COMPARING DISTINCT LEAF FUNCTIONALITIES OF ACER RUBRUM AND ACER SACCHARUM UNDER EXTREMELY HIGH TEMPERATURES IN SUBTROPICAL REGIONS

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Abstract. *Acer* spp. plants are popular colorful foliage species used for landscape gardening, as their unique ornamental value is an important developmental resource for introduction and cultivation. For this study, *Acer saccharum* and *Acer rubrum* were employed as research models. *Acer buergerianum*, which is a native Chinese species of the same genus, was used as a control to compare differences in the anatomical characteristics of leaves, physiological photosynthetic parameters, and leaf construction costs of the three species and to explore their adaptability to extreme climatic conditions. The results revealed that the thickness of the leaf tissues and photosynthetic capacities of *A. rubrum* and *A. saccharum* were lower than that of *A. buergerianum*. Further, the costs of leaf construction for both *A. rubrum* and *A. saccharum* were significantly lower than that of *A. buergerianum*. Finally, *A. saccharum* had lower inputs in leaf construction, which facilitated the rapid occupation of higher ecological niches in suitable environments. However, in contrast to *A. saccharum*, *A. rubrum* possessed thicker succulent leaf tissues and strong photosynthetic capacity; thus, they were more likely to survive in hot dry environments. This study is informative for guiding selective plant introduction in subtropical regions.

Keywords: *adaptability, leaf construction cost, Acer spp., extreme climate, subtropics*

Introduction

Plant species with commercial value have been introduced into new habitats in large numbers over the centuries (e.g., Sitka spruce (*Picea sitchensis*) and Pecan (*Pseudotsuga menziesii*) (Wang et al., 2006; Zhang et al., 2015). In China, many exotic species have been introduced into botanical gardens and tree gardens, while the use of myriad ornamental plants in landscaping has increased considerably (Fang et al., 2021; Li et al., 2023a). Nevertheless, it is important to consider not only the commercial value of plant species in their selection, but also their ability to adapt to their new environments. Factors such as temperature, precipitation, soil, habitat, pests, and diseases may prevent plants from growing and developing properly (Long et al., 2017). Successful cases have demonstrated that plants introduced from similar habitats, or the same climate types,

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typically adapted more easily to new environments and were less difficult to domesticate. Consequently, they can be rapidly propagated and planted on a large scale (Zhu et al., 2019). For example, pecan has been cultivated on a large scale since it was introduced in China from the United States more than 100 years ago (Zhang et al., 2015). *Platanus orientalis*, introduced to China in the 19th century, is well enjoyed and loved by the Chinese people, with many regions using them as street trees and for landscaping (Cui et al., 2022; Shen et al., 2023).

Continual increases in global temperatures in recent years makes it possible for progressively more high-latitude plants to migrate to lower latitudes. But , the weather extremes associated with global climate change have also challenged the survival of introduced plants (Zhu et al., 2020). It has been suggested that heat stress becomes prominent when species are introduced from cold to warmer habitats. Plants may respond to environmental changes by altering their morphological traits, physiological and biochemical processes, and trade-offs in nutrient investments (Tang et al., 2021; Paing et al., 2021). Leaves are the most important and highly plastic organ exposed to the external environment, their structures, physiological, and biochemical characteristics reflect the impacts of environmental factors and plant responses to habitats (Ni et al., 2022). It has been revealed that elevated minimum temperatures and differences in monthly and seasonal precipitation limits the growth and development of *Caryopteris mongolia* (Yu et al., 2023). When the environment changes drastically, *Cunninghamia lanceolate* leaves enhance adaptation to the environment by increasing the cost of leaf development, while increasing nutrient investments to maintain their growth (Li et al., 2023b). The cost of leaf construction (CC) is one of the universally applicable indices for the evaluation and prediction of the invasive potential of plants, which can measure the energy invested in plant leaf development and reflect the energy allocation strategies of plants at the leaf level (Villar et al., 2001; Li et al., 2023b). Williams (2006) proposed that calculating leaf construction costs based on the leaf dry weight calorific values, leaf ash, and nitrogen contents may be employed to reflect the relationships between energy investments and repayments in constructed leaves, and evaluate the tolerance of plants against adversity. Some studies have found that invasive plants may enhance resource competitiveness by reducing leaf investments and increasing the accumulation biomass with lower energy investments (Williams et al., 2006).

