Comments to the authors.

The paper has potential for publication, however, it lacks important information for acceptance for publication. The introduction does not contextualize the central problem of the paper, there are no hypotheses and the objective is not clear. The methodology lacks several pieces of information about how the paper was carried out. The main problem is the statistical analysis performed; in my opinion, another analysis should be performed to compare the four sources. Since the analysis used in the paper is not consistent with what the authors wanted to demonstrate, the results and discussion are scattered throughout the manuscript. I have included some correction suggestions in the attached file.

Introduction

The introduction lacks contextualization of the paper's theme. The authors need to improve the definition of the problem. The paper has no hypotheses. Improving the contextualization of the introduction will help the authors to support the hypotheses. What is the problem of the paper? What is the central question of the paper? The objective of the paper needs to be clear.

Methodology

What is the sample size? This information needs to be included. There is a lot of missing information in the methodology. Mainly how many individuals were measured. Include a topic about the statistical analyses. Explain in detail which analyses were performed. I could not understand which analysis was performed. I would like to emphasize the importance of detailing the statistical analysis. I suggest that you compare the four different sources. Perhaps a one-way ANOVA would be more appropriate.

Results

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Discussion

The discussion gives a general idea of what happened to the plants in the study, however, the authors did not compare four sources (note: at least the text does not indicate this), so it should be rewritten after the suggested corrections.

Conclusion

You cannot conclude this way. Not without the other suggested corrections.

Elucidation of the adaptability of *Cinnamomum camphora* seedlings from different provenances via analyzing photosynthetic characteristics and anatomical structure

Yufeng Liu[1,2], Yanmeng Guo[1,2], Ruobing Zou[1,2], Yu Ji[1,2], Mengyuan Li[1,2],Yang You[1,2]

1 College of Horticulture and Landscape Architecture, Henan Institute of Science and Technology, Xinxiang 453003, Henan, China
2 Henan Engineering Technology Research Center of Characteristic Horticultural Plants Development and Utilization, Henan Institute of Science and Technology, Xinxiang 453003, Henan, China
Corresponding Author: Yang You
College of Horticulture and Landscape, Henan Institute of Science and Technology, Xinxiang, Henan, 453003, China;
Email address: Youyang1028@126.com

Abstract:

This study compared the adaptability of *Cinnamomum camphora* seedlings from various provenances to provide insights into the practice of garden introduction. Three-year-old *Cinnamomum camphora* seedlings from four different provenances were grown in the same environment in Henan Province. The variations in photosynthetic parameters, stomatal characteristics, and anatomical structures, as well as the influence of provenance climate on leaf characteristics and overall photosynthetic capacity, were assessed. The results revealed that the net photosynthetic rates of *C. camphora* seedlings from four different provenance sites exhibited a "double-peak" curve and a photosynthetic "lunch break" phenomenon, which was strongly positively correlated with stomatal conductance, transpiration rate, and SPAD value. Obviously different in stomatal characteristics were observed among the seedlings from four provenances. The seedlings from Fuzhou and Wuhan exhibited larger stomatal width, area, resulting in superior stomatal gas exchange than that in the seedlings from other provenances. Conversely, *C. camphora* seedlings from Shanghai exhibited smaller stomatal area and density, indicating poorer gas exchange and reduced adaptability. The stem cortex cells, stem phloem, stem pith diameter, leaf palisade tissue thickness, and leaf thickness of the seedlings from Shanghai were significantly lower than those of the seedlings from other provenances, indicating that these structural characteristics do not exhibit any photosynthetic advantages over other provenances. In contrast, the seedlings from Fuzhou and Wuhan exhibited larger stem pith diameter, thicker mesophyll cell , and greater leaf thickness, which enhanced their photosynthetic capabilities. Among the seedlings from the four different origins, those from Fuzhou and Wuhan exhibited the best overall photosynthetic ability and strongest adaptability. Conversely, the seedlings from Shanghai exhibited the poorest overall photosynthetic ability and weakest adaptability. Despite similarities in climate, the environmental conditions of different provenances did not appear to have a significant correlation with leaf anatomy. This study provided

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valuable insights for the introduction of *C. camphora* in various regions in China.

