

Environmental adaptability of the genus *Carex*-A case study of *Carex heterostachya* and *Carex breviculmis* in northwest China

Xiaoqi Wang

North West Agriculture and Forestry University

Yuhan Feng

North West Agriculture and Forestry University

Xuwei Feng

North West Agriculture and Forestry University

Wanting Liu

North West Agriculture and Forestry University

Jinguo Hua

North West Agriculture and Forestry University

Fei Xie

North West Agriculture and Forestry University

Wenli Ji (✉ jiwenli@nwsuaf.edu.cn)

North West Agriculture and Forestry University

Research Article

Keywords: *Carex*, photosynthesis, leaf structural traits, leaf anatomical traits

Posted Date: August 24th, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1982084/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at *Plant Ecology* on June 17th, 2023. See the published version at <https://doi.org/10.1007/s11258-023-01328-y>.

Abstract

Carex heterostachya (CH) and *Carex breviculmis* (CB) are easy to develop lawns in a short period and exhibit high ornamental value in northwest China with high summer temperatures, uneven rainfall, and poor soil. Several questions are raised, including what type of plant functional traits has they formed for long-term survival and adaptation to this environment, which plant is more adaptable, as well as which leaf functional traits are critical to photosynthetic characteristics. After exploring the leaf functional traits of the two plants by gas exchange technology and field emission electron scanning technology, the following conclusions are drawn: (a) CB is a slow investment-return plant, which exhibits strong environmental adaptability and plasticity, and is resistant to barrenness, drought and shade. CH is a kind of quick investment-return plant, with high photosynthetic efficiency, well-developed transport tissue, and relatively shade-tolerant. The soil with low water content and poorer soil is suitable for CB cultivation, and CH is suitable for cultivation in the environment with sufficient light and rich nutrients. At the same time, both CB and CH can be used to enrich the diversity of understory landscape. (b) *Carex* have strong environmental adaptability, large variation in leaf structure traits, as well as strong plasticity. Leaf anatomical characters are stable, whereas there are differences in the interspecific variability and plasticity. (c) Specific leaf area (SLA) can serve as the main factor affecting the photosynthetic availability of *Carex*, the thickness of the stratum corneum(CUT), the thickness of the upper(UET) are secondary factors. These finding can provide a theoretical basis for the cultivation and application of *Carex* and the expansion of turfgrass germplasm resources.

1 Introduction

The genus *Carex* is characterized by its wide distribution and considerable number of species(Schütz 2000). It is the largest genus of the Cyperaceae family, with nearly 2,000 species worldwide. If it can be developed and utilized scientifically, the diversity of turfgrass species can significantly increase, such that people's needs for turfgrass can be met to a certain extent. CB and CH are common plants of the genus *Carex*. We have suggested that they are easy to develop lawns in a short period and exhibit high ornamental value. They can still grow well in the shade of forests. In the future, the focus should be placed on their high development and utilization value in landscape applications. Existing research has suggested that CH is distributed in northeast China and Hebei, Shanxi, Shandong, Henan, Shaanxi Provinces of China, as well as Russia and the Far East (Zhang et al. 1995). CB is extensively distributed in Inner Mongolia and northeast China. Moreover, it is also distributed in the former Soviet Union, Mongolia, Japan, as well as Southeast Asian countries (Xiao et al. 1995). It is therefore revealed that the two *Carex* species have a wide range of environmental adaptability. A question is raised that whether this environmental adaptability can be accounted for by leaf functional traits and photosynthetic characteristics. With CH and CB introduced into college campuses in northwest China as the examples, several questions are raised, including what type of plant functional traits has the *Carex* species formed for long-term survival and adaptation to this environment. which plant is more adaptable, what are the correlations between individual leaf functional traits, as well as how photosynthesis works.

The existing research on *Carex* (Cyperaceae) has been primarily limited to plant phylogeny (Oda et al. 2019), classification (Group et al. 2021), seed germination (Kettenring & Galatowitsch 2007; Kettenring et al. 2006), as well as mycorrhizal status of the genus *Carex* (Miller et al. 1999). There has been rare research on the environmental adaptability and survival adaptation strategies related to the genus *Carex*. In the long-term evolution and development, plants interact with the environment to form plant functional traits, so as to adapt to changes in the external environment (Maza-Villalobos et al. 2022). For instance, the relatively stable leaf structure traits are capable of indicating the maximization of carbon harvest (Correa et al. 2018; Taylor et al. 2012). The leaf thickness will increase significantly at the extremely high CO₂ concentration in the environment (Teng et al. 2006; Think et al. 2018). The leaf physiological traits-Photosynthesis has been found as the physiological basis for plant growth and development (Evans 2013). Leaf anatomical features can indicate plant stress resistance (Chen et al. 2016), which includes drought resistance. Besides, the plasticity and variability of their structural and anatomical traits can be obtained, thus well indicating the adaptation strategies of plants in a variety of ecological environments. Plants with high coefficient of variation and plasticity index exhibit a higher sensitivity to the environment potential adaptability (Valladares et al. 2000).

Existing research has suggested that leaf functional traits and photosynthesis are coordinated with each other for a long period (Nam et al. 2017; Wright et al. 2004). Exploring the correlation between leaf functional traits and photosynthetic characteristics can provide more insights into the adaptability of plants to the environment (Ali et al. 2016; Tribouillois et al. 2015). Tholen et al. (2012) investigated the factors for plant photosynthetic capacity according to the anatomical structure of leaves. They have suggested that plants with thick or dense leaves show certain advantages under strong light, and mesophyll cells output photosynthetic products more efficiently with the increase of the leaf vein density, thus facilitating more efficient production of photosynthetic products. Dong et al. (2022) investigated the reference indicators for screening high-light-efficiency germplasms of the genus *Herperis*. They highlighted that the ratio of palisade tissue to sponge tissue can serve as a vital reference indicator for screening high-light-efficiency germplasm resources of this genus. Using the above method, Li and Tian (2022) investigated the correlation between leaf morphology and photosynthetic physiological characteristics exhibited by six garden plants in Lanzhou City. It is preferred that the dry matter content of emerging leaves is the explanatory variable with the most significant effect on the photosynthetic characteristics. The research on the evaluation index of light efficiency or the main driving factor of plant ecological adaptation and resource acquisition of *Carex* species is relatively limited for the genus *Carex*. There is no significance difference between the palisade tissue and the sponge tissue in the *Carex* species, such that a question is raised that whether their leaf anatomical character is correlated with photosynthetic properties. Accordingly, correlation analysis and redundancy analysis were used to explore the internal relationship between photosynthetic characteristics and leaf functional traits, to clarify plant growth strategies and explain the physiological and ecological responses of plants in heterogeneous environments. It lays a theoretical basis for screening grass species with the potential to be ideal turfgrass in the future.

2 Materials And Methods

2.1 Plant Materials and growth condition

In 2000, the plant seeds were purchased from a seedling company in Shandong Province, China, and were sown on the campus of Northwest Agriculture and Forestry University Yangling demonstration area, Shaanxi Province(108°5'18"E, 34°5'4"N) in the same period. After two *Carex* species have grown in the shade for years, they naturally formed a lawn with high ornamental value, thus playing a role in beautifying the campus environment (Fig. 1)(Table 1). The optimal growing season was selected for plants in summer (end of July) for this experiment

Table 1
Growth of CH and CB

Index	CH	CB
turfgrass height(cm)	26.507	15.750
turfgrass density(plant/cm ⁻²)	1.2	1
ground over age(%)	98	95
length of leaves(cm)	60.160	26.283
width of leaves(cm)	0.3	0.2
leaf index	238.630	68.259

The introduction site is characterized by a temperate continental monsoon climate. The annual precipitation is 635.1mm, Average evaporation 993.2 mm, the annual average temperature is 12.9°C, the annual average sunshine hours are 2163.8h, and the annual accumulated temperature $\geq 10^{\circ}\text{C}$ is 4184°C. The distribution of precipitation in summer (June to August) is extremely uneven, often accompanied by summer drought and sub-drought. In early summer, it is often dry and less rainy, with more than 5 strong winds. Hot and high temperature, the average temperature is higher than 25 °C, and the extreme maximum temperature can reach 42 °C. Furthermore, the soil of the introduction land is poor, and the contents of organic matter, nitrogen and available phosphorus are low(0.06–0.1%)(Dou et al. 2015).

2.2 Diurnal variation of photosynthetic parameters

Photosynthetic Diurnal variation parameters were developed using a LI-6400XT portable photosynthesis measurement system, and the light source was natural sunlight. The middle position of the leaves was measured, and the following contents were examined every 2h from 8:00 to 18:00, including net photosynthetic rate (Pn), transpiration rate (Tmmol), stomatal conductance (Gs), air CO₂ concentration (Ca), intercellular CO₂ concentration (Ci), air temperature(Ta), relative humidity(RH) and photosynthetically active radiation (PAR). One plant was repeated four times. The following calculation

was conducted after the measurement: light use efficiency (LUE) = P_n/PAR , water use efficiency (WUE) = P_n/Tr , Stomatal limitation(L_s)= $(C_a-C_i)/C_a$.

2.3 Photosynthetic light–Response Curves Measurements

LI-6400XT portable photosynthesis system (Li-Cor Inc., Lincoln, Nebraska, USA) with a red–blue LED light source (6400-02B), in 9:00–11:00, setting PAR of 1200, 1000, 800, 600, 500, 400, 300, 200, 150, 100, 50, 20, 0 $\mu\text{mol}/\text{m}^2/\text{s}$, the CO_2 injection system setting value was 400 $\mu\text{mol}/\text{mol}$, and the flow rate was 500 $\mu\text{mol}/\text{s}$.

