

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

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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. So, 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. The result of this study suggests that (1) CB is a slow investment-return plant with strong environmental adaptability and plasticity in long-term shaded environments. It is characterized by its weak photosynthetic capacity, smaller specific leaf area, low CO₂ compensation point, high water utilization rate, high maximum carboxylation rate, as well as dark breathing rate. Moreover, it also has a thick cuticle, and epidermal cells make CB resistant to drought and barrenness. (2) CH is a quick investment-return plant, which is characterized by its higher photosynthetic rate, transpiration rate, stomatal conductance, as well as larger specific leaf area. With the increase of the temperature and photosynthetically active radiation, CH maintains high photosynthetic capacity by decreasing the transpiration rate and increasing the utilization rate of light energy. Its conducting tissue is well developed. CH have lower light saturation points and light compensation points, and CH was more shade-tolerant than CB. (3) *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. (4) 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 (Z. H. Zhang, Sun, & Wang, 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, Sun, & Gao, 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, Fuse, Yamashita, & Tamura, 2019), classification (Group et al., 2021), seed germination (Kettenring & Galatowitsch, 2007; Kettenring, Gardner, & Galatowitsch, 2006), as well as mycorrhizal status of the genus *Carex* (Miller, Smith, Jastrow, & Bever, 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, García-Ramírez, Endress, & Lopez-Toledo, 2022). For instance, the relatively stable leaf structure traits are capable of indicating the maximization of carbon harvest (Correa, de Araujo, & Scudeller, 2018; Taylor et al., 2012). The leaf thickness will increase significantly at the extremely high CO₂ concentration in the environment (Teng et al., 2006; Thinh, Kumagai, Shimono, & Kawasaki, 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, Wright, Lasso, Kitajima, & Pearcy, 2000).

Existing research has suggested that leaf functional traits and photosynthesis are coordinated with each other for a long period (Nam, Kim, & Kim, 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, Boom, and Zhu (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. M. Y. 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, 34deg5'4"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 (Figure 1)(Table 1). The optimal growing season was selected for plants in summer (end of July) for this experiment.

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 [?]10degC is 4184degC. 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 , and the extreme maximum temperature can reach 42 . 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, Chu, Wang, Chu, & Wang, 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 (Trmmol), stomatal conductance (Gs), air CO₂concentration (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(Ls)=(Ca-Ci)/Ca.

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 μmol/m²/s, the CO₂injection system setting value was 400 μmol/mol, and the flow rate was 500 μmol/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 (Pnmax), and dark breathing rate (Rd) of the two types of plants can be obtained.

$$Pn(I) = \alpha \frac{1-\beta I}{1+\gamma I} I - Rd(1)$$

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

2.4 CO₂–Response Curves Measurements

When the photosynthetic CO₂ response was performed, the generated reaction substrate had a certain hysteresis. Thus, the CO₂ concentration controlled by the instrument is first reduced from the atmospheric concentration (nearly 400 μmol/mol) to 50 μmol/mol during the observation. The CO₂ concentration of the sample chamber is 400, 300, 200, 150, 100, 50, 400, 400, 600, 800, 1000, 1200, 1500 μmol/mol. Photosynthetically active radiation was set to 600 μmol/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 CO₂ saturation point (CSP), CO₂ compensation point (CCP), initial carboxylation rate (η), photorespiration rate (Rp)and maximum net photosynthetic rate (Pnmax) can be calculated. The maximum carboxylation rate and maximum electron conductivity of the two plants were calculated using the fitaci function.

$$Pn(Ca) = \eta \frac{1-\beta Ca}{1+\gamma Ca} Ca - Rp(2)$$

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 \pm 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(Figure 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 Ta, the increase of Trmmol and the lower WUE. In general, the WUE of CB was significantly higher ($P < 0.01$) than that of CH (Figure 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(Figure 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(Figure 4). When the carbon dioxide concentration was nearly 0-1000 $\mu\text{mol}\cdot\text{mol}^{-1}$, 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 $\mu\text{mol}\cdot\text{mol}^{-1}$, 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 Rd between CH and CB ($P > 0.05$), and LCP, LSP. Pmax of CB are significantly higher than CH ($P < 0.05$). The CCP and Rp of CH were significantly higher than CB ($P < 0.05$), and there was no significant difference in η , Amax, CSP, and Jmax between the two plants ($P > 0.05$). The Vcmax of CB was significantly higher than CH ($P < 0.01$).