Keywords: provenances; *Cinnamomum camphora* seedlings; photosynthetic characteristics; anatomical structures

Introduction

Plant species with widespread distribution typically exhibit a high degree of intraspecific variation in functional traits, which is reflected in their phenotypic diversity. This diversity may originate from genetic differences arising because of local adaptation and phenotypic plasticity (Ren et al, 2020). Investigating the environmental adaptability of plants has a significant practical value for their conservation, cultivation, and introduction. To examine the influence of environmental and genetic factors on physiological and ecological traits of plants, researchers have conducted common garden experiments by planting specimens from different provenances in the same environment. This method eliminates the confounding effects of provenance-related environmental factors and facilitates the assessment of adaptive traits in plants, including the establishment of stable inheritance (Albaugh et al., 2018).

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For many years, the study of plant photosynthesis has been a major focus in ecology, plant physiology, and environmental restoration (Yang, Yang & Gao, 2023). Photosynthesis is a critical process through which plants metabolize, accumulate metabolites, and grow (Luo, Wang & Zeng, 2020), and it is influenced by both environmental and physiological factors. Key photosynthetic parameters, such as net photosynthetic rate (Pn), transpiration rate (Tr), and stomatal conductance (Gs), can reflect the growth status of plants (Gao, 2023) and provide a foundation for deeper understanding of plants' adaptability. Stomata are essential for leaf function, acting as valves that regulate the exchange of carbon and water between plant leaves and the atmosphere. Their evolution has enabled early land plants to successfully transition from marine to terrestrial environments (Mcadam et al., 2021; Wang, 2015). The degree to which stomata open and close directly impacts vital physiological processes in plants, including transpiration, photosynthesis, and respiration (Liu et al., 2018). The position of stomata changes throughout the leaf growth process, gradually becoming fixed until the leaf matures (Yang, Chen & Xian, 2023). Stomatal characteristics not only influence the microenvironment but also respond to climate change (Simonin & Roddy, 2018). Stomatal traits, including density, shape, and size, result from long-term adaptations of plants to external environmental factors during evolution and are highly sensitive to environmental changes (Zhu, Kang & Liu, 2011). Stomatal parameters are predominantly assessed to reflect plants' responses to climate change (Hu, Ji & An, 2015). The leaves of angiosperms serve as the most direct and sensitive organs for sensing environmental conditions such as light, temperature, and water. The phenotypic characteristics of leaves directly reflect the quality and growth status of the plant (Zhang et al, 2023). The anatomical structure of plant leaves is influenced by the long-term natural environment. Changes in the thickness of epidermal cells, palisade tissue, and sponge tissue in leaves affect the photosynthetic regulation of plants (Bacelar et al, 2004), and leaf anatomy primarily regulates the adaptation of plants to light (Niinemets & Tenhunen, 1997).

Cinnamomum camphora L. Presl. is a significant tree species in the subtropical regions of China, primarily distributed in the southern areas of the Yangtze River, where it often occurs as an associated species in natural settings (Leng, Wan & Liu, 2023). The roots, stems, and leaves of *C. camphora* emit a distinct camphor aroma and exhibit various pharmacological activities including antibacterial, antioxidant, anti-inflammatory, insecticidal, analgesic, and anticancer (Zhang et al., 2019). *C. camphora* holds considerable potential for development and application in horticultural therapy. Additionally, *C. camphora* plays a vital role in soil and water conservation and environmental protection, which can absorb atmospheric smoke and dust and exhibit strong resistance to harmful gases such as sulfur dioxide (Wang et al., 2024). Current research on *C. camphora* primarily focuses on physiological changes under stress (Zhang, Zhang & Gan, 2014; Zhao & Li, 2016; Wang et al., 2019; Chen et al., 2024; Luo et al., 2020; Luo et al., 2019)and gene expression (Liu, 2020). However, studies employing common garden experiments to investigate the adaptation mechanisms of *C. camphora* from different provenances are scarce.