The light–response curves were fitted using a modified Right-Angle Hyperbolic Model(Ye 2007; Ye & Yu 2008), The fitting model formula was as Eq. (1). After fitting and calculation, the light saturation point (LSP), light compensation point (LCP), apparent quantum efficiency (α), maximum net photosynthetic rate ($P_{n\text{max}}$), and dark breathing rate (R_d) of the two types of plants can be obtained.

$$P_n I = \alpha \frac{1 - \beta I}{1 + \gamma I} I - R_d$$

1

Where I denotes the photosynthetically active radiation; β and γ represent coefficients

2.4 CO_2 –Response Curves Measurements

When the photosynthetic CO_2 response was performed, the generated reaction substrate had a certain hysteresis. Thus, the CO_2 concentration controlled by the instrument is first reduced from the atmospheric concentration (nearly 400 $\mu\text{mol}/\text{mol}$) to 50 $\mu\text{mol}/\text{mol}$ during the observation. The CO_2 concentration of the sample chamber is 400, 300, 200, 150, 100, 50, 400, 400, 600, 800, 1000, 1200, 1500 $\mu\text{mol}/\text{mol}$. Photosynthetically active radiation was set to 600 $\mu\text{mol}/\text{mol}$.

The light–response curves were fitted using a modified Right-Angle Hyperbolic Model(Ye & Yu 2009). The fitting model formula was as Eq. (2). After fitting and calculation, the CO_2 saturation point (CSP), CO_2 compensation point (CCP), initial carboxylation rate (η), photorespiration rate (R_p) and maximum net photosynthetic rate ($P_{n\text{max}}$) can be calculated. The maximum carboxylation rate and maximum electron conductivity of the two plants were calculated using the fitaci function.

$$P_n C_a = \eta \frac{1 - \beta C_a}{1 + \gamma C_a} C_a - R_p$$

2

Where β and γ represent coefficients

2.5 Leaf functional traits measurements

Physiological characters: Using the third leaf at the top of each plant, the plants were determined for leaf area(LA), leaf thickness(LT), leaf saturated fresh weight(LSFW), Leaf fresh weight (LFW), and leaf dry weight(LDW) Collected 3 leaves of each plant species for 4 replicates, and calculate after measurement: Specific leaf area(SLA) = LA/LDW, Leaf dry matter content(LDMC) = LDW/LSFW, Leaf relative water content(LRWC)=(LFW-LDW)/(LSFW-LDW), Leaf tissue density(LTD) = LDW/(LT*LA).

Anatomical characters: The complete leaves of each plant growing in the sun were selected, and the leaf tissue near the middle or lower position was cut. First, the cut tissue blocks were quickly put into 4% glutaraldehyde at 4°C overnight for more than 12 h. Then rinsed and dehydrated with PBS buffer solution and different concentration gradients (30%, 50%, 70%, 80%, 90%, 100%) of ethanol. The samples were dried with a critical point dryer (EMCPD300), sprayed with gold by a sputter coater (Q150TS), and lastly magnified to 300 times with a field emission scanning electron microscope (Nano SEM-450) for observation and photography. Lastly, the high of siliceous papillosethe, the thickness of the stratum corneum(CUT), the thickness of the upper(UET) and lower epidermal cells (LET), thickness of the main vein(MVT), the vessel area (VA), main vessel vascular bundle structure area(VBA), vessel area/vascular bundle area(VA/VBA), the number of vesicle cells(BC) were calculated. 3–5 leaves of the respective plant species were collected for four replicates.

Coefficient of Variation(CV) = SD/mean*100%, Plasticity index(PI)=(MAX-MIN)/MAX.

2.6 Statistical analyses

Photosynthetic parameters were calculated in the Zipao Ye photosynthetic calculation model software 4.1.1. The data were analyzed using one-way analysis of variance using SPSS 26. The correlation was analyzed through Pearson and redundancy analysis. Before the RDA analysis, detrended correspondence analysis (DCA) was conducted on the leaf photosynthetic parameters. The results indicated that the maximum gradient length was 0.4, less than 3. Accordingly, the linear response model and Canoco 5.0 software were used for RDA analysis. Plotted in Origin 2019. Data in the graph are expressed as the mean ± SD.

3 Result

3.1 Photosynthetic Characteristics of two *Carex* species

3.1.1 Diurnal variation of photosynthetic parameters

With the increase of PAR, Ta and the decrease of RH(Fig. 2), Ca, Pn, Gs, Trmmol of the two plants tended to increase, while Ci tended to decrease. LUE peaked twice in one day. Both CH and CB reached the maximum Pn at 12:00, but the maximum Pn, Trmmol, Gs, Ci of CH were significantly higher than CB ($p < 0.01$). The Trmmol peak of CH appeared at 10:00, which was earlier and significantly higher than CB($p < 0.01$). The LUE peak of CH appeared at 12:00, later than CB. Under the high temperature and strong PAR environment, the LUE of CH also was significantly higher than that of CB ($P < 0.01$). The diurnal course of

CB's WUE was bimodal, whereas that of CH was unimodal. WUE of CB exhibited a significant "photosynthetic noon break" phenomenon at 12:00, correlated with the increase of T_a , the increase of Trmmol and the lower WUE. In general, the WUE of CB was significantly higher ($P < 0.01$) than that of CH (Fig. 3).

3.1.2 Light response curve parameters, CO₂ response curve parameters

The changes of the light response curves of YS and QL are similar (Fig. 4). When the photosynthetically active radiation value was nearly 0-600 $\mu\text{mol}\cdot\text{m}^2\cdot\text{s}$, both showed an approximate linear increase, and the net photosynthetic rate increased with the increase of PAR. When the light saturation point was approached, the photosynthetically active radiation reached 600–1200 $\mu\text{mol}\cdot\text{m}^2\cdot\text{s}$, and the light response curve tended to be flat, thus showing a certain saturation phenomenon.

The change rules of the CO₂ response curves of YS and QL are similar (Fig. 4). When the carbon dioxide concentration was nearly 0-1000 $\mu\text{mol}\cdot\text{mol}$, both achieved an approximate linear increase, and the net photosynthetic rate increased with the increase of the carbon dioxide concentration; near the CO₂ saturation at the carbon dioxide concentration of 1000–1500 $\mu\text{mol}\cdot\text{mol}$, the carbon dioxide response curve tended to be flat, thus showing a certain saturation phenomenon.

As can be seen in Table. 2 that there was no significant difference in the α and R_d between CH and CB ($P > 0.05$), and LCP, LSP. P_{max} of CB are significantly higher than CH ($P < 0.05$). The CCP and R_p of CH were significantly higher than CB ($P < 0.05$), and there was no significant difference in η , A_{max} , CSP, and J_{max} between the two plants ($P > 0.05$). The V_{cmax} of CB was significantly higher than CH ($P < 0.01$).

3.2 Physiological characters and Anatomical characters

As depicted in Table. 3, Fig. 5 and Fig. 6, the LT, LA and SLA of CH were significantly larger than those of CB ($P < 0.01$). The LRWC and LDWC of CB were significantly higher than CH ($P < 0.05$). LTD of CB was significantly higher than CH ($P < 0.01$). The anatomical structure of the leaves was roughly "V"-shaped in cross section, comprising epidermal cells, mesophyll cells and leaf veins. There were huge air cavities between them, which can help plants reduce the damage to cells caused by flooding in a water-wet and anoxic environment (Sun et al. 2020). Moreover, and there were major vascular bundles with large area in the main vein, and there were also many others distributed in the mesophyll. The vascular bundle structure distributes mechanical tissues up and down. It can be seen from the Table 2 that: (1) epidermal characteristics exhibited by leaves: CUT of CB was significantly larger than CH ($P < 0.01$), which was 1.8 times of CH, and CH had sp with a height of 18.175 μm , while CB does not; UET of CB was significantly larger than that of CH ($P < 0.01$). (2) Conducting tissue characteristics: The VBA of CH was significantly larger than CB ($P < 0.05$); VA of CH was significantly larger than that of CB ($P < 0.01$), which was 2.2 times that of CB; VA/VBA of CH was extremely significant greater than CB ($P < 0.01$) was 1.6 times that of CB; (3) Stress-resistant structure: there were larger vesicular cells at the main veins of CH and CB, The number

of vesicular cells in CB was significantly higher than that in CH ($P < 0.01$). The number was 2 times the difference.

Table 2
Light response curve parameters, CO₂ response curve parameters

Spiece		CH	CB
Photoresponse parameters	α	0.084 ± 0.059 aA	0.090 ± 0.007 aA
	Pmax($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	8.736 ± 0.308 bA	9.178 ± 0.150 aA
	LSP($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	670.792 ± 18.485 bA	812.367 ± 25.392 aA
	LCP($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	9.163 ± 2.174 bA	10.163 ± 3.453 aA
	Rd ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.690 ± 0.281 aA	0.752 ± 0.089 aA
CO ₂ Response Parameters	η	0.039 ± 0.004aA	0.038 ± 0.003 aA
	Amax($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	14.741 ± 1.330 aA	14.140 ± 0.569 aA
	CSP($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	1150.207 ± 31.293 aA	1132.385 ± 90.935 aA
	CCP($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	83.517 ± 7.965 aA	68.630 ± 1.034 bA
	Rp($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	3.166 ± 0.113 aA	2.446 ± 0.203 bA
	Vcmax($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	27.967 ± 0.612 bB	29.056 ± 0.550 aA
	Jmax($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	66.160 ± 2.727 aA	63.662 ± 3.365 aA
Note: Different small letters following each value within a Column indicate significant differences at $p < 0.05$, different capital letters following each value within a Column indicate significant differences at $p < 0.01$.			