Both *Acer rubrum* and *Acer saccharum* are *Acer* species originating from North America, which were introduced to China for urban parks and gardens due to the unique ornamental value of their leaves (Zhu et al., 2019). Influenced by latitude differences and climate types, these trees may suffer from certain physiological maladaptations when transferred from colder climates to subtropical China for cultivation. Furthermore, urban trees must struggle for their survival under higher warming patterns due to the urban heat island (UHI) effect (Percival, 2023). Although earlier studies demonstrated variations in the acclimatization of *A. saccharum* from different seed sources in subtropical regions (Zhu et al., 2019, 2020), the acclimatization of different species of North American *Acer* spp. plants to subtropical regions will require further exploration.

In the summer of 2022, China's Yangtze River basin region was hit by unusually persistent high temperatures and droughts, with maximum temperatures exceeding 40 degrees Celsius for 20 consecutive days in some areas, accompanied by a catastrophic drought that occurs once in 120-140 years, which posed new challenges for the survival of introduced plants of the *Acer* spp. (*Table 1*) (Liu et al., 2023b; Zhang et al., 2024). Consequently, for this study, we selected two *Acer* spp. plants (*A. rubrum*, and

A. saccharum) (introduced from Canada) as research models, and the native Chinese *A. buergerianum* as a control. There was before that, a common garden was established for experiments, where we focused on the structural characteristics of the plant leaves, photosynthetic properties, chlorophyll content, and differences in the costs of leaf development. This is to evaluate the acclimatization of the two North American maples. We hypothesized that 1) *A. rubrum* and *A. saccharum* are less environmentally adaptable than *A. buergerianum* and, 2) leaf construction cost for *A. rubrum* and *A. saccharum* is less costly than for *A. buergerianum*.

Table 1. *Climatic characteristics of the trial site and the country of origin (August 2022)*

Site	Ontario	Hefei
Latitude	43°40′ N	31°87′ N
Longitude	79°24′ W	117°23′ E
Warmest maximum temperature (°C)	19.37	40.1
Summer precipitation (mm)	81.9	52.0

Note: https://slt.ah.gov.cn/tsdw/swj/stbcjcypj/121204441.html and https://climate.weather.gc.ca/

Materials and methods

Experimental site and test materials

The study site is located in the experimental base of Anhui Agricultural University in Hefei City (31°87'N, 117° 25E), which has a subtropical humid monsoon climate, with a mean annual frost-free period of ~228 d, a mean annual air temperature of 15.8°C, annual precipitation of 1172 mm, a yellowish-brown loam soil with a deep texture, and a pH of from 5.8-6.1. In this study, two introduced *Acer* species (*A. rubrum*, and *A. saccharum*) were employed as the study models, whereas the native Chinese *Acer* species (*A. buergerianum*) was used as the control. The *A. rubrum* and *A. saccharum* seeds were purchased from the Forestry Seed Center of Ontario in 2013 and sown the same year. At the time of the experiments, the age of the seedlings was 10 y.

Experimental design

Seedlings of the three trees were planted in a 400 m^2 experimental garden in the fall of 2013, with 25 plants of each species. A 4 m isolation zone was set up in different plots to avoid interactions between groups (*Figure 1*). Uniform horticultural management was adhered to during planting.

