207008	Xianggelila Yunnan	3350

from herbarium specimens. The Sample treatment includes four steps according to the method of Wang *et al.* [12]: 1) leaf blades were selected from each specimen, cut into $1 \times 1 \text{ cm}^2$ pieces, and place it into a 10 ml centrifuge tube; 2) after the addition of glacial acetic acid and 30% H_2O_2 , the mixture was heated at 60°C for 6 h in a water bath; 3) take out the samples and wash them clean, then separate the adaxial and abaxial epidermis under the stereomicroscope; 4) the separated epidermis were dyed using 1% safranin solution to make section with glycerin to mounted and then sealed with nail polish.

2.3. Microscopic Image and Data Acquisition

Include two steps: 1) microscope images were acquired with the LUMIX LX3-GK attached to a ZEISS Axioskop 20 microscope; 2) collect image data on computer using Adobe photoshop CC 2018 and ImageTool 2.0 software.

2.4. Measurement of Stomatal Traits

For the present analyzes, two indices [stomatal area (SA) and stomatal index (SI)] were utilized to describe stomatal quantitative characters. Stomatal shape is elliptic in all species examined. Therefore, their areas (in **Table 2**) can be conveniently calculated from the area formula of the ellipses. SI values were computed as in

$$SI = S / (E + S) \times 100\%, \quad (1)$$

where S = number of stomata per unit area, and E = number of epidermal cells per same unit area. Stomatal terminology was based on that proposed by Dilcher [13], while the classification of pavement cells was based on the work of Wang and Tao [14].

Table 2. Summary of selected leaf epidermal features in tribe Lilieae taxa.

Taxa	SA (μm^2)	SI (100%)	Adaxial epidermis		Abaxial epidermis	
			Shape of cells	Pattern of anticlinal walls	Shape of cells	Pattern of anticlinal walls
<i>Cardiocrinum cathayanum</i>	2886.23	62.61	Irregular	Deep sinuous	Irregular	Deep sinuous
<i>C. giganteum</i> var. <i>yunnanense</i>	2887.55	66.02	Irregular	Deep sinuous	Irregular	Deep sinuous
<i>Fritillaria anhuiensis</i>	1634.34	68.57	Linear	Straight	Linear	Straight
<i>F. crassicaulis</i>	3601.14	65.74	Linear	Straight	Linear	Straight
<i>F. tortifolia</i>	2504.05	69.77	Linear	Straight	Irregular	Sinuolate
<i>L. apertum</i>	3401.53	64.94	Irregular	Sinuuous	Irregular	Sinuuous
<i>Lilium bakerianum</i> var. <i>delavayi</i>	3454.68	65.01	Polygonal	Arched	Irregular	Arched
<i>L. brownii</i>	2608.17	67.05	Irregular	Sinuolate	Irregular	Sinuolate
<i>L. duchartrei</i>	2605.53	65.28	Irregular	Sinuolate	Irregular	Sinuolate
<i>L. leucanthum</i>	2756.52	67.98	Irregular	Sinuuous	Irregular	Sinuuous
<i>L. meleagrinum</i>	3003.21	63.18	Irregular	Microsinuous	Irregular	Sinuuous
<i>L. nanum</i>	3303.31	62.41	Polygonal	Straight	Irregular	Straight
<i>L. pardanthinum</i>	3294.48	68.73	Irregular	Sinuuous	Irregular	Sinuuous
<i>L. primulinum</i> var. <i>burmanicum</i>	4388.73	65.56	Irregular	Deep Sinuous	Irregular	Deep Sinuous
<i>L. primulinum</i> var. <i>ochraceum</i>	4298.25	65.80	Irregular	Deep Sinuous	Irregular	Deep Sinuous
<i>L. sealyi</i>	3931.82	66.31	Polygonal	Straight	Irregular	Sinuuous
<i>L. sulphureum</i>	2820.76	65.42	Polygonal	Straight	Irregular	Straight
<i>L. taliense</i>	2922.59	64.47	Irregular	Sinuuous	Irregular	Sinuuous
<i>L. tsingtauense</i>	2414.38	67.09	Irregular	Sinuuous	Irregular	Sinuuous
<i>L. wenshanense</i>	3551.88	65.14	Polygonal	Straight	Irregular	Sinuuous
<i>Notholirion bulbuliferum</i>	4092.67	68.37	Linear	Straight	Linear	Straight
<i>N. campanulatum</i>	4512.38	70.48	Linear	Straight	Linear	Straight

2.5. Statistical Analysis

Analysis of variance (ANOVA) followed by the least significant difference test (LSD) was performed on stomatal traits to indicate any significant difference among the taxa studied. The correlations of two stomatal indices (SA and SI) and altitude were disposed of by Bivariate Correlations Analysis. Pearson's coefficient of correlation was determined to assess the correlations between the different indices. Only correlations significant at the 1% level or higher are discussed. Statistical and plot analyzes were performed using the software SPSS 27 and Origin 2022, respectively.