This study aimed to explore the adaptive responses of *C. camphora* seedlings from four different provenances using common garden experiments. Their photosynthetic characteristics, stomatal traits, anatomical structures, and other relevant factors were compared. This study will provide valuable insights for the introduction of *C. camphora* in northern Chinese regions.

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1 Materials and methods

1.1 Experimental site

The experimental site is located at Xindong Farm in the Hongqi District of Xinxiang City, Henan Province (E113°87′, N35°30′). This region has warm temperate continental monsoon climate, characterized by four distinct seasons: cold winters, hot summers, cool autumns and dry spring. Annual average temperature of approximately 14 °C. The highest recorded temperature reaches approximately 42.7 °C, whereas the lowest drops to approximately −21.3 °C. The annual average air relative humidity is 68%, and the maximum depth of frozen soil is 280 mm. Annual average precipitation is 656.3 mm, with the peak occurring from June to September accounting for approximately 409.7 mm or 72% of the total annual precipitation often accompanied by heavy rainfall. The average annual sunshine duration is approximately 1928.5 h. The frost-free period lasts approximately 220 days. The soil pH is approximately 8.2, and the surrounding vegetation primarily consists of artificially planted experimental tree species and crops.

1.2 Experimental material

Table 1 shows the details regarding the area from which the test materials were collected. The seeds of *C. camphora* from various provenances were germinated using a stratification treatment before cultivating in pots. On April 7, 2023, the

3-year-old seedlings were transferred to Xindong Farm for field maintenance. The planting spacing was 1 m × 1 m, and consistent field management measures were implemented. Prior to planting the seedlings, an appropriate amount of urea and compound fertilizer was applied to the test field. After planting, adequate root watering was performed. Additionally, urea and compound fertilizer were regularly administered on a monthly basis. The seedlings were watered, and soil was loosened and mulched according to prevailing weather conditions, along with weeding and other cultural management practices.

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1.3 Experimental design

1.3.1 Leaf photosynthetic parameters

From October 28, 2023, for 3 consecutive days of favorable weather, the Li-6400XT portable photosynthesis measurement system (Li-Cor, Lincoln, Nebraska, USA) was used to measure various photosynthetic parameters. Measurements were conducted hourly from 9:00 to 17:00 each day, with each measurement completed within 30 min. The gas parameters assessed included net photosynthetic rate (Pn), stomatal conductance (Gs), transpiration rate (Tr), and intercellular CO_2 concentration (Ci). Additionally, water utilization efficiency(WUE = $Pn \cdot Tr^{-1}$) and the limit value for stomatal conductance (Ls = $1 - Ci \cdot Ca^{-1}$) were calculated. The primary real-time external factors monitored included leaf vapor pressure difference (VPD), Ta, and RH. The instrumental environmental parameter settings were as follows: leaf chamber light intensity 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and flow rate 500 $\mu mol \cdot s^{-1}$. Relative chlorophyll content was assessed using a SPAD-502 chlorophyll meter (Konica Minolta, Japan). From each provenance, five experimental seedlings exhibiting robust and uniform growth were selected and marked, ensuring that no obstructions were present between the measured leaves. Each leaf underwent repeated measurements yielding five sets of data, which were subsequently averaged.

1.3.2 Leaf stomatal characteristics

The timing for stomatal measurements and criteria for test strain selection were aligned with those for photosynthetic parameter measurements. Measurements were conducted bi-hourly from 9:00 to 17:00 daily, with each measurement completed within 30 min, using the methods by Kübarsepp et al. (Kübarsepp et al., 2020) involving the blotting technique. This technique involved the use of transparent, non-elastic nail polish to capture imprints of the lower epidermis of the leaves. These imprints were mounted on a microscope slide using a tape, and observations were made using an optical microscope at 40× magnification. The epidermal imprint was observed from below, and 10 fields of view were randomly selected for image capture. ImageJ software was used to measure stomatal length (SL), width (SW), area (SS), and density (DS). The average of measurement data from each provenance site was calculated.