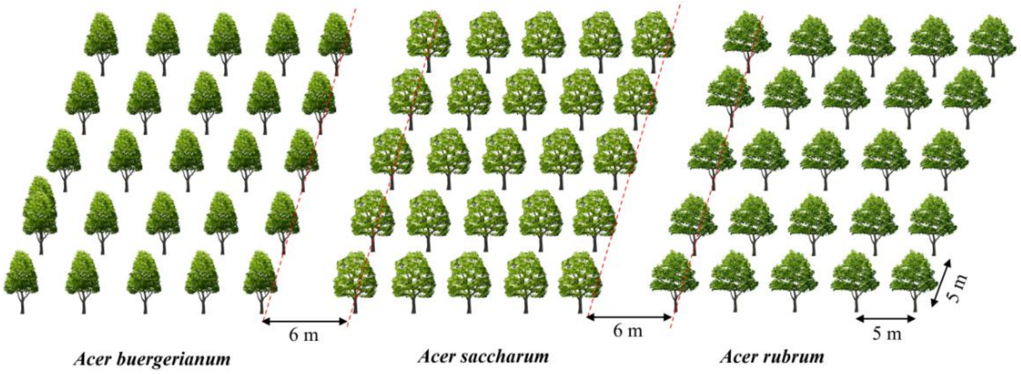

Figure 1. *Planting diagram of experimental garden*

Sampling and measurement

Photosynthetic physiology

In August 2023, 10 healthy plants from each tree species were randomly selected as experimental materials, from which the net photosynthetic rates (Pn, umol·m^{-2}·s^{-1}), stomatal conductance (Gs, mmol·m^{-2}·s^{-1}),leaf transpiration rates (Tr, mmol·m^{-2}·s^{-1}) and water use efficiency (WUE, mmol·mol^{-1})were measured using a LI-6400 Portable Photosynthesis System (LiCor, Lincoln, NE, USA) on a sunny day between 9:00 a.m. and 11:00 a.m (Li et al., 2020; Liu et al., 2021).

$$\mathrm{WUE}=\mathrm{Pn}/\mathrm{Tr} \tag{Eq.1}$$

Leaf structure

Healthy and mature leaves from the tree canopies were collected in four directions (east, south, west, and north), with 16 leaves collected from each plant. The collected leaves were placed into self-sealing bags, labeled, and transferred to the laboratory. Subsequently, they were washed and the central portions (0.5 x 0.5 cm) of the leaf blades were extracted, which retained the main veins. The samples were then fixed with a FAA solution for 24 h, dehydrated with gradient ethanol, made transparent with xylene, embedded in paraffin wax, sealed with neutral gum, and photographed for observation under a microscope. The thicknesses of the leaf blades and epidermis, as well as those of the fenestrated tissues and sponge tissues, were determined using ImageJ software(Liu et al., 2023a).

The leaves were treated via the nail polish blotting method, and the leaves of the different *Acer* spp. were fixed with FAA fixative for 24 h. They were then made into a carrier slice and placed under an optical microscope for observation, where the stomatal diameter, area, and densities were measured via ImageJ software (Liu et al., 2023a).

The *Acer* spp. leaf samples were placed in a 5% NaOH solution, fixed with FAA fixative for 24 h, boiled in a water bath for ~30 min until the leaf flesh was separated. Following boiling, the leaves were removed with tweezers, and placed into pure water, rinsed with distilled water several times, and then made into a carrier slice and placed under an optical microscope for observation. The diameters of the secondary leaf veins and the densities of the leaf veins were measured using ImageJ software (Carins Murphy et al., 2013).

Photosynthetic pigment content

Next, the leaf samples were segmented into thin filaments following the removal of the midrib. Weighed volumes (0.2 g) of the leaves were placed in 10 mL of acetone and anhydrous ethanol mixed in equal amounts in a test tube with a lid, and the extraction was carried out in darkness at room temperature. The absorbances at 663 nm, 645 nm, and 470 nm were determined using an ultraviolet spectrophotometer after 24 h of observation. Subsequently, the chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll content, and carotenoid values were calculated according to the formula (Li et al., 2017). Among them:

$$\mathrm{Chl\ a}=(12.72A_{663}-2.59A_{645})\times V/\,(W\times 1000) \tag{Eq.2}$$

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$$\text{Chl b}＝(22.88A_{663}-4.67A_{645})\times V/(W\times 1000) \quad \text{(Eq.3)}$$

$$\text{Total chlorophyll }＝(20.29A_{645}+8.05A_{663})\times V/(W\times 1000) \quad \text{(Eq.4)}$$

$$\text{Carotenoid} =(1000A_{470}-2.05\text{Chl a}-114.8\text{Chl b})\times V/(W\times 1000) \quad \text{(Eq.5)}$$

where, A is the absorbance value; V is the total volume of the extract, ml; and W is the fresh mass of the leaf, g.