3. Results

A summary of the micromorphological characteristics of the leaf epidermis is given in **Table 2**, and depicted in **Figure 1**, and **Figure 2**. The pavement cell properties of 22 species were described. Two stomatal indices, SA and SI, for 22 species were used for linear regression with increasing altitude, respectively.

3.1. Qualitative Character of Leaf Epidermis

The pavement cells of the tribe Liliae as seen under light microscope are linear, polygonal or irregular in form (**Figure 1**, **Figure 2**, and **Table 2**). It is interesting that the shape of cells in the upper and lower epidermis in most taxa is uniform except five taxa. These taxa are *Fritillaria tortifolia*, *Lilium bakerianum* var. *delavayi*, *L. nanum* var. *nanum*, *L. sulphureum*, *L. wenshanense*, and *L. sealyi*. In general, both in *Notholirion* and *Fritillaria*, the shape of the pavement cells is linearly specific, and in *Cardiocrinum* the epidermal cells are irregular in shape. While *Lilium* taxa possessed both polygonal or irregular form, it is dependent on species.

The pattern of anticlinal walls separates the 22 taxa into two groups. Group one comprises genus *Fritillaria*, *Notholirion*, and some taxa of *Lilium*, namely *L. bakerianum* var. *delavayi*, *L. nanum* var. *nanum*, and *L. sulphureum*, have straight anticlinal cell walls (**Figure 1**, **Figure 2**, and **Table 2**), while the second group comprising genus *Cardiocrinum* and the rest taxa of *Lilium*, have microsinuous to deep sinuous anticlinal cell walls (**Figure 1**, **Figure 2**, and **Table 2**).

Only one species, namely *F. tortifolia*, possessed trichomes on the abaxial surfaces (**Figure 2**), while the other species lacked epidermal hairs. Additionally, this species is hypostomatic (stomata on the abaxial surface only).

3.2. Quantitative Character of SA and SI

ANOVA indicated that the differences between SI of different genus were indistinctive, except *Lilium* and *Fritillaria* ($p = 0.048$). As for SA, there is not any distinction between *Lilium* and *Cardiocrinum*, *Lilium* and *Fritillaria*, *Cardiocrinum* and *Fritillaria*. However, the “ p -value” of the difference between *Fritillaria* and *Notholirion* is 0.008, which is significant. While the difference between *Lilium* and *Notholirion* ($p = 0.040$), *Cardiocrinum* and *Notholirion* ($p = 0.038$) is least

significant.

3.3. Relationship between Stomatal Traits and Altitude

As the leaf epidermis traits were different between taxa, we analyzed the relationships between the leaf epidermis traits and altitude separately. SA increased with elevation. There was a good positive correlation between altitude and SA