1.3.3 Anatomical structure of stems and leaves

On October 28, 2023, annual branches and leaves of seedlings were collected, with

5–6 samples taken from each site. For leaf sampling, a segment measuring 1.0 mm on each side of the midrib was obtained, resulting in a total length of approximately 3.0–5.0 mm. For branch sampling, a smooth, knotless section of similar length was selected. The samples were fixed (using 50% FAA fixative), dehydrated, embedded in paraffin, sliced, dewaxed, stained, and sealed to obtain complete tissue sections suitable for microscopic observation. ImageJ software was used to measure upper and lower epidermis thickness (UET, LET), palisade tissue thickness (PT), spongy tissue thickness (ST), mesophyll thickness (MT), and leaf thickness (LT). Additionally, the stem epidermal cell thickness (EpT), cortical cell thickness (CoT), xylem thickness (XyT), phloem thickness (PhT), and pith diameter (PiD) were recorded. The palisade to spongy tissue ratio (P/S (= PT/ST), cell structure compactness (CTR (= TP/LT), and cell structure looseness (SR (= ST/LT) were calculated.

1.3.4 Data processing

ImageJ software was used to measure stem and leaf anatomies and stomatal data. Excel 2020 was used for data processing and visualization. The SPSS 2023 data processing system was used for data analysis. Additionally, Origin 2024 was used to create correlation heatmaps. Comprehensive membership function formulas (1) and (2) were applied for calculations, where X_j represents the measured value of indicator j at provenance site i, and X_{min} denotes the minimum value. If a positive correlation exists between the measured index and growth, membership function (1) is used; conversely, if a negative correlation is observed, the inverse membership function (2) is applied. The detailed methodology is given by Xu et al. (Xu et al., 2022).

The membership function value formula is given by:

$$U(X_j) = (X_j - X_{min})/(X_{max} - X_{min}) \quad (1)$$

The inverse membership function value formula is expressed as:

$$U(X_j) = 1 - (X_j - X_{min})/(X_{max} - X_{min}) \quad (2)$$

2 Results

2.1 Environmental parameters

The diurnal variations of environmental factors at the measurement site are illustrated in Figure 1. Both the overall air temperature (Ta) and leaf vapor pressure difference (VPD) initially exhibited an increasing trend, followed by a decrease. An upward trend was observed in the morning, reaching a peak between 11:00 and 14:00, followed by a downward trend. However, the relative humidity (RH) within the sample chamber displayed an opposite trend. At noon, leaves transpire significant amount of water, resulting in a higher VPD, which indicates greater transpiration demand. Consequently, VPD serves as a more accurate reflection of the water storage and loss in leaves. Both Ta and VPD increased between 11:00 and 14:00, contributing to the observed decrease in RH.

2.2 Photosynthetic characteristics

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The net photosynthetic rate (Pn) of seedlings from the four provenances exhibited a “double-peak” curve. Notably, the Pn values for the seedlings from Fuzhou (FZ), Shenzhen(SZ), and Wuhan (WH) provenances were low at 12:00. However, the seedlings from Shanghai (SH) exhibited the lowest Pn value at 14:00, demonstrating a photosynthetic “lunch break” phenomenon (Figure 2A). The daily average Pn for the seedlings across four provenances followed this order: WH > FZ > SZ > SH (Table 2). The trends in stomatal conductance (Gs) and transpiration rate (Tr) were generally similar; the seedlings from FZ, SZ, and WH exhibited low values at 12:00 and 16:00. Conversely, for the seedlings from SH, Gs and Tr peaked at 12:00 before dropping to low levels at 16:00 (Figures 2B and D). The daily average Gs and Tr for the seedlings exhibited a trend of FZ > WH > SZ > SH (Table 2), with considerable differences observed between the seedlings from SH and those from FZ and WH. The intercellular carbon dioxide (CO_2) concentration (Ci) of all seedlings displayed a trend opposite to that of the stomatal limitation value (Ls) and water utilization efficiency (WUE) (Figures 2C, E, and F). Specifically, Ci for the seedlings from SH peaked at 12:00, coinciding with low values of Ls and WUE. In contrast, seedlings from FZ, WH, and SZ exhibited minimum Ci value at 14:00, with Ls peaking at this time and WUE peaking at 15:00. No significant differences were observed among the daily average Ci, Ls, and WUE of *C. camphora* seedlings across the four provenances. Additionally, the SPAD values for the seedlings from SH were significantly lower than those for the seedlings from other provenances, exhibiting a trend of WH > SZ > FZ > SH (Table 2).