Table 3
Physiological characters and Anatomical characters of CH and CB

Spiece		CH			CB		
			CV%	PI		CV%	PI
Physiological characters	LT(mm)	0.211 ± 0.006 aA	2.684	0.062	0.167 ± 0.004 bB	2.552	0.021
	LA(cm ²)	22.090 ± 0.092 aA	0.416	0.012	11.338 ± 0.555 bB	4.897	0.129
	SLA(m ² ·kg ⁻¹) ₁₎	140.552 ± 0.317 aA	0.225	0.016	126.530 ± 1.023 bB	0.809	0.019
	LTD(mg·mm ⁻³) ₃₎	0.038 ± 0.001 bB	4.515	0.105	0.047 ± 0.002 aA	3.729	0.082
	LRWC(%)	0.069 ± 0.075 bA	109.170	0.229	0.049 ± 0.052 aA	106.545	0.256
	LDMC(g·kg ⁻¹) ₁₎	3.327 ± 0.050bA	1.504	0.036	6.269 ± 1.126 aA	17.959	0.358
Anatomical characters	CUT(um)	2.578 ± 0.126 bB	4.903	0.129	4.570 ± 0.144 aA	3.143	0.073
	SP (um)	18.175 ± 1.901	10.459	0.224	/	/	/
	UET(um)	25.092 ± 0.435 bB	1.734	0.041	29.118 ± 0.947 aA	3.253	0.077
	LET(um)	11.945 ± 0.738 aA	6.180	0.169	11.602 ± 0.978 aA	8.426	0.206
	MVT(um)	205.728 ± 4.465 aA	2.170	0.049	197.320 ± 11.178 aA	5.665	0.130
	VBA(um ⁻²)	8269.177 ± 276.859 aA	3.348	0.079	5873.731 ± 35.397 bA	0.603	0.015
	VA(um ²)	918.852 ± 31.997 aA	3.482	0.080	405.723 ± 69.320 bB	17.086	0.341
	VA/VBA	0.116 ± 0.001 aA	0.755	0.017	0.069 ± 0.011 bB	16.488	0.331
	BC	3 ± 0.471 bB	14.142	0.250	6 ± 0.943 aA	14.142	0.250

Note: Different small letters following each value within a Column indicate significant differences at p < 0.05, different capital letters following each value within a Column indicate significant differences at p < 0.01. CV: Coefficient of variation; PI: means plasticity index

The coefficient of variation (CV) of two species leaf structure traits reached 0.225%–109.170%, and the plasticity coefficient (PI) were 0.005–0.256. The degree of variation of leaf structure traits was relatively large. LRWC exhibited the highest variability (CV: 109.170% and 106.545%, respectively) and the strongest plasticity (PI: 0.229 and 0.256, respectively). SLA achieved the lowest variability (CV: 0.225 and 0.809, respectively) (PI: 0.016 and 0.019, respectively). The CV of leaf anatomical traits ranged from 0.603–17.086%, and the PI were 0.017–0.341. The all CV and PI of leaf anatomical traits were lower, so they showed stronger stability than leaf structural traits. In terms of different plant species, the interspecific differences in leaf structural traits were not large, but in leaf anatomical traits were large. The CB's CV of VA, VA/VBA were significantly larger than those of CH. It has greater plasticity and better adaptability to the current habitat than CH.

3.3 Correlations among multiple leaf functional traits in *Carex*

Among leaf structural traits, LT, SLA, LA, LTD, and LDWC were correlated with photosynthetic characteristics. LT, LA, SLA were highly significantly positively correlated with photo (LT-photo, $r = 0.98$), G_s (SLA, $r^2 = 0.99$), $Trmmol$ (SLA, $r^2 = 1.00$), LUE (LA, SLA, $r^2 = 0.99, 0.99$), and V_{cmax} (SLA, $r^2 = 0.90$), and were significantly correlated with WUE (SLA, $r^2 = -1.00$), LSP (SLA, $r^2 = -0.99$) and R_p (LA, $r^2 = -0.94$). LTD, LDWC were significantly negatively correlated with photo (LTD, $r^2 = -0.97$), G_s (LTD, $r^2 = -0.98$), $Trmmol$ (LTD, $r^2 = -0.98$), LUE (LTD, $r^2 = -0.96$), and V_{cmax} ($r^2 = -0.91, -0.91$). LTD, LDWC with a very significant positive correlation with WUE (LTD, $r^2 = 0.97$) and LSP (LTD, $r^2 = 0.98$). LTD and R_p showed a significant positive correlation ($r^2 = 0.90$).

Among leaf anatomical traits, CUT, UET, VBA, VA, VBA/VA, BC were correlated with photosynthetic characteristics. CUT and UET showed a significant negative correlation with photo ($r^2 = -0.95, -0.91$), G_s ($r^2 = -0.98, -0.93$), LUE ($r^2 = -1.00, -0.98$), and $Trmmol$ ($r^2 = -1.00, -0.96$), and a significant positive correlation with WUE ($r^2 = 0.99$). VBA, VA, VA/VBA showed a significant positive correlation with photo (VA, $r^2 = 0.96$), G_s (VA, $r^2 = 0.94$), LUE (VA, $r^2 = 0.97$) and $Trmmol$ (VA, $r^2 = 0.97$), as well as a significant negative correlation with WUE (VA, $r^2 = -0.96$) and LSP (VA, $r^2 = -0.94$).

3.4 Key factors for the light efficiency of the *Carex* species

To further screen the critical variables from multiple traits with significant correlations, it is considered that the coefficients of variation of the leaf structural traits and the leaf anatomical traits are significantly different. At first, the leaf functional traits affecting photosynthetic characteristics were classified into two matrices, one for the leaf structural traits and the other the for leaf anatomical traits. The built-in algorithm of the Canoco software was adopted to screen six vital explanatory variables from the leaf morphological characters. The explanatory variables of the first axis and the second axis reached 52.48% and 12.95%, suggesting that the first and second axes accounted for 65.43% of the variation in photosynthetic characteristics exhibited by the two *Carex* species. SLA (explainability of 52.00%, $P =$

0.012) exhibited the longest arrow length and significantly affected the photosynthetic characteristics ($P < 0.05$). Five important leaf anatomical characters were screened using the built-in algorithm of the Canoco software. The explanatory variables of the first and second axis reached 52.24% and 22.60%, suggesting that the first two axes accounted for 74.83% of the variation in photosynthetic characteristics of the two *Carex* species. The arrow length of CUT (explainability of 51.70%, $P = 0.016$) was the longest, and the effect on the photosynthetic characteristics was significant ($P < 0.05$). UET facilitated the second principal component (explainability of 20.10%, $P = 0.024$), and the effect on the photosynthetic characteristics was also significant ($P < 0.05$). The results of RDA and Pearson analysis were consistent.

The above three significant explanatory variables (SLA, CUT, UET) were re-analyzed, suggesting that the explanatory variables of the first axis (SLA) accounted for 52.17% (more than half) of the variation of the photosynthetic characteristics, reaching the significant level of $P = 0.001$. There was a small angle between the arrow directions of SLA and LUE, Trmmol, photo, and Gs (acute angle), suggesting that SLA shows a strong positive correlation with LUE, Trmmol, photo, as well as Gs. There was a relatively large angle between the arrows of SLA and WUE, LSP, and Rp (obtuse angle), suggesting that the correlation between SLA and WUE, LSP, and Rp was significantly negative.

4 Discussion

4.1 Analysis of environmental adaptability of two *Carex* species from the angle of photosynthetic characteristics

4.1.1 Diurnal variation characteristics of photosynthetic parameters

The Relative humidity (RH) and the air CO_2 concentration (Ca) tended to decrease, and the cell vapor pressure inside and outside of leaves increased with the increase of the photosynthetically active radiation (PAR), air temperature (Ta) and leaf temperature (Duursma et al. 2014). A higher intercellular CO_2 concentration (Ci) was used for photosynthesis to reduce the leaf temperature and the plant increasing stomatal conductance (Gs) (Urban et al. 2017) and increase the transpiration rate (Trmmol) (Monteiro et al. 2016). When Ta reached the highest peak, plants responded to the high temperature environment, and the water loss was reduced, the stomata was closed, Gs was decreased (Urban et al. 2017), and Trmmol was reduced due to the effect of stomata (Monteiro et al., 2016).