Calorific value and ash content of leaf blade

The leaves were cleared at 105°C for 30 min, then dried at 65°C to balance the weight and crushed. The ash concentrations of the leaves were determined through combusting at 500°C in a muffle furnace for 6 h and weighing the remaining residue. The dry weight calorific value was determined using an oxygen bomb calorimeter (Model6400, Parr): Approximately 0.5 g of the plant sample powder was used to determine the calorific value following complete combustion. Three replicates were determined for each sample, where the average value was taken as the dry weight calorific value. Benzoic acid was used for calibration prior to the measurements. Construction cost per unit leaf dry mass (CC_m, $g\cdot glouse\cdot g^{-2}$) was estimated from ΔHc, N concentration, and Ash, according to (Williams et al., 2006):

$$CC_m = \frac{(0.06968H_C-0.065)\ \times(1-Ash)+\frac{7.5\times K\times N}{14.0067}}{0.87} \quad \text{(Eq.6)}$$

where, Hc is the calorific value of the leaf de-ash ($KJ\cdot g^{-1}$); Ash is the leaf ash content (%); k is the valence of the redox form of nitrogen (the most important source of nitrogen for higher plants under most field conditions is NO_3^-) so in this experimental calculation, k=+5; and N is the leaf nitrogen content ($mg\cdot g^{-1}$) (Li et al., 2011). The cost of leaf construction per unit area (CC_a, $g\cdot glucose.m^{-2}$) is the ratio of the cost of leaf construction per unit mass to the specific leaf area (SLA), i.e., $CC_a = CC_m/SLA$.

Statistical analysis

Microsoft Excel 2010 and SPSS Statistic 26 were used for the statistical analysis of the data. R 4.1. was employed for One-Way ANOVA to compare differences in the leaf structures, photosynthetic physiologies, photosynthetic pigment contents, and leaf construction costs of the different *Acer* spp. trees. The least difference significance method (LSD) was used to conduct the post-test, at a significance level of 0.05. The correlations between the quantitative indicators used Pearson's phase relationship, and all graphs were plotted using the“ggplot2”package (Ginestet, 2011).

Results

Structural differences in the leaves of different Acer spp.

The anatomical structures of the leaf blades of the *Acer* species under study reflected their drought resistance. Typically, thicker leaf tissues translated to a more robust plant resistance against drought. The thickness of the *A. buergerianum* leaf tissue was significantly higher than those of *A. rubrum* and *A. saccharum* ($p<0.05$). Conversely, the thickness of the *A. saccharum* leaf blades, upper epidermis, spongy and fence tissue were lowest among all three *Acer* spp. samples. It could be inferred that *A. buergerianum* was the most drought resistant species, while *A. saccharum* was less so (*Figure 2*).

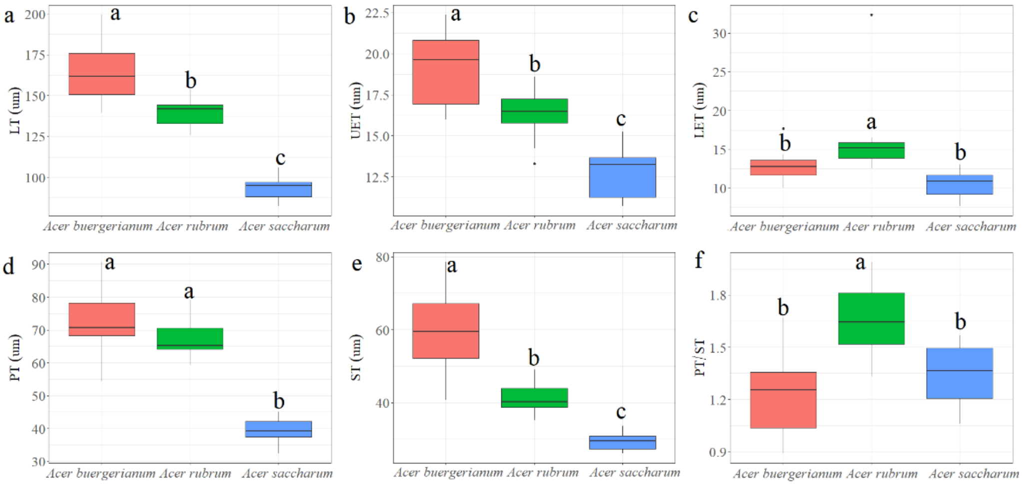

Figure 2. *Anatomical structure of leaves of different Acer species. LT, leaf thickness; UET, thickness of upper; LET, thickness of lower; PT, palisade tissue thickness; ST, sponget issue thickness. The significance level was p<0.05, with a 95% mean confidence interval, by LSD. Letters indicate variations between different treatments*