The RH was significantly negatively correlated with the WUE (Table 3). Furthermore, the VPD was extremely significantly negative correlated with the Pn and SPAD value ($P < 0.01$), while exhibiting a significant negative correlation with Gs and Tr. This suggested that the WUE of camphor is a crucial factor influencing environmental humidity. Furthermore, VPD was identified as a significant environmental variable that induces diurnal variations in Pn, Gs, and Tr.

2.3 Stomatal characteristics

The observation of the lower epidermis of *C. camphora* seedlings revealed that the stomata and guard cells exhibited a spindle shape, whereas the lower epidermal cells (LE) were square, rectangular, or round(Figure 3). No significant difference was observed in stomatal length (SL) and stomatal width (SW) among the seedlings from different provenances (Table 4); however, the difference in stomatal area (SS) between the seedlings from SZ and FZ was more considerable. Notably, SW and SS were positively correlated. Considerable variation in stomatal density (DS) existed among the seedlings from four provenances. Specifically, no significant difference was observed in DS among the seedlings from FZ, SZ, and WH. In contrast, DS of the seedlings from SH was significantly different from that of seedlings from WH and SZ but was not significantly different from that of seedlings from FZ. DS exhibited the following trend: SZ > WH > FZ > SH, whereas SS exhibited the following trend: FZ > WH > SH > SZ. DS and SS exhibited an inverse relationship in the seedlings from FZ, WH, and SZ. A significant positive correlation was observed between SL of the seedlings and the longitude of the provenance ($P < 0.05$; Table 5). Additionally, SS was significantly correlated with annual average temperature, annual rainfall, and the altitude of the provenance. DS and provenance latitude exhibited a highly significant negative correlation ($P < 0.01$). The geographical gradient indicated that SL increases from south to north, whereas DS decreases from west to east. Furthermore, higher average temperatures, annual rainfall, and provenance altitudes were associated with smaller SS.

2.4 Anatomical structure of the stems and leaves

The primary functions of the stem are transportation and support. In the stems, the epidermis has a protective role, whereas the cortex comprises multiple layers of parenchyma cells that contain chloroplasts for photosynthesis. The xylem is responsible for transporting water and inorganic salts, whereas the phloem transports photosynthetic products to various plant organs, with nutrients stored in the pith. In the anatomical structure of *C. camphora* stems, various tissue components exhibited notable morphological differences, and the epidermis, cortex, and stele were distinctly identifiable (Figure 4). The lacunar and parenchyma tissues in the cortex of seedlings from different provenances were well-differentiated and developed, with vascular bundles forming distinct annular strips. The cortical cell (Co) consisted of several layers of parenchyma cells that exhibited uneven thickness among the seedlings from various sources, and the boundaries of the vascular columns were clearly defined. The thickness of the stem cortical cell (CoT), thickness of the phloem (PhT), and pith diameter (PiD) were significantly greater in the seedlings from FZ, SZ, and WH than in those from SH (Table 6). This indicated that the photosynthetic conditions of the stems of seedlings from SH were inferior to those of the stems of seedlings from other provenances, resulting in lower nutrient storage.