The diurnal variation of photosynthetic parameters can indicate the adaptability of plants to the environment and is an essential method to investigate the effect of environmental factors on plant growth and metabolism (Schurr et al. 2006). (1) CH: CH is characterized by its stronger photosynthetic capacity, higher net photosynthetic rate (Pn), and more organic matter accumulated per unit time and unit leaf area. Higher Trmmol and Gs can facilitate the water vapor exchange between CH leaves and the external environment, the accumulation of the photosynthetic products, as well as the increase of the

growth rate (Xinqiang et al. 2020). C_i is capable of determining the amount of carbon source providing plant photosynthesis (Tominaga et al. 2018), and the light use efficiency (LUE) can indicate the plant efficiency in fixing solar energy (Akmal & Janssens 2004). The higher the value, the more vigorous the plant growth will be. In general, CH can provide carbon source for its own photosynthesis, and the fixing solar energy is a higher efficiency than that of CB. Lastly, the Trmmol of CH peaked earlier, suggesting that CH can respond to high temperatures and high PAR in time, while closing stomata, decreasing Trmmol to reduce plant water loss, and maintaining high light energy utilization for photosynthesis. (2) CB: CB is more easily affected by the ambient temperature and the effective radiation of light. At high temperatures and in strong light environments, it can effectively reduce transpiration and water loss by reducing stomatal conductance, enhancing stomatal limit value, effectively using water in leaves, as well as maintaining its own growth through low photosynthesis. It is an excellent ground cover with drought resistance and water saving characteristics, consistent with the research conclusions drawn by Yang et al. (2014).

4.1.2 Photoresponse parameters

In general, plants exhibiting low light compensation point (LCP) and light saturation point (LSP) are recognized as typical shade-tolerant plants (Zhang et al. 2004). The LCPs of CB and CH are less than $20 \mu\text{mol m}^{-2} \cdot \text{s}^{-1}$, and their LSPs are all less than $1000 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, similar to the shade-tolerant *Liriope spicata* (Thunb.) Lour (Qiu et al. 2014). The LCP and LSP of green moss grass obtained by Yang et al. (2014) were higher than the those in this study, probably because the green moss grass in this study grows in the shade for a long period. CH exhibits a more significant ability to utilize low light than CB. CH is more suitable to cultivate CH in low light or shading environments, whereas CB may be well grown in semi-shading environments.

4.1.3 CO₂ Response Parameters

CO₂ compensation point (CCP) and CO₂ saturation point (CSP) are crucial indicators for determining whether plants exhibit the genetic characteristics of high light efficiency. Plants with lower CCP are characterized by high photosynthetic rate, low respiration rate, and fast growth (Dong et al. 2016). The maximum carboxylation rate (V_{cmax}) of leaves represents a vital rate-limiting reaction in the process of photosynthesis, thus playing a critical role in the rate of photosynthesis (Schurr et al. 2006). The CCP of CB is significantly lower than CH, and the V_{cmax} of CB is significantly higher than that of CH, thus making CB exhibit high light efficiency and high growth potential. Using CO₂ for photosynthesis is beneficial to produce organic matter and facilitate the growth of CH. Thus, CH grows faster into lawns. The photorespiration rate (R_p) indicates the ability of plants to use high concentrations of O₂ for respiration to consume photosynthetic products under light conditions. The high R_p rate of CH hinders the accumulation of photosynthetic products to a certain extent (Hagemann & Bauwe 2016).

4.2 Analysis of Environmental Adaptability of two Carex species from the Angle of leaf structural traits and leaf anatomical characters

4.2.1 Differences in leaf structural traits and leaf anatomical traits

Leaf is a bridge connecting plant physiology and external environment, thus exhibiting a significant ability to perceive heterogeneous environments. It is a survival strategy for plants to adapt to environmental changes by regulating the functional traits of leaves to cope with different habitats (García-Cervigón et al. 2021). Leaf morphology is capable of affecting the photosynthetic area of leaves, while leaf area (LA) can indicate the ability of plants to intercept light (Huang et al. 2021; Milla & Reich 2007). (1) CH: The leaves of CH promote the plants to capture different degrees of light energy and perform stronger photosynthesis. The larger vessel area (VA), vascular bundle area (VBA), and vessel area/vascular bundle area (VA/VBA) of CH suggest that its conducting tissue is well developed, thus facilitating the photosynthetic reaction with CO₂ and H₂O as the raw materials. Existing research has suggested that the conduction of water by leaves is positively correlated with photosynthetic capacity (Brodrigg & Feild 2000), so it more significantly contributes to the efficient delivery of nutrients and photosynthetic products by plants to ensure the normal plant growth. CH shows a siliceous papillose structure outside the stratum corneum, thus leading to its strong self-protection ability and its significantly larger SLA than that of CB, suggesting that it has strong adaptability to the resource-rich environment and less investment in the construction of "defensive" resources (Cornelissen et al. 2003). (2) CB: CB is more resilient to barren and arid environments. It extends leaf life and reduces nutrient loss primarily by reducing leaf thickness and increasing leaf tissue density (Wright et al. 2004). LDMC is often adopted to characterize the ability of plants to preserve nutrients (van Bodegom et al. 2014). The size of leaf tissue density (LTD) indicates the plant's water demand and the plant's resistance (Jones 2004) (e.g., resistance to high temperature and drought). As revealed by the higher LRWC, LDWC and LTD values of CB, its leaves generally exhibit higher osmotic regulation function and stronger drought resistance. Besides, the plants use more carbon storage to resist the structural structure of defense to enhance self-resistance (Wiley & Helliker 2012). Accordingly, the plants exhibit a high ability to resist damage from abiotic factors and require less water. In terms of leaf anatomy, CB's thicker cuticle (CUT) and epidermal cells can help the plants reduce water transpiration (Guan et al. 2011). Larger vesicular cells play an essential role in maintaining cellular water potential. CB uses large vacuoles to regulate leaf extension and curling, which can prevent the loss of water potential in plants under drought stress and improve their ability to adapt to drought, thus affecting leaf morphology and light and water use capacity (Xiang et al. 2012).

The theoretical analysis of leaf economic spectrum suggests that CH is a fast investment-income species and tends to select survival strategies with strong photosynthetic ability, larger than leaf area but short

lifespan. Besides, CB refers to a slow investment-income species and tends to select weak photosynthetic ability, smaller SLA, and longer lifespan. The two completely different survival strategies are the result of species adapting to the environment in the long-term evolution, thus revealing the optimal allocation of resources among plants of different life forms among their own functional traits based on their needs.

4.2.2 Variability and plasticity of leaf structural traits and leaf anatomical traits

Leaf tissue structure has strong variability and plasticity. Traits with a coefficient of variation greater than 50% are considered ecologically adaptive traits, and those achieving a smaller coefficient of variation are considered relatively stable system evolution traits, thus revealing the potential adaptive capacity of species (Abrams et al. 1994). The plasticity index can indicate the ability of a species to resist environmental stress, and a higher level of plasticity suggests a stronger system regulation ability (Valladares et al. 2007). Among the leaf structural traits of the two plants, LRWC exhibited the greatest variability and plasticity, thus suggesting the results of adaptation to external drought stress. Northwest China is characterized by higher temperatures and higher evaporation in summer. To improve their water retention and drought resistance, the plants increase the relative water content of leaves, and the plant cell wall is more elastic, thus becoming helpful to reduce the decline of leaf water potential when plants lose water and adapt to the water-deficit environment. The leaf anatomical traits of CH exhibit relatively low plasticity and variability, and all traits are relatively stable, all of which belong to evolutionary traits. The plasticity and variability of CB are stronger than those of CH, suggesting that CB is capable of maintaining the relative stability and adaptability of leaves in heterogeneous ecosystems through plasticity, thus enhancing the resistance and resilience to biotic and abiotic factors in the system. In terms of the anatomical structure, CB can regulate the conducting tissue, which connects the above-ground and underground structures of the ecosystem, to adapt environment. The conducting tissue is a vital structure for the adaptation of desert wetlands and oasis riparian plants to the environment (Zhou et al. 2012). Thus, the plasticity of conducting tissue can enhance the ability of CB to absorb water and salt to better adapt to the environment.

4.3 Key factors for the light efficiency of the *Carex* species

Correlation analysis (Pearson) is a method to investigate the linear correlation between two variables, while redundancy analysis (RDA) refers to a method to study the correlation between groups of variables, which is capable of prioritizing explanatory variables and ranking the significance of their effect (Liu et al. 2021).

In this study, Correlation analysis shows that among leaf structural traits, SLA has the strongest correlation with photosynthetic characteristics (r value is close to ± 1). Among leaf anatomical traits, CUT and UET have the strongest correlation with photosynthetic characteristics (r value is close to ± 1). SLA has the greatest effect on photo, Gs, Trmmol, LUE, Vcmax and photosynthetic characteristics, which shows a very significant positive correlation. SLA shows a significant negative correlation with WUE, LSP, and Rp. Wright's research suggested that SLA is a trait correlated with light capture and photosynthetic

capacity(Wright et al. 2004). The larger the SLA, the greater the LA will be, which is beneficial to the plant to capture more light energy(Vincent 2001) and achieve a higher metabolic rate per unit mass of plant(Wright et al., 2004), thus increasing the growth rate of plants. SLA is significantly negatively correlated with WUE, LSP, and R_p , consistent with the study of Niinemets U et al. suggesting that shade-loving plants exhibits thinner leaves, larger SLA, better photosynthetic capacity. LSP and R_d and chlorophyll a/b will be lower, and the chlorophyll concentration will be higher(Niinemetts et al. 1998). With lower photosynthetic capacity, the water transpiration rate and R_p also decrease. Among the leaf anatomical traits, CUT most significantly affects the photosynthetic characteristics exhibited by the two *Carex* species. CUT had a strong positive correlation with WUE and LSP, and had a strong negative correlation with G_s and T_{mmol} . CUT can enhance the reflection of solar radiation, which is beneficial to prevent the loss of water and improve the utilization rate of water(Goodwin & Jenks 2005). The plant photosynthesis can be promoted by reducing water transpiration through thicker cuticles. Moreover, CUT is capable of reducing the damage of high temperature to parenchyma and protecting against mechanical injuries and environmental changes(Dominguez et al. 2011). UET shows a strong positive correlation with R_p and WUE, as well as a strong negative correlation with LUE and T_{mmol} . At high altitudes, plants gain more resources to sustain growth by increasing the thickness of their epidermal cells (Thakur et al. 2019). The thickened epidermal cell may enhance the capability to light energy capture(Bernado et al. 2021).