The characterization of the leaf stomata and veins of the three Acer species revealed that the leaf stomatal conductance of *A. buergerianum* was significantly higher than those of *A. saccharum* and *A. rubrum*. The leaf stomatal density of *A. buergerianum* was the highest at 846.78 no·per·mm^{-2}, with *A. saccharum* at 440.74 no·per·mm-2, followed by the lowest for *A. rubrum* at 357. 83 no·per·mm^{-2}. In contrast, the vein densities of both the fine leaves and leaves were significantly higher in *A. saccharum* and *A. rubrum* than for *A. buergerianum* ($p<0.05$), as they invested more in their leaf vein network systems (*Figure 3*).

Differences in photosynthetic capacities of the different Acer spp. samples

Among the three *Acer* samples under study, *A. buergerianum* possessed the highest leaf net photosynthetic rate, transpiration rate, and water use efficiency, which were significantly higher than those of *A. rubrum* and *A. saccharum* ($p<0.05$). In terms of the net photosynthetic rate, the order was *A. buergerianum* > *A. rubrum* > *A. saccharum* (*Figure 4*).

The quantification of the photosynthetic pigment contents of the leaves of the three *Acer* species indicated that the total chlorophyll, chlorophyll a, chlorophyll b, and carotenoid contents of *A. buergerianum* and *A. rubrum* leaves were not significantly different, albeit considerably higher than those of *A. saccharum* ($p<0.05$) (*Figure 5*). This suggested that *A. buergerianum* and *A. rubrum* had more potential for organic matter production than did *A. saccharum* under the same conditions in the subtropics.

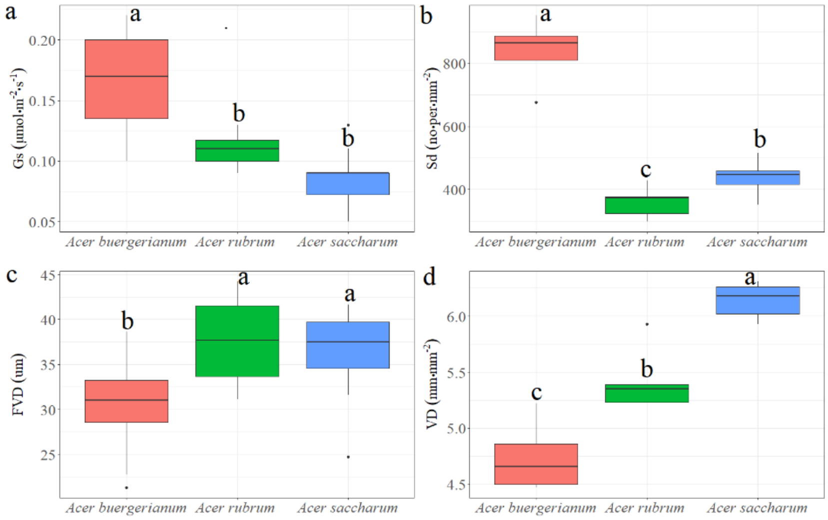

Figure 3. *Characteristics of stomata and veins in different Acer species. Gs, Stomatal conductance; Sd, Stomatal diameter; FVD, Fine vein diameter; VD, Vein density. The significance level was p<0.05, with a 95% mean confidence interval, by LSD. Letters indicate variations between different treatments*

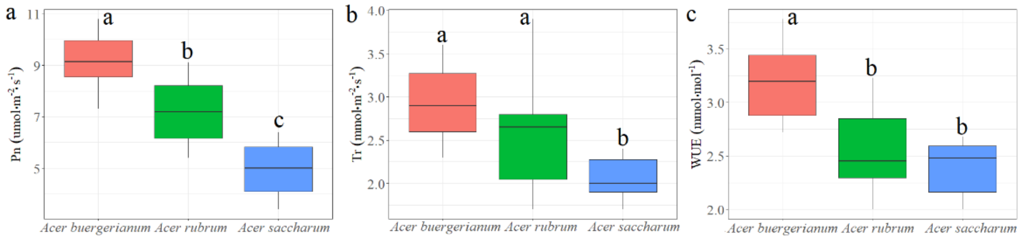

Figure 4. *Photosynthetic indexes of different Acer species. Pn, net photosynthetic rates; Tr, leaf transpiration rates; WUE, water use efficiency. The significance level was p<0.05, with a 95% mean confidence interval, by LSD. Letters indicate variations between different treatments*