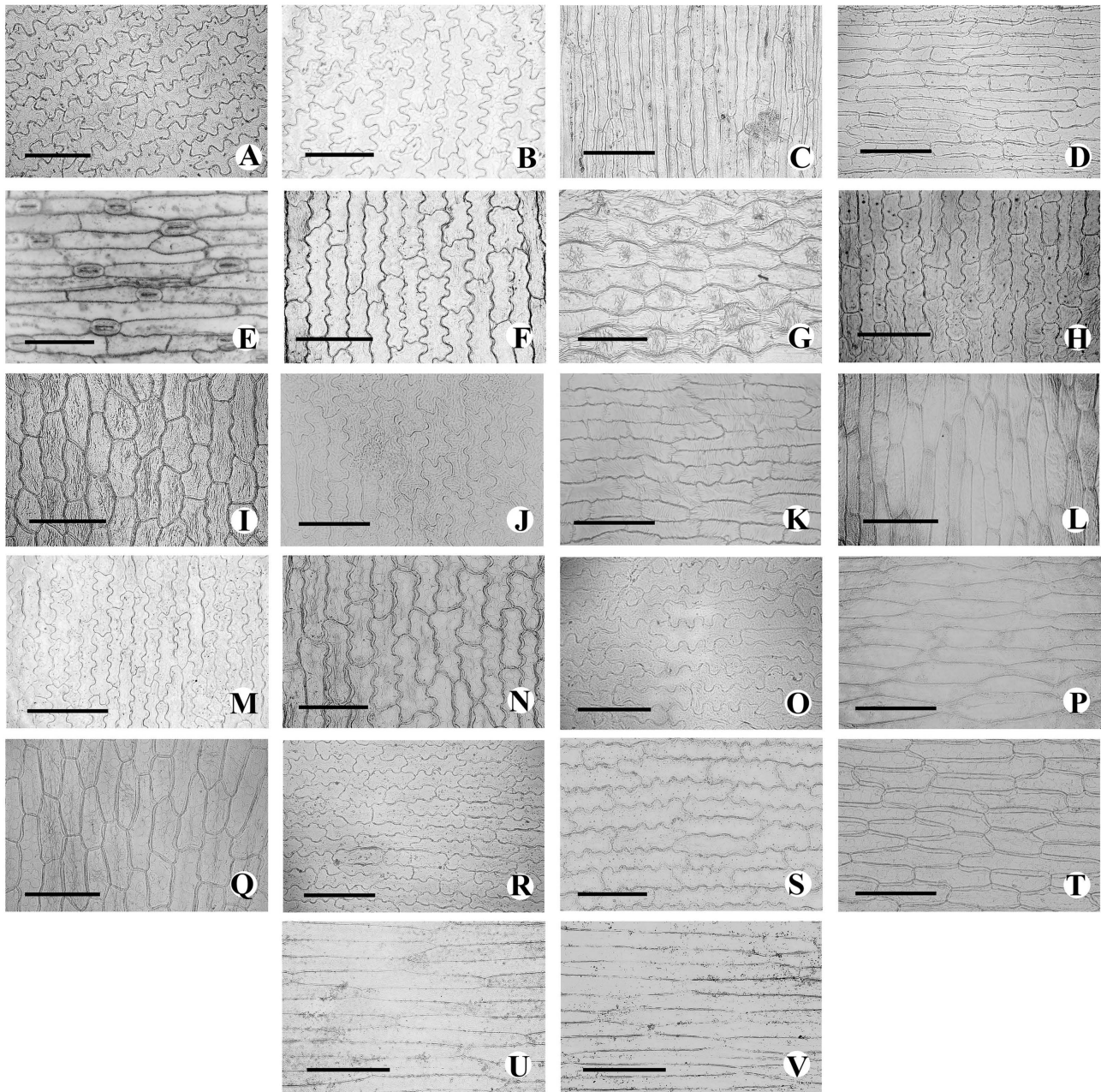


Figure 1. Micromorphological characteristics of the adaxial leaf surfaces. (A) *Cardiocrinum cathayanum*; (B) *C. giganteum* var. *yunnanense*; (C) *Fritillaria anhuiensis*; (D) *F. crassicaulis*; (E) *F. tortifolia*; (F) *Lilium apertum*; (G) *L. bakerianum* var. *delavayi*; (H) *L. brownii*; (I) *L. duchartrei*; (J) *L. leucanthum*; (K) *L. meleagrinum*; (L) *L. nanum*; (M) *L. pardanthinum*; (N) *L. primulinum* var. *burmanicum*; (O) *L. primulinum* var. *ochraceum*; (P) *L. sealyi*; (Q) *L. sulphureum*; (R) *L. taliense*; (S) *L. tsingtauense*; (T) *L. wenshanense*; (U) *Notholirion bulbuliferum*; (V) *N. campanulatum*. Scale bars = 100 μ m.