By optimizing the explanatory variables and ranking the significance of their effects, it was concluded that SLA, UET and CUT can serve as reliable indicators to study the variation of photosynthetic characteristics of two species of *Carex*. Moreover, SLA has the strongest effect on the photosynthetic characteristics of the two *Carex* species. The SLA of CH is significantly larger than that of CB, suggesting that CH exhibits higher photosynthetic efficiency and high utilization of light energy. In brief, SLA can serve as an essential indicator to screen the germplasm resources of the genus *Carex* with high efficiency.

Conclusion

CH and CB have different resource acquisition strategies after undergoing long-term environmental adaptation and evolution. CB refers to a slow investment-return plant. The variability and plasticity of leaf functional traits of CB were stronger, and it exhibits strong environmental adaptability in long-term shaded environments. And CB are high water utilization, high CO_2 utilization capacity, drought resistance and barren resistance. The advantage of CH is that CH can better adapt and maintain photosynthesis with the increase of T_a and PAR. CH is a quick investment-return plant. CH has a well-developed conducting tissue, thus leading to its higher efficiency in transporting nutrients and accumulating organic matter. Furthermore, CH photosynthetic efficiency is high, which has high efficiency in capturing and fixing solar energy. Both CH and CB have shade tolerance, but CH is more than CB. Lastly, SLA can serve as the main indicators to evaluate the light efficiency of *Carex*.

CH and CB have extensive applications, especially in areas with continental monsoon climates. They are beneficial to increase the diversity of turfgrass species and meet people's more demand for turfgrass to a

certain extent. Moreover, they can be employed in shading environments and beside buildings, thus increasing the stratification of landscapes in the configuration of landscape. Lastly, CB can be planted in places with poorer soil water content and poorer soil nutrients to rapidly grow lawns. CH and CB are potential turfgrasses.

Declarations

Funding: This work was supported by the Natural Science Foundation of China (32071859).

Competing Interests: The authors have no relevant financial or non-financial interests to disclose.

Author Contributions: Xiaoqi Wang and Wenli Ji planned and designed the research. Xiaoqi Wang, Yuhan Feng, Xuewei Feng, Wanting Liu, Jinguo Hua, Fei Xie performed experiments and conducted fieldwork. Xiaoqi Wang analysed data. Xiaoqi Wang wrote the initial manuscript, and all authors contributed to its revision.

Acknowledgments

Sincere thanks to the support of the Natural Science Foundation of China (32071859).

References

1. Abrams M.D., Kubiske M.E. and Mostoller S.A. 1994. Relating wet and dry year ecophysiology to leaf structure in contrasting temperate tree species. *Ecology* 75: 123–133.
2. Akmal M. and Janssens M. 2004. Productivity and light use efficiency of perennial ryegrass with contrasting water and nitrogen supplies. *Field crops research* 88: 143–155.
3. Ali A.M., Darvishzadeh R., Skidmore A.K., van Duren I., Heiden U. and Heurich M. 2016. Estimating leaf functional traits by inversion of PROSPECT: Assessing leaf dry matter content and specific leaf area in mixed mountainous forest. *International Journal of Applied Earth Observation and Geoinformation* 45: 66–76.
4. Bernado W.d.P., Rakocevic M., Santos A.R., Ruas K.F., Baroni D.F., Abraham A.C., Pireda S., Oliveira D.d.S., Cunha M.D. and Ramalho J.C. 2021. Biomass and Leaf Acclimations to Ultraviolet Solar Radiation in Juvenile Plants of *Coffea arabica* and *C. canephora*. *Plants* 10: 640.
5. Brodribb T. and Feild T. 2000. Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. *Plant, Cell & Environment* 23: 1381–1388.
6. Chen L.H., Zhang D.J., Yang W.Q., Liu Y., Zhang L. and Gao S. 2016. Sex-specific responses of *Populus deltoides* to *Glomus intraradices* colonization and Cd pollution. *Chemosphere* 155: 196–206.
7. Cornelissen J.H.C., Lavorel S., Garnier E., Diaz S., Buchmann N., Gurvich D.E., Reich P.B., ter Steege H., Morgan H.D., van der Heijden M.G.A., Pausas J.G. and Poorter H. 2003. A handbook of protocols for

- standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.
8. Correa M.M., de Araujo M.G.P. and Scudeller V.V. 2018. Comparative leaf anatomy of twenty species of *Chrysobalanaceae* R. Br. *Flora* 249: 60–66.
 9. Dominguez E., Heredia-Guerrero J.A. and Heredia A. 2011. The biophysical design of plant cuticles: an overview. *New Phytologist* 189: 938–949.
 10. Dong M.Y., Wang J.X., WU M., Zhou Z.Y., Cheng S. and Li Y.H. 2022. Leaf structure and photosynthetic characteristics of two species of *Hesperis*. *ACTA PRATACULTURAE SINICA* 31: 172–184.
 11. Dong Q., Li L.L., Liu Y.M. and Liu D.Y. 2016. Photosynthetic Characteristics of Ten Species of Wild Ground Cover Plants. *Northern Horticulture*: 93–97.
 12. Dou Q., Chu H.L., Wang H.H., Chu W.H. and Wang C.Y. 2015. Resource and Distribution of Macrofungi in the Campus of Northwest A&F University. *Journal of Northwest Forestry University* 30: 174–181.
 13. Duursma R.A., Barton C.V., Lin Y.-S., Medlyn B.E., Eamus D., Tissue D.T., Ellsworth D.S. and McMurtrie R.E. 2014. The peaked response of transpiration rate to vapour pressure deficit in field conditions can be explained by the temperature optimum of photosynthesis. *Agricultural and Forest Meteorology* 189: 2–10.
 14. Evans J.R. 2013. Improving photosynthesis. *Plant Physiology* 162: 1780–1793.
 15. García-Cervigón A.I., García-López M.A., Pistón N., Pugnaire F.I. and Olano J.M. 2021. Co-ordination between xylem anatomy, plant architecture and leaf functional traits in response to abiotic and biotic drivers in a nurse cushion plant. *Annals of Botany* 127: 919–929.
 16. Goodwin S.M. and Jenks M.A. 2005. Plant cuticle function as a barrier to water loss. *Plant abiotic stress*: 14–36.
 17. Group G.C., Roalson E.H., Jiménez-Mejías P., Hipp A.L., Benítez-Benítez C., Bruederle L.P., Chung K.S., Escudero M., Ford B.A. and Ford K. 2021. A framework infrageneric classification of *Carex* (Cyperaceae) and its organizing principles. *Journal of Systematics and Evolution* 59: 726–762.
 18. Guan Z.-J., Zhang S.-B., Guan K.-Y., Li S.-Y. and Hu H. 2011. Leaf anatomical structures of *Paphiopedilum* and *Cypripedium* and their adaptive significance. *Journal of Plant Research* 124: 289–298.
 19. Hagemann M. and Bauwe H. 2016. Photorespiration and the potential to improve photosynthesis. *Current opinion in chemical biology* 35: 109–116.
 20. Huang L., Niinemets Ü., Ma J., Schrader J., Wang R. and Shi P. 2021. Plant age has a minor effect on non-destructive leaf area calculations in moso bamboo (*Phyllostachys edulis*). *Symmetry* 13: 369.
 21. Jones H.G. 2004. Irrigation scheduling: advantages and pitfalls of plant-based methods. *Journal of Experimental Botany* 55: 2427–2436.
 22. Kettenring K.M. and Galatowitsch S.M. 2007. Temperature requirements for dormancy break and seed germination vary greatly among 14 wetland *Carex* species. *Aquatic Botany* 87: 209–220.