Differences in leaf construction between Acer spp. samples

Among the three *Acer* spp. samples *A. buergerianum* had the highest cost of leaf construction per unit mass (2.19 g·glouse·g^{-2}), which was 78.04% higher than that of *A. saccharum* (1.23 g·glouse·g^{-2}) and 45.03% higher than that of *A. rubrum* (1.51 g·glouse·g^{-2}). *A. buergerianum* also had the highest cost of leaf construction per unit area (178.29 g·glouse·m^{-2}), which was 78.80% higher than *A. rubrum* (99.71 g·glouse·g^{-2}) and 191.60% higher than *A. saccharum* (61. 14 g·glouse·m^{-2}). In terms of specific leaf area, the maximum specific leaf area of *A. saccharum* leaves was significantly higher than that of *A. buergerianum* and *A. rubrum* (*Figure 6*).

Pearson correlation analysis showed that CC$_m$ and CC$_a$ were significantly positively correlated with the LT, UET, PT, ST, Pn, Tr, WUE, Gs, and photosynthetic pigments. However, they were highly significantly negatively correlated with the VD ($p < 0.01$), while for the specific leaf area CC$_a$ was significantly negatively correlated with the LT, UET, PT, ST, Pn, Tr, WUE, Gs, and photosynthetic pigments and substantially positively correlated with the VD ($p < 0.05$). This indicated that thicker leaves with higher photosynthetic capacities increased the cost of leaf construction (*Figure 7*).

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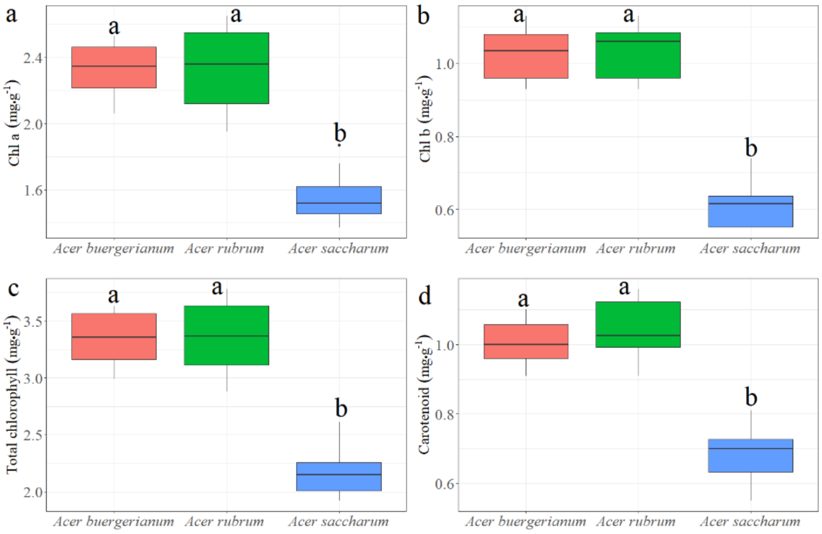

Figure 5. *Photosynthetic pigments of different Acer species. Chl a, chlorophyll a; Chl b, chlorophyll b. The significance level was $p<0.05$, with a 95% mean confidence interval, by LSD. Letters indicate variations between different treatments*

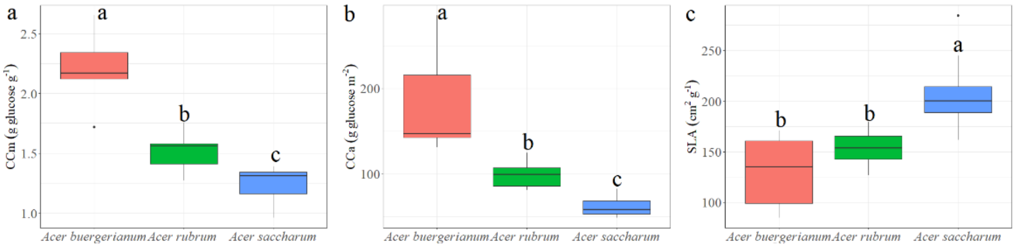

Figure 6. *Different leaf construction costs of the three Acer species. CC_m, Construction cost per unit leaf dry mass; CCa, Construction cost per unit leaf dry area; SLA, specific leaf area. The significance level was $p<0.05$, with a 95% mean confidence interval, by LSD. Letters indicate variations between different treatments*