Plant leaves serve as the primary organs for photosynthesis. Epidermal cells of the leaves of *C. camphora* seedlings were closely arranged, featuring a visible cuticle membrane (Figure 4). The leaf palisade tissue was situated in the upper part of the leaf (ventral surface), whereas the spongy tissue was located in the lower part (dorsal surface), characteristic of typical heterofacial leaves. The spongy tissue thickness (ST) of the leaves of *C. camphora* seedlings from four provenances was consistently thicker than the palisade tissue thickness (PT). The palisade tissue, palisade to spongy tissue ratio (P/S), and structural compactness (CTR) of *C. camphora* seedlings from WH and SZ were significantly thicker than other provenances, indicating that their leaf structural characteristics were more conducive to photosynthesis. In contrast, the upper epidermal thickness (UET), PT, mesophyll cell thickness (MT), leaf thickness (LT), P/S, and CTR of the seedlings from SH were thinner than those of the seedlings from other provenances, suggesting that the leaf photosynthetic structures of the seedlings from SH were somewhat less effective.

The latitude of the provenance was significantly negatively correlated with UET ($P < 0.05$) and was extremely significantly negatively correlated with the P/S and CTR ($P < 0.01$; Table 8). Additionally, it was very significantly positively correlated with structural looseness (SR). From west to east, the geographical gradient exhibited a gradually decreasing trend for UET, P/S, and CTR and a gradually increasing trend for SR. Furthermore, annual rainfall and ST were significantly negatively correlated ($P < 0.05$), and soil pH and LET were significantly positively correlated ($P < 0.05$).

2.5 Correlation analysis

Using the Pearson product-moment correlation coefficient calculation method, a correlation coefficient matrix was obtained for each individual indicator, and a correlation heatmap was constructed for these indicators (Figure 4). The Pn was significantly positively correlated with Gs, Tr, and PT; very significantly positively correlated with the SPAD value; and significantly negatively correlated with lower epidermis thickness (LET). Furthermore, Gs was very significantly positively correlated with Tr, suggesting that stomatal behavior is a crucial factor influencing transpiration. The stomata were primarily located in lower epidermis of the leaves (Figure 4) and were significantly negatively correlated with LET (Figure 5). Chloroplasts, predominantly observed in the palisade tissue, were positively correlated with PT. It is indicated that chlorophyll content and stomatal presence in leaves are the vital factors affecting photosynthesis. CO_2 serves as the primary raw material for plant photosynthesis, with intercellular CO_2 primarily accumulating in the stomatal gap. In this study, Ci was significantly negatively correlated with WUE and significantly positively correlated with ST, indicating that the *C. camphora* seedlings from various sources can effectively utilize CO_2 for photosynthesis. Simultaneously, water can be effectively utilized to enhance the accumulation of organic matter. Tr and SPAD value were significantly positively correlated, indicating that the intensity of visible photosynthesis directly influences WUE. Conversely, Tr and WUE were negatively correlated. Under the conditions of drought, high temperature, or other stressors, plants typically reduce water consumption by decreasing Tr, thereby reallocating more water for the synthesis of organic matter to adapt to their environment. Furthermore, CoT and PhT were very significantly positively correlated. CoT refers to the thickness of cortical cells containing chloroplasts in plant stems, which leads to the seedlings appearing green in color. PhT serves as a conduit for transporting photosynthetic products within plant stems and is closely linked to the process of photosynthesis. In this study, SW was significantly positively correlated with SS. DS was significantly positively correlated with P/S, very significantly positively correlated with CTR, and negatively correlated with cell SR. This indicated that the short axis of the stomatal pore is a crucial factor influencing SS, and it was hypothesized that PT and ST are important determinants affecting DS.

2.6 Comprehensive evaluation of the photosynthetic capacity

To thoroughly assess the advantages and disadvantages of *C. camphora* seedlings from different provenances, their photosynthetic capacity and related indicators were comprehensively evaluated using the membership function analysis method. Among the evaluated indicators, the Ls, WUE, xylem thickness (XyT), LET, and SR were negatively correlated with photosynthetic indicators. Consequently, the inverse

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membership function calculation formula was employed to calculate their function values. In contrast, other indicators exhibited positive correlations with photosynthetic indicators, for which the standard membership function calculation formula was used. The average membership functions of *C. camphora* seedlings from different provenances were subsequently ranked (Table 9). FZ、WH and SH provenances exhibited the highest (0.781、0.746) and lowest (0.066) average membership function values, respectively, with the values exhibiting the trend of FZ > WH > SZ > SH. This suggested that the overall performance of *C. camphora* seedlings from FZ was superior, and that of the seedlings from SH exhibited the least favorable comprehensive performance.