23. Kettenring K.M., Gardner G. and Galatowitsch S.M. 2006. Effect of light on seed germination of eight wetland *Carex* species. *Annals of Botany* 98: 869–874.
24. Li J.X. and Tian Q. 2022. Leaf morphology and photosynthetic physiological characteristics of
25. six garden plants in Lanzhou. *Journal of Northwest A & F University (Natural Science Edition)* 50: 72–80.
26. Liu F.T., Wang X.Q., Chi Q.H. and Tian M. 2021. Spatial variations in soil organic carbon, nitrogen, phosphorus contents and controlling factors across the "Three Rivers" regions of southwest China. *Science of the Total Environment* 794.
27. Maza-Villalobos S., García-Ramírez P., Endress B.A. and Lopez-Toledo L. 2022. Plant functional traits under cattle grazing and fallow age scenarios in a tropical dry forest of Northwestern Mexico. *Basic and Applied Ecology*.
28. Milla R. and Reich P.B. 2007. The scaling of leaf area and mass: the cost of light interception increases with leaf size. *Proceedings of the Royal Society B: Biological Sciences* 274: 2109–2115.
29. Miller R.M., Smith C.I., Jastrow J.D. and Bever J.D. 1999. Mycorrhizal status of the genus *Carex* (Cyperaceae). *American Journal of Botany* 86: 547–553.
30. Monteiro M.V., Blanuša T., Verhoef A., Hadley P. and Cameron R.W. 2016. Relative importance of transpiration rate and leaf morphological traits for the regulation of leaf temperature. *Australian Journal of Botany* 64: 32–44.
31. Nam J.M., Kim J.H. and Kim J.G. 2017. Effects of light intensity and plant density on growth and reproduction of the amphicarpic annual *Persicaria thunbergii*. *Aquatic Botany* 142: 119–122.
32. Niinemets U., Kull O. and Tenhunen J.D. 1998. An analysis of light effects on foliar morphology, physiology, and light interception in temperate deciduous woody species of contrasting shade tolerance. *Tree Physiology* 18: 681–696.
33. Oda J., Fuse S., Yamashita J. and Tamura M.N. 2019. Phylogeny and Taxonomy of *Carex* (Cyperaceae) in Japan I. C. sect. *Rarae*. *Acta Phytotaxonomica Et Geobotanica* 70: 69–85.
34. Qiu J., Wang K., Duan Y., Guan H. and Wei H. 2014. Study on leaf morphology and photosynthetic characteristics of *Ophiopogon japonicus* and *Liriope spicata*. *Acta Botanica Boreali-Occidentalia Sinica* 34: 727–732.
35. Schurr U., Walter A. and Rascher U. 2006. Functional dynamics of plant growth and photosynthesis—from steady-state to dynamics—from homogeneity to heterogeneity. *Plant, Cell & Environment* 29: 340–352.
36. Schütz W. 2000. Ecology of seed dormancy and germination in sedges (*Carex*). *Perspectives in plant ecology, evolution and systematics* 3: 67–89.
37. Sun Y., Wang C.T., Chen H.Y.H. and Ruan H.H. 2020. Response of Plants to Water Stress: A Meta-Analysis. *Frontiers in Plant Science* 11.
38. Taylor S.H., Franks P.J., Hulme S.P., Spriggs E., Christin P.A., Edwards E.J., Woodward F.I. and Osborne C.P. 2012. Photosynthetic pathway and ecological adaptation explain stomatal trait diversity

- amongst grasses. *New Phytologist* 193: 387–396.
39. Teng N., Wang J., Chen T., Wu X., Wang Y. and Lin J. 2006. Elevated CO₂ induces physiological, biochemical and structural changes in leaves of *Arabidopsis thaliana*. *The New phytologist* 172: 92–103.
 40. Thakur D., Rathore N. and Chawla A. 2019. Increase in light interception cost and metabolic mass component of leaves are coupled for efficient resource use in the high altitude vegetation. *Oikos* 128: 254–263.
 41. Thinh N.C., Kumagai E., Shimono H. and Kawasaki M. 2018. Effects of elevated atmospheric CO₂ concentration on morphology of leaf blades in Chinese yam. *Plant Production Science* 21: 311–321.
 42. Tholen D., Boom C. and Zhu X.-G. 2012. Opinion: prospects for improving photosynthesis by altering leaf anatomy. *Plant science* 197: 92–101.
 43. Tominaga J., Shimada H. and Kawamitsu Y. 2018. Direct measurement of intercellular CO₂ concentration in a gas-exchange system resolves overestimation using the standard method. *Journal of Experimental Botany* 69: 1981–1991.
 44. Tribouillois H., Fort F., Cruz P., Charles R., Flores O., Garnier E. and Justes E. 2015. A Functional Characterisation of a Wide Range of Cover Crop Species: Growth and Nitrogen Acquisition Rates, Leaf Traits and Ecological Strategies. *Plos One* 10.
 45. Urban J., Ingwers M., McGuire M.A. and Teskey R.O. 2017. Stomatal conductance increases with rising temperature. *Plant signaling & behavior* 12: e1356534.
 46. Valladares F., Gianoli E. and Gómez J.M. 2007. Ecological limits to plant phenotypic plasticity. *New Phytologist* 176: 749–763.
 47. Valladares F., Wright S.J., Lasso E., Kitajima K. and Pearcy R.W. 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology* 81: 1925–1936.
 48. van Bodegom P.M., Douma J.C. and Verheijen L.M. 2014. A fully traits-based approach to modeling global vegetation distribution. *Proceedings of the National Academy of Sciences of the United States of America* 111: 13733–13738.
 49. Vincent G. 2001. Leaf photosynthetic capacity and nitrogen content adjustment to canopy openness in tropical forest tree seedlings. *Journal of Tropical Ecology* 17: 495–509.
 50. Wiley E. and Helliker B. 2012. A re-evaluation of carbon storage in trees lends greater support for carbon limitation to growth. *New Phytologist* 195: 285–289.
 51. Wright I.J., Reich P.B., Westoby M., Ackerly D.D., Baruch Z., Bongers F., Cavender-Bares J., Chapin T., Cornelissen J.H.C., Diemer M., Flexas J., Garnier E., Groom P.K., Gulias J., Hikosaka K., Lamont B.B., Lee T., Lee W., Lusk C., Midgley J.J., Navas M.L., Niinemets U., Oleksyn J., Osada N., Poorter H., Poot P., Prior L., Pyankov V.I., Roumet C., Thomas S.C., Tjoelker M.G., Veneklaas E.J. and Villar R. 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.
 52. Xiang J.-J., Zhang G.-H., Qian Q. and Xue H.-W. 2012. SEMI-ROLLED LEAF1 Encodes a Putative Glycosylphosphatidylinositol-Anchored Protein and Modulates Rice Leaf Rolling by Regulating the Formation of Bulliform Cells. *Plant Physiology* 159: 1488–1500.

53. Xiao Y.F., Sun F.Z. and Gao j. 1995. A study on wild turfgrass - *Carex breviculmis*. Journal of Grassland and Forage Science: 29–32.
54. Xinqiang Q., Yushun Z., Haixia Q., Min W., Yanping W., Haochen Y. and Zhenguang L. 2020. Estimation of leaf water use efficiency threshold values for water stress in winter wheat (*triticum aestivum* L.). Journal of Sensors 2020.
55. Yang X.J., Wu J.Y., Teng W.J. and Yuan X.H. 2014. Daily and seasonal variation of photosynthetic characteristics of *Carex leucochlora*. PRATACULTURAL SCIENCE 31: 102–107.
56. Ye Z.P. 2007. A new model for relationship between irradiance and the rate of photosynthesis in *Oryza sativa*. Photosynthetica 45: 637–640.
57. Ye Z.P. and Yu Q. 2008. A coupled model of stomatal conductance and photosynthesis for winter wheat. Photosynthetica 46: 637–640.
58. Ye Z.P. and Yu Q. 2009. Comparison of the response curves of photosynthesis to intercellular and atmospheric CO₂. Chinese Journal of Ecology 28: 2233–2238.
59. Zhang J.Z., Shi L., Shi A.P. and Zhang Q.X. 2004. Photosynthetic responses of four *Hosta* cultivars to shade treatments. Photosynthetica 42: 213–218.
60. Zhang Z.H., Sun M.Y. and Wang G.H. 1995. Excellent turfgrass - *Carex heterostachya*. Bulletin of Biology: 26.
61. Zhou H., Li W., Ayup M. and Xu Q. 2012. Xylem hydraulic conductivity and embolism properties of desert riparian forest plants and its response to drought stress. Chinese Journal of Plant Ecology 36: 19–29.

Figures



Figure 1

high ornamental value of CH(left) and CB(right)

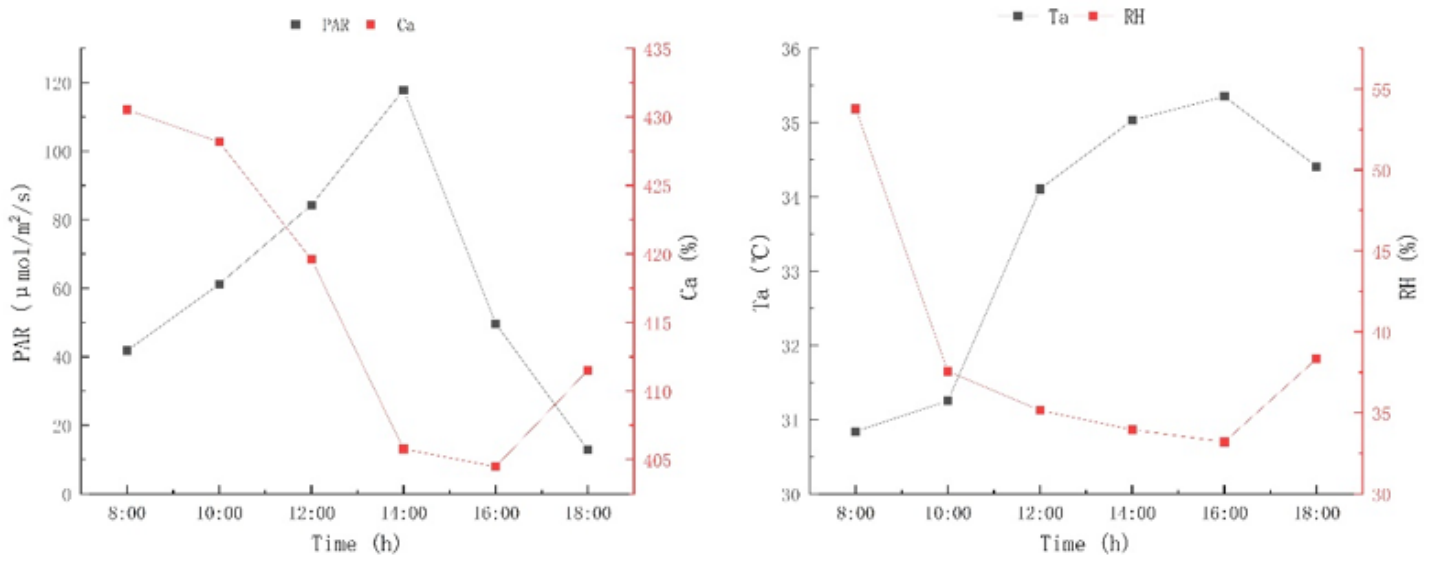


Figure 2

Diurnal variation of photosynthetically active radiation (PAR), atmospheric CO₂ concentration (Ca), atmospheric temperature (Ta) and relative humidity (RH)