3.2 Physiological characters and Anatomical characters

As depicted in Table. 3, Figure 5 and Figure 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, Wang, Chen, & Ruan, 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 18.175um, 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.

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% to 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, $r = 0.98$), Gs (SLA, $r^2 = 0.99$), Trmmol (SLA, $r^2 = 1.00$), LUE (LA, SLA, $r^2 = 0.99, 0.99$), and Vcmax (SLA, $r^2 = 0.90$), and were significantly correlated with WUE (SLA, $r^2 = -1.00$), LSP (SLA, $r^2 = -0.99$) and Rp (LA, $r^2 = -0.94$). LTD, LDWC were significantly negatively correlated with photo (LTD, $r^2 = -0.97$), Gs (LTD, $r^2 = -0.98$), Trmmol (LTD, $r^2 = -0.98$), LUE (LTD, $r^2 = -0.96$), and Vcmax ($r^2 = -0.91, -0.91$). LTD, LDWC with a very significant positive correlation with WUE (LTD, $r^2 = 0.97$) and LSP (LTD, $r^2 = 0.98$). LTD and Rp 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 ($r^2 = -0.95, -0.91$), Gs ($r^2 = -0.98, -0.93$), 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, $r^2 = 0.96$), Gs (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, $r^2 = -0.94$).

3.5 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 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, Ingwers, McGuire, & Teskey, 2017) and increase the transpiration rate (Trmmol) (Monteiro, Blanuša, Verhoef, Hadley, & Cameron, 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, Walter, & Rascher, 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). Ci is capable of determining the amount of carbon source providing plant photosynthesis (Tominaga, Shimada, & Kawamitsu, 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, Wu, Teng, and Yuan (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 (J. Z. Zhang, Shi, Shi, & Zhang, 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, Wang, Duan, Guan, & Wei, 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 CO₂saturation 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(Q. Dong, Li, Liu, & Liu, 2016). The maximum carboxylation rate (Vcmax) 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 Vcmax 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 (Rp) indicates the ability of plants to use high concentrations of O₂ for respiration to consume photosynthetic products under light conditions. The high Rp 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, García-López, Pistón, Pugnaire, & Olano, 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 (Brodribb & 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, Douma, & Verheijen, 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, Zhang, Guan, Li, & Hu, 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, Zhang, Qian, & Xue, 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, Kubiske, & Mostoller, 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, Gianoli, & Gomez, 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, Li, Ayup, & Xu, 2012). Thus, the plasticity of conducting tissue can enhance the ability of CB to absorb water and salt to better adapt to the environment.

4.4 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, Wang, Chi, & Tian, 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 Rp, consistent with the study of Ninemets U et al. suggesting that shade-loving plants exhibits thinner leaves, larger SLA, better photosynthetic capacity. LSP and Rd and chlorophyll a/b will be lower, and the chlorophyll concentration will be higher(Niinemets, Kull, & Tenhunen, 1998). With lower photosynthetic capacity, the water transpiration rate and Rp 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 Gs and Trmmol. 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, Heredia-Guerrero, & Heredia, 2011). UET shows a strong positive correlation with Rp and WUE, as well as a strong negative correlation with LUE and Trmmol. At high altitudes, plants gain more resources to sustain growth by increasing the thickness of their epidermal cells (Thakur, Rathore, & Chawla, 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 CO₂ utilization capacity, drought resistance and barren resistance. The advantage of CH is that CH can better adapt and maintain photosynthesis with the increase of Ta 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.

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Data Accessibility Statement

Data openly available in a public repository.

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Table:

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

Table 2 Light response curve parameters, CO₂response curve parameters

Spiece	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	Spiece	CH	CH	CH	CB	CB	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)	140.552±0.317 aA	0.225	0.016	126.530±1.023 bB	0.809	0.019
	LTD(mg·mm ⁻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)	3.327±0.050 bA	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±11.1785.665 aA		0.130
	VBA(um ⁻²)	8269.177±276.833 aA	3.48	0.079	5873.731±35.397 bA	0.603	0.015
	VA(um ²)	918.852±31.9973 aA	4.82	0.080	405.723±69.32017.086 bB		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

Figure:

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 (Pn), transpiration rate (Trmmol), stomatal conductance (Gs), CO₂ concentration (Ci), 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_i0.05 , **P_i0.01)

Figure 8. RDA analysis map between photosynthetic characteristics and leaf morphological characters and leaf anatomical traits

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