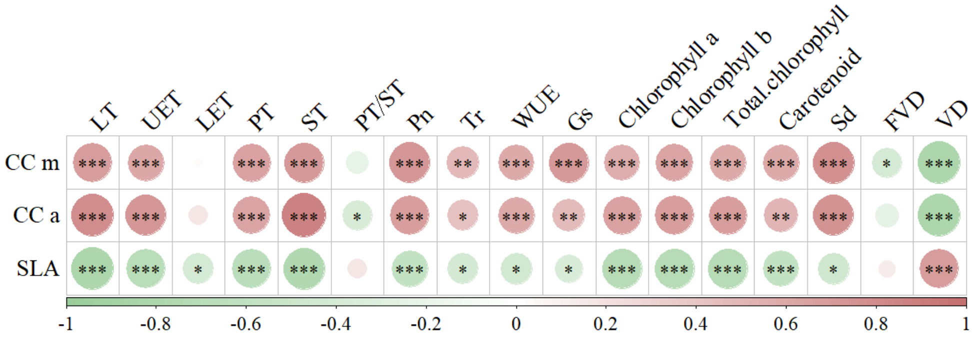

Figure 7. *Correlations between leaf construction costs with leaf structures and photosynthetic characteristics. LT, leaf thickness; UET, thickness of upper; LET, thickness of lower; PT, palisade tissue thickness; ST, sponget issue thickness; Pn ,net photosynthetic rates; Tr, leaf transpiration rates; WUE, water use efficiency; Gs, Stomatal conductance; Chl a, chlorophyll a; Chl b, chlorophyll b; Sd, Stomatal diameter; FVD, Fine vein diameter; VD, Vein density*

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Discussion

Structural characteristics of Acer leaf blades

Plant leaves are sensitive to environmental changes during growth and development and have strong plasticity; thus, the anatomical structures of leaves can reflect, to a certain extent, the adaptability of plants to adversity induced stress (Wu et al., 2022). In general, leaf fenestration organization and epidermal thickness are adaptations to arid habitats. A thicker epidermis can effectively prevent strong light irradiation from consuming too much water via transpiration, and tight fenestration organization is also conducive to the storage of water, which makes plants more drought-resistant (Tian et al., 2016; Ni et al., 2022). Earlier research results as to the anatomical structures of the leaf blades of *Populus euphratica*, *Quercus pubescens*, and other plants suggested that the thicker the leaf epidermis, fenestrated tissues, and leaf blades, the more drought-resistant the plant will be (Li et al., 2015; Song et al., 2021; Laoué et al., 2024). Consistent with our expected results, *A. buergerianum* leaves had a thicker epidermal layer and fenestrated tissues, which effectively prevented water evaporation. They also exhibited stronger water retention functions, and likely possessed stronger adaptations to arid environments. This was followed by *A. rubrum*, while *A. saccharum* had thinner leaves, and thereby a weaker water retention capacity. Thus, they were less adapted to drought than *A. buergerianum* and *A. rubrum*, which aligned with some preceding results (Zhu et al., 2019).