3 Discussion

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3.1 Photosynthetic and stomatal characteristics

Stomatal closure is recognized as a primary factor contributing to decline in Pn (Figueras et al., 2004). In this study, Pn of *C. camphora* seedlings from four provenances exhibited a "double-peak" curve. The trends in Pn, Gs, and Tr were largely congruent (Figures 2A, B, and D), with a positive correlation among the three variables (Figure 5). This suggested a synergistic relationship between stomatal opening and Pn. Both stomatal and non-stomatal limitations influence photosynthesis (Rao & Chaitanya, 2016). Farquhar et al. (Farquhar & Sharkey, 1982) suggested that a decrease in Pn, accompanied by an increase in Ls and decrease in Ci, indicates that the decline in Pn is primarily due to stomatal factors; conversely, if Ls decreases and Ci increases, non-stomatal factors become the main contributors to the reduction in Pn. In *C. camphora* seedlings from FZ, SH, and SZ, Ls increased but Ci decreased at noon, suggesting that stomatal closure was the principal reason for the decline in Pn. Conversely, in *C. camphora* seedlings from WH, Ls decreased and Ci increased, indicating that non-stomatal factors were the primary cause of the reduction in Pn. These findings demonstrated that under high temperature and intense light conditions at noon, plants adjust Gs to optimize CO_2 fixation from the atmosphere while mitigating the adverse effects of strong radiation and elevated temperatures. The Pn of *C. camphora* seedlings from SH was significantly lower than that of seedlings from other provenances (Figure 2A). This reduced photosynthetic capacity indicated weaker adaptability of the seedlings from SH than those from other provenances. Decrease in Gs and leaf water potential contributes to lowering Pn, which in turn reduces assimilate production and ultimately leads to reduced growth and yield (Nikinmaa et al., 2013). The stomata serve as the primary channels for two essential processes: entry of CO_2 into the mesophyll cells during photosynthesis and water loss through transpiration. The efficiency of gas exchange is determined by DS and SS (Sack &Buckley, 2016). In this study, the short axis of the stomata and SS were significantly positively correlated (Figure 4), suggesting that SS is primarily influenced by the angle of stomatal opening and closing. Differences in SS and DS were observed among the seedlings from four provenances (Table 3). Notably, except for SH, smaller SS correlated with greater DS in other three provenances. This is consistent with the results of Cao et al. regarding mulberry stomata (Cao et al., 2020).

Specifically, SS exhibited a trend of FZ > WH > SZ, whereas DS exhibited a trend of SZ > WH > FZ. The SW and SS of *C. camphora* seedlings from FZ and WH were higher, suggesting that they were better at gas exchange than the seedlings from other provenances. WUE, defined as the dry mass produced per unit mass of water consumed, reflects the relationship between leaf water consumption and material accumulation (Wu, Tian & Xie, 2020). Pn of *C. camphora* seedlings from FZ was lower than that of seedlings from WH and SZ. However, the seedlings from FZ exhibited the highest Tr; consequently, their WUE was the lowest among the seedlings from four provenances, indicating greater photosynthetic water requirement and higher overall tolerance, although with reduced drought resistance. The photosynthetic capacity of plants is closely linked to the content of chlorophylls, which not only capture and transmit light energy but also facilitate its conversion (Hu et al., 2010). The relative chlorophyll content of *C. camphora* seedlings exhibited a trend of WH > SZ > FZ > SH (Table 2), and the chlorophyll content was observed to be extremely significantly positively correlated with Pn.