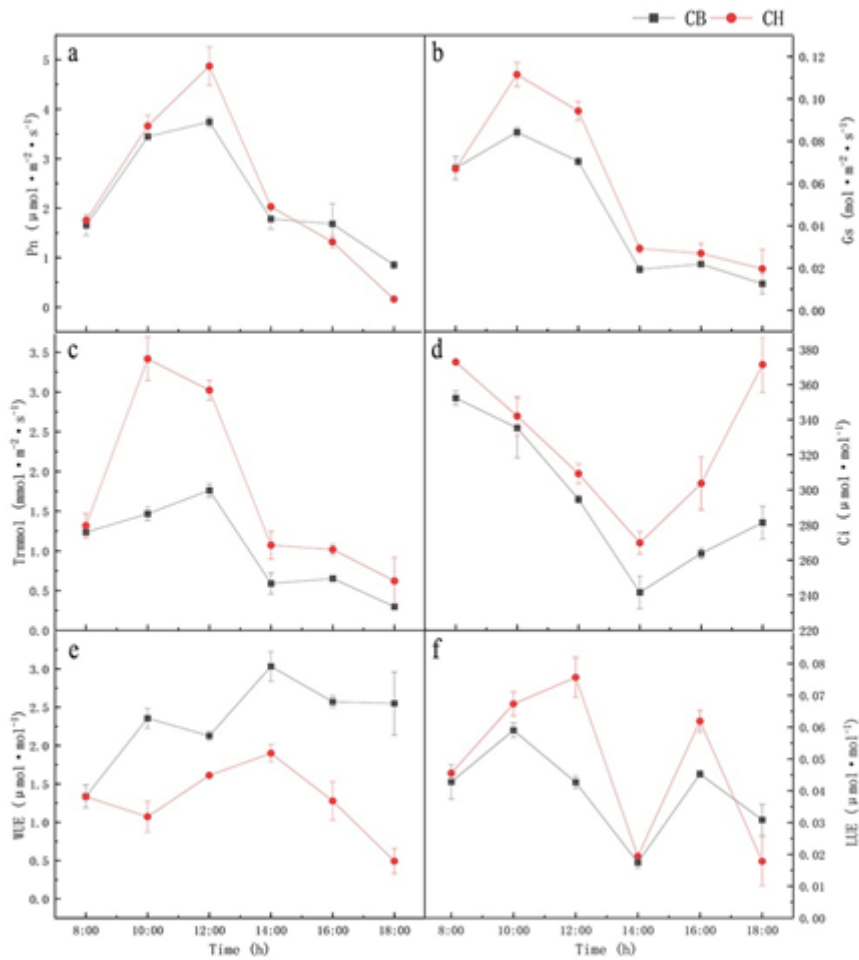


Figure 3

Diurnal variation curves of net photosynthetic rate (P_n), transpiration rate (T_{rmmol}), stomatal conductance (G_s), CO₂ concentration (C_i), light energy use efficiency (LUE), water use efficiency (WUE) of two plants.

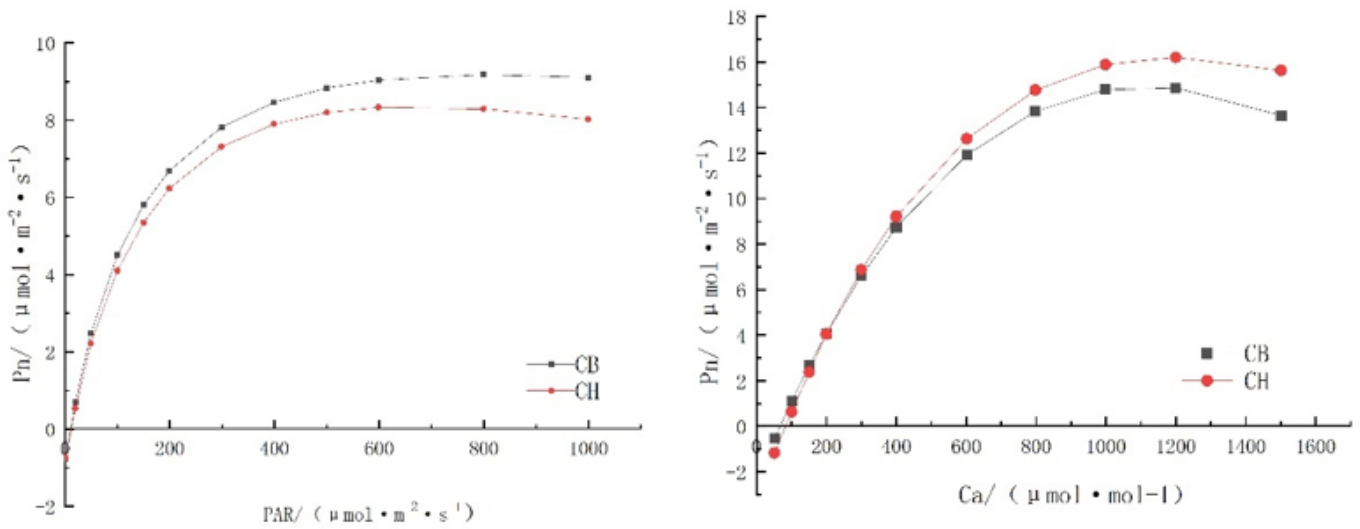


Figure 4

Light response curve and carbon dioxide response curve

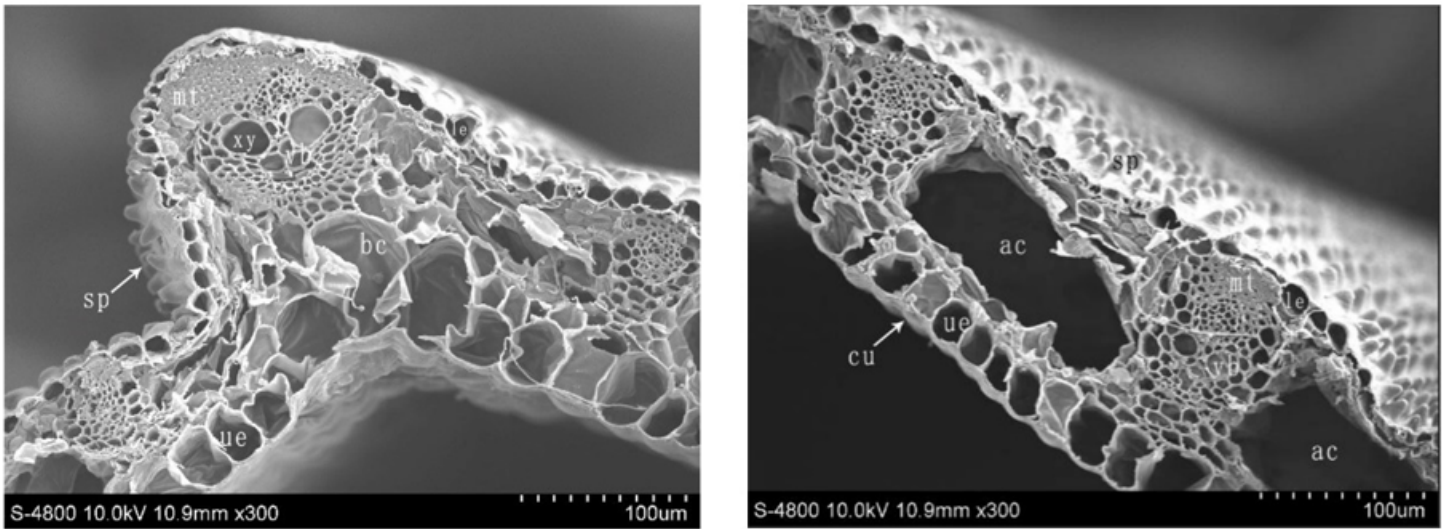


Figure 5

Morphological and anatomical structure of CH (left picture: main veins of leaves)

Note: Upper epidermis ue Lower epidermis le Bulliform cells bc Air cavaera ac vascular bundle vb mechanical organization mt xylem duct xy Phloem ph siliceous papillose sp cuticle cu