Stomata are interfacial channels for gas and water exchange in plant leaves, which play important roles in maintaining stable carbon levels, while regulating hydraulic structures and nutrient uptake in plants (Guo et al., 2023; Alon et al., 2024). Through the regulation of stomatal density and size, plants are able to achieve more efficient CO_2 assimilation and H_2O exchange to adapt to environmental vagaries (Guo et al., 2023). *A. buergerianum* was found to possess small and dense stomata that balanced the gas exchange area and enabled a faster response rate to the environment. Further, it had strong drought resistance, a higher net photosynthetic rate, and improved regulation under drought conditions with the morphology of a typical arid plant. This was consistent with the findings of Cao (2019), who found, after studying the anatomical structures of the leaves of seven species of *Morus alba*, that small and dense stomata were more favorable to plant survival under drought conditions. There were no significant differences in the stomatal density between *A. saccharum* and *A. rubrum*; however, the stomatal dimensions of *A. rubrum* were significantly larger than that of *A. saccharum* ($p<0.05$). In terms of stomatal characterization, those of *A. rubrum* were weaker than *A. saccharum* in their response to drought stress. The spatial relationships between veins and stomata have been shown to have the potential to greatly influence gas exchange efficacy relative to carbon investments (Fiorin et al., 2015). It is generally accepted that species with higher secondary vein densities have higher photosynthetic rates and hydraulic conductivity (He et al., 2024). In this study, leaf vein density and fine vein diameter of *A. saccharum* and *A. rubrum* were significantly larger than that of *A. buergerianum* ($p<0.05$), and *A. saccharum* and *A. rubrum* invested more photosynthetic products into the construction of the leaf vein network system to ensure the “safety” of water transport (Walls, 2011).

Leaf photosynthetic physiology

The robustness of the photosynthetic abilities of plant leaves determines their capacity for organic matter production, which is correlated with the survival and development of individual plants (Nión et al., 2024). The chlorophyll content and net photosynthetic intensity are key indicators of a plant's photosynthetic capacity. The concentrations of chlorophyll a, chlorophyll b, and total chlorophyll of *A. rubrum* and *A. buergerianum* in this study were significantly greater than those of *A. saccharum*; thus, their photosynthetic capacities were also greater. This was consistent with the net photosynthetic intensity of the leaves, which demonstrated the superiority of the organic matter production capacity of *A. rubrum* over *A. saccharum* under high temperature arid environments, which provided material security for the survival of the species. On one hand, this might have been related to the photosynthetic optimal temperature of *A. saccharum*, which was previously shown to range from 27°C - 31°C (Gunderson et al., 2000); however, the experimental temperatures were clearly beyond this range. Drought affects stomatal closure, and reduced stomatal conductance limits photosynthesis (Damour et al., 2009), as was evidenced by the stomatal conductance characteristics (*Figure 3*).

Leaf construction costs

Leaf construction costs are intimately related to the leaf economics spectrum and may reflect, to some extent, the strategies of plants to adapt to their environments (Villar et al., 2001). The high cost of leaf construction typically implies higher resilience, while a low leaf construction cost represents a higher growth rate (Li et al., 2021, 2023b). *A. buergerianum* had significantly larger CC_a and CC_m than the other two *Acer* species, as well as a stronger environmental adaptability. This may have been due to the fact that *A. buergerianum* (as a native tree species) was better adapted to local climatic characteristics, which confirmed the conjecture of our hypothesis 2. In contrast, introduced *Acer* spp. species invested more photosynthetic energy into their leaf structures, defenses against pests and diseases, and growth and reproduction, which was consistent with the results of previous similar studies (Li et al., 2011; Barros et al., 2020). The specific leaf area can reflect a plant's growth responses to some extent, where plants with high SLA have a greater ability to maintain nutrients. Exotic plant species usually have a higher specific leaf area compared with native species (Kaur et al., 2024), which was consistent with our findings. Barros et al. (2021) suggested that exotic species exhibited a lower CC_a and higher SLA than native species in new environments as an adaptive mechanism. In this way, more nutrients were significantly positively correlated with photosynthetic pigments and intensity. This suggested that larger leaves were primarily applied to improving the photosynthetic physiology of plants and to enhance tissue structures.

Conclusion

The results of this study revealed that under extremely high temperatures and drought conditions, the leaf tissue thickness and net photosynthetic rate of *A. rubrum* were significantly higher than that of *A. saccharum* ($p<0.05$) with an improved accumulation of photosynthetic organic matter and better adaptation to the environment. The CC_m and CC_a of *A. buergerianum* were 78.04% and 191.60% higher than that of *A. saccharum*, and 45.03% and 78.80% higher than that of *A. rubrum*. It proved that *A. buergerianum* puts more photosynthetic products into the construction of leaves, while the introduced maple puts photosynthetic products into the construction of other structures. Our results provide a reference for cross-regional plant introductions, as well as a guide for landscape tree planning.

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