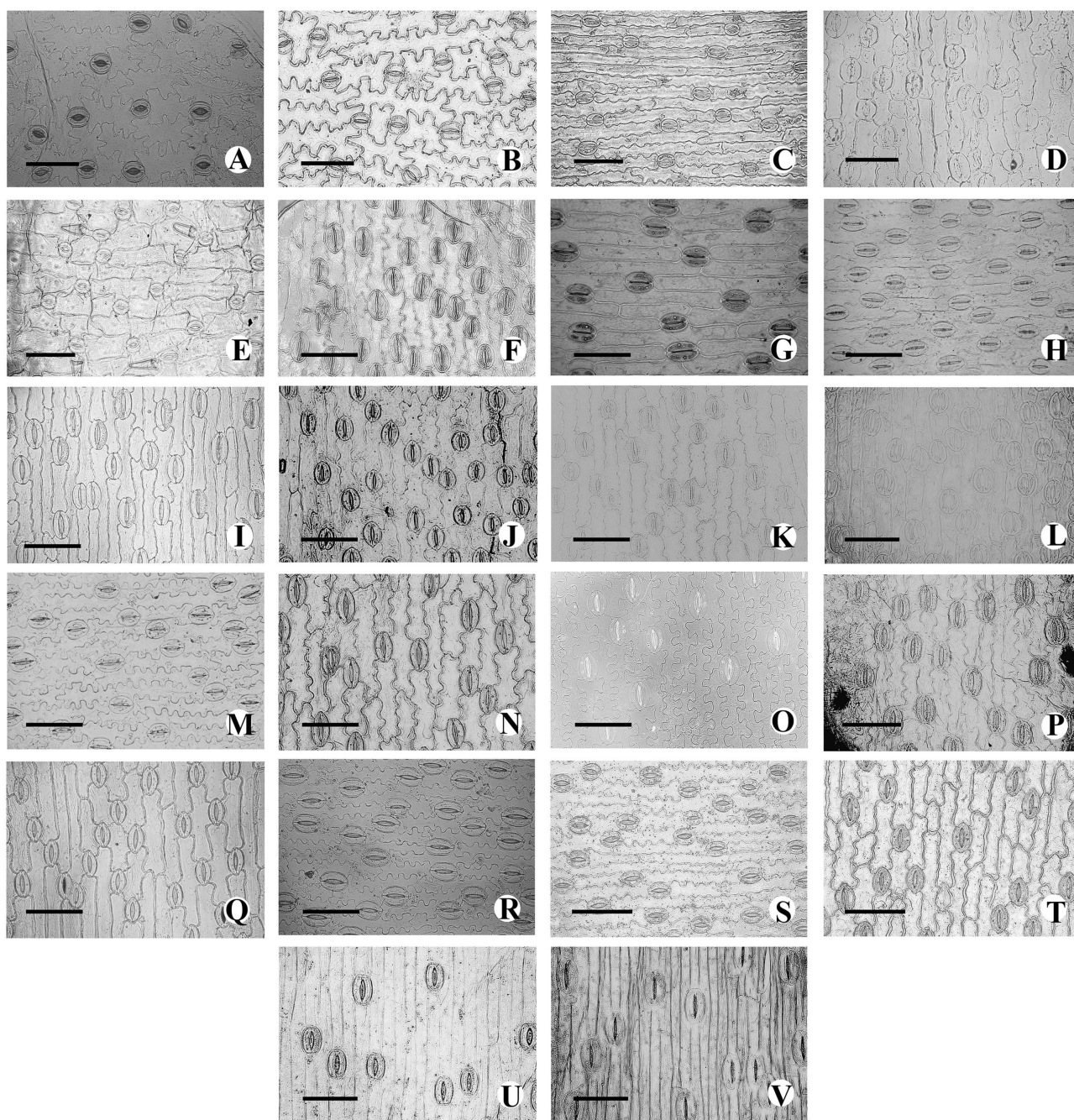


Figure 2. Micromorphological characteristics of the abaxial leaf surfaces. (A) *Cardiocrinum cathayanum*; (B) *C. giganteum* var. *yunnanense*; (C) *Fritillaria anhuiensis*; (D) *F. crassicaulis*; (E) *F. tortifolia*; (F) *Lilium apertum*; (G) *L. bakerianum* var. *delavayi*; (H) *L. brownii*; (I) *L. duchartrei*; (J) *L. leucanthum*; (K) *L. meleagrinum*; (L) *L. nanum*; (M) *L. pardanthinum*; (N) *L. primulinum* var. *burmanicum*; (O) *L. primulinum* var. *ochraceum*; (P) *L. sealyi*; (Q) *L. sulphureum*; (R) *L. taliense*; (S) *L. tsingtauense*; (T) *L. wenshanense*; (U) *Notholirion bulbuliferum*; (V) *N. campanulatum*. Scale bars = 100 μ m.

across Liliaceae ($r^2 = 0.294$, $p = 0.009$, **Figure 3(A)**), indicating that increases in altitude were generally accompanied by increasing stomatal area.