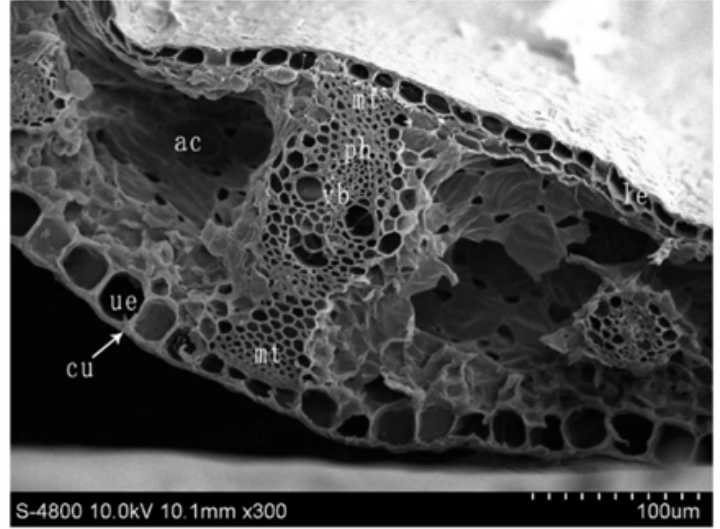
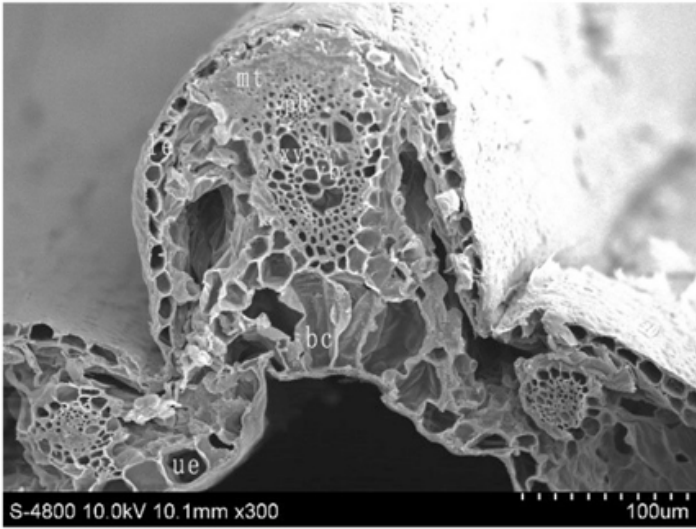


Figure 6

Morphological and anatomical structure of CB (left picture: main vein of leaf)

Note: Upper epidermis ue Lower epidermis le Bulliform cells bc Air cavaera ac vascular bundle vb
mechanical organization mt xylem duct xy Phloem ph siliceous papillose sp cuticle cu

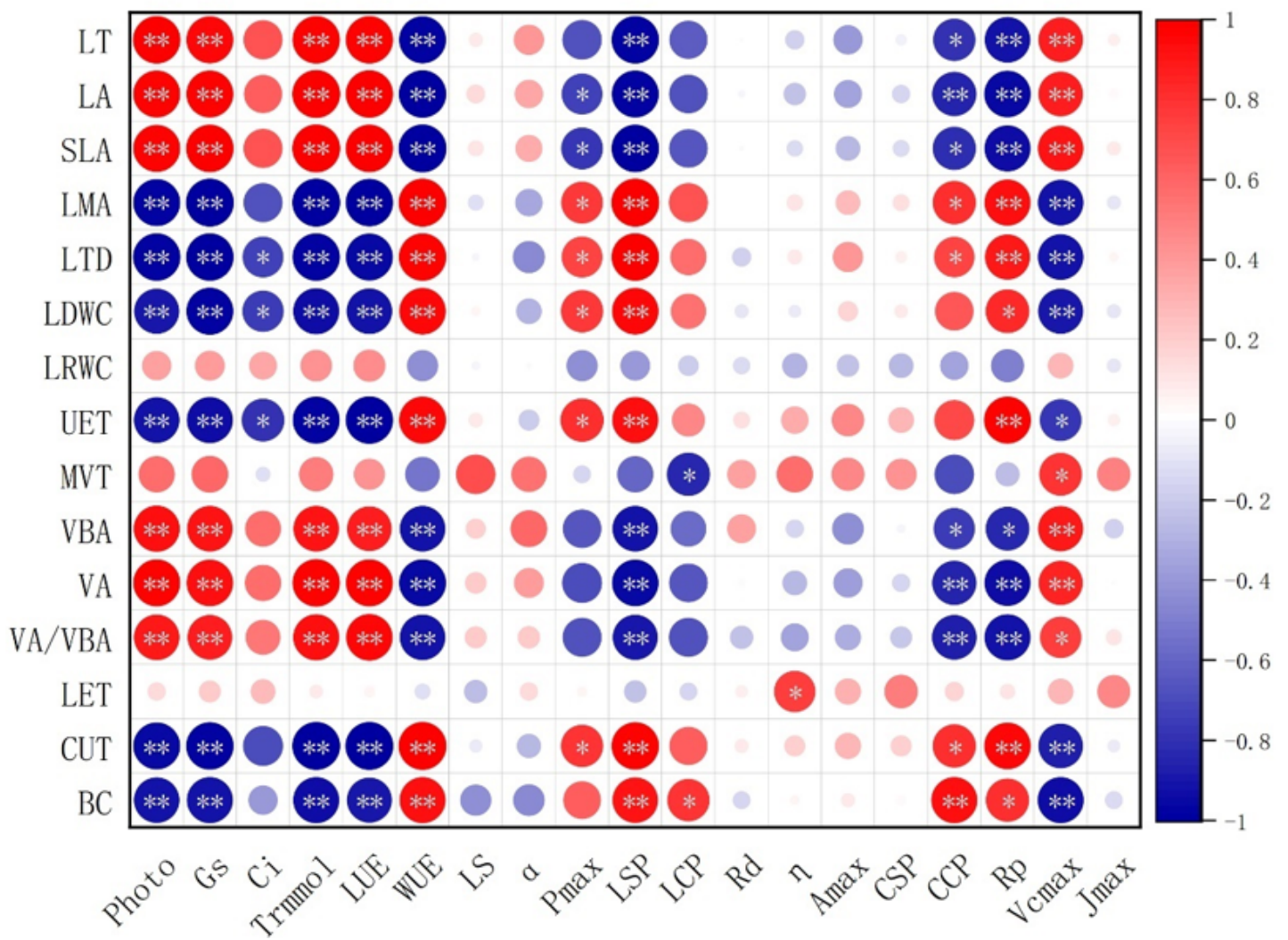


Figure 7

Heat map of correlations between photosynthetic parameters, leaf structural traits, and leaf anatomical traits in two *Carex* species(*P 0.05 , **P 0.01)

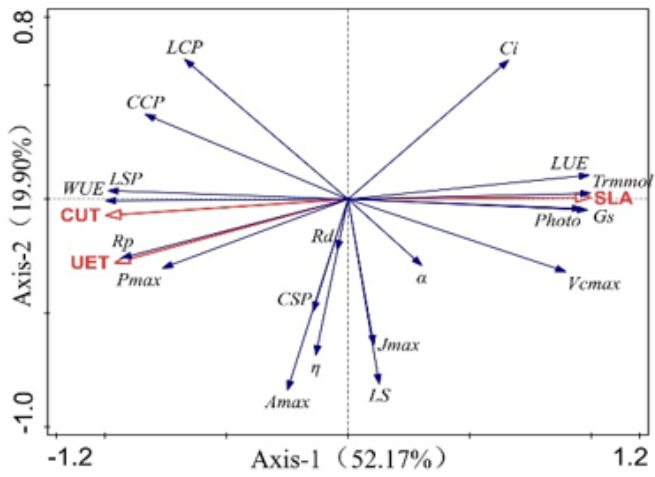
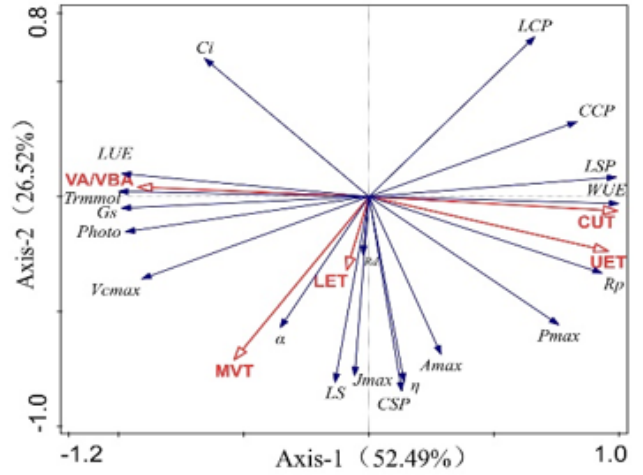
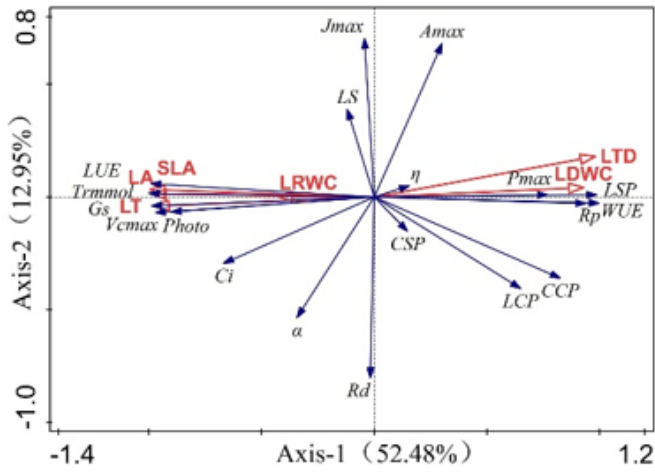


Figure 8

RDA analysis map between photosynthetic characteristics and leaf morphological characters and leaf anatomical traits