SI tended to decrease with increasing elevation. SI was inversely related to the altitude ($r^2 = -0.254$, $p = 0.017$, **Figure 3(B)**), indicating that increases in altitude were generally accompanied by decreasing stomatal number.

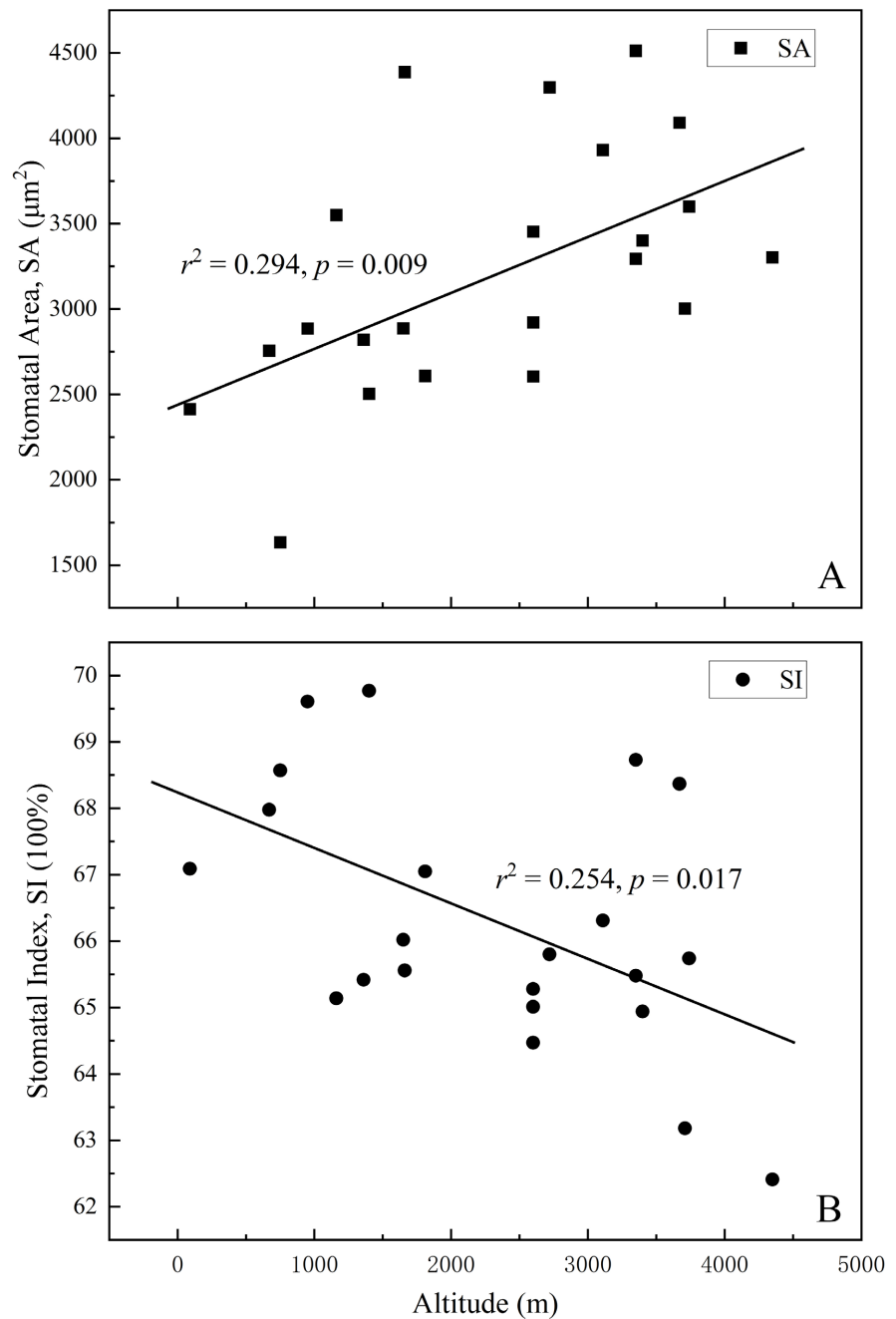


Figure 3. The relationships between stomatal traits and altitude.

4. Discussion

Taxonomic Implications of Leaf Epidermal Features

Given that the quantitative stomatal characters play only a minor role in delimiting genera, it is plausible to assume that they seem influenced mainly by environmental rather than genetic. For example, ANOVA shows that SI can distinguish only *Lilium* and *Fritillaria* ($p = 0.048$). Similarly, SA was slightly useful to delimit generic circumscriptions between *Fritillaria* and *Notholirion* ($p = 0.008$), *Lilium* and *Notholirion* ($p = 0.040$), *Cardiocrinum* and *Notholirion* ($p = 0.038$).

Contrary to the quantitative stomatal characters, the shape of the epidermal cells and the pattern of the anticlinal walls provide some useful taxonomic information to distinguish the genus. For example, *C. cathayanum* and *C. giganteum* var. *yunnanense* are very close to each other in phylogenetics but live in the different habitat characteristics (Table 1). However, there are few differences between these two taxa for epidermis character (Table 1, Table 2; Figure 2(A), Figure 2(B); Figure 3(A), Figure 3(B)). An equivalent situation has been found in *L. primulinum* var. *burmanicum* and *L. primulinum* var. *ochraceum* (Table 1, Table 2; Figure 2(L), Figure 2(M); Figure 3(N), Figure 3(O)).

In general, both in *Notholirion* and *Fritillaria*, the shape of the epidermal cells is linearly specific, while *Lilium* taxa possess either a polygonal or irregular form. The morphogenesis of lobed plant cells has been considered to controlled by microtubule and/or actin filament organization [15], indicating the shape of epidermis is correlated with genetic factors.

Some variation has been found between different species, and it has been observed that each species has its own unique combination of features that set them apart from each other. As a result, leaf epidermal features provide some taxonomic information at the species level. However, none of the stable traits are unique to a genus. Consequently, the epidermal characters of the leaves can only play a very minor role in defining the genus.

Among leaf morphological characters, trichomes are one of the most important traits contributing to plant's passive resistance to pathogens, pests and drought [16]. In the sampled species, only *F. tortifolia*, possessed trichomes on the abaxial surfaces (Figure 3). In fact, the species was collected from the wild in Yumin County, Xinjiang, and without being stressed by pests and diseases. Xinjiang is one of China's major drought-prone regions, especially in Yumin County. The annual average rainfall in Yumin County is 304.1 mm [17], which is far less than the other location of the present study.

Stomatal variability is mainly caused by environmental factors such as radiation, humidity, temperature, etc. [3]. As altitude increases, environmental factors increase or decrease [18]. However, the environmental factors in this study do not change linearly, but temperature. Theoretically, as temperature drops, water stress exacerbates. The drop in temperature may lead to physiological drought of plants [12]. Plants respond to drought stress by activating hormonal and genetic mechanisms that reduce the number of stomata [19]. This may be the reason for the negative correlation between SI and altitude changes in the present study ($r^2 = -0.254$, $p = 0.017$, Figure 3(B)).

As air temperature continuously drops and plant physiological drought strengthens, water conservation to resist drought becomes the first essential problem to maintain the survival of plants [20]. Through regulating stomatal development and opening-closing movement, plants adapt to the environment and compensate for the insufficient water caused by low-temperature physiological drought [12]. In this study, an analysis of the relationship between altitude and SA showed these two parameters were positively correlated ($r^2 = 0.294$, $p = 0.009$, Figure

3(A)), indicating that increases in altitude were generally accompanied by increasing stomatal area. Generally, there is a clear negative relationship between the size of the stomatal pore and sensitivity to increasing drought [21]. As a result, species at higher altitudes may become less sensitive to physiological drought through stomatal enlargement.

Stomatal traits are interrelated and act together and should not be viewed in isolation. Plants regulate the allocation of energy within the plant through a trade-off between traits to improve plant adaptability. Therefore, the adaptation of plants to the environment is the common adaptation of multiple traits [4].

5. Conclusions

Thus, the pattern of leaf epidermal cells and anticlinal walls provides some useful taxonomic information to distinguish species. However, none of the stable traits are exclusive to a genus. Consequently, the epidermal characters of the leaves can only play a very minor role in distinguishing the genus in tribe Liliae.

The results of the present study confirmed that variations in the SA and SI of 22 species belong to tribe Liliae at different locations showed a clear correlation with altitude. From a plant physiological point of view, this linear change in stomata may be related to adaptation to the physiological drought induced by temperature drops.

As a result, the pattern of leaf cells and anticlinal walls is influenced by genetic factors, while the stomatal area and stomatal index are influenced by environmental factors. Members of the tribe Liliae have a relatively stable elevation range, which is related to their long-term adaptation to the local environment in the structure of their leaf epidermis.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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