3.2 The anatomical structure of stems and leaves

Compared with the seedlings from SH, the CoT, PhT, and PiD of the stems of *C. camphora* seedlings from FZ, SZ, and WH were significantly higher, facilitating the accumulation of photosynthetic pigments. The accumulation of photosynthetic products is linked to transportation. Therefore, the photosynthetic conditions in FZ, SZ, and WH were superior to those in SH. Changes observed in the upper and lower epidermises of leaves and P/S provide evidence of the plants' ability to adapt to varying environmental conditions (Oliveira et al., 2018). In this study, the ST was higher than the PT under natural conditions without stress, which is consistent with the findings of Afas et al. (Afas, Marron & Ceulemans, 2007) in poplar leaves. Chloroplasts are predominantly located in palisade tissue of leaves, which are closely linked to photosynthetic efficiency (Silva & Santos, 2023). In our study, PT was significantly positively correlated with both Pn and SPAD values. Leaf anatomical features, including the epidermis, palisade, and spongy parenchyma, are finely tuned to optimize WUE and photosynthesis (Ackerson & Krieg,1977). In our study, ST was significantly negatively correlated with Ls and WUE and significantly positively correlated with Ci. Additionally, LET was significantly negatively correlated with Pn, Tr, and SPAD values (Figure 5). Palisade tissue serves as the primary site for chloroplasts in plant leaves and is integral to leaf photosynthesis. ST is located adjacent to lower epidermis, with the interstitial spaces within ST serving as the primary sites for CO_2 storage in plants. Consequently, thicker ST leads to enhanced CO_2 storage, which is intricately linked to photosynthesis and associated reactions. It is evident that the parameters of PT and ST are critical indicators influencing various photosynthetic metrics. In this study, the leaf PT, P/S, and CTR of seedlings from WH and SZ were significantly higher than those of the seedlings from other provenances, suggesting that the seedlings from WH and SZ possess superior photosynthetic structures. Conversely, UET, PT, MT, LT, P/S, and CTR of seedlings from SH were observed to be the lowest, indicating a less effective photosynthetic structure.

Based on the anatomical examination of the stems and leaves of *C. camphora* seedlings from the four provenances, it can be concluded that the photosynthetic structure of seedlings from SH was the least favorable. Furthermore, this study reported extremely significant or significant positive correlation between CTR and both DS and P/S, whereas SR was significantly negatively correlated with DS and P/S. It was speculated that PT and ST also influence plant photosynthesis by affecting DS.

3.3 Adaptability of *Cinnamomum camphora* seedlings

Plants' adaptation to the environment is a complex process. The structure of leaf tissue is sensitive to surrounding environmental conditions, and leaf morphological characteristics are closely related to plant growth strategies and resource utilization (Yu et al., 2019). In this study, significant or extremely significant differences were observed in the anatomical structure of *C. camphora* leaves (specifically, UET, P/S, CTR, and SR) across different geographical distribution areas, indicating that these plants have undergone local adaptation. However, the correlation between the anatomical structure of *C. camphora* leaves and other environmental factors of the original provenance appears weak; this suggested that though environmental factors influence *C. camphora* leaves, their contribution is relatively minor (Table 8). Moreover, all original provenances of *C. camphora* have subtropical monsoon climate, where there has been no significant change in the climatic environment. Our findings are consistent with those of Chen et al., who examined changes in the leaf functions of *Machilus pauhoi* seedlings from various provenances under common garden environments (Chen et al., 2019). Despite the adaptability of the test materials, which have undergone 3 years of growth in a common garden, notable differences in the anatomical structure of leaves persist among various sources. This variability may arise from the varying degree of adaptability to garden environment exhibited by the seedlings.

4 Conclusions

Commented [RC11]: They cannot conclude that way. Not without the indicated corrections.

The ability of a single index to evaluate the adaptability of plants is limited. Through the comprehensive evaluation of the photosynthetic characteristics and anatomical structure of *C. camphora* seedlings, suggested that seedlings from SH provenance were inferior to those of *C. camphora* seedlings from other provenances, resulting in reduced competitiveness (Table 9). In contrast, the seedlings from FZ and WH exhibited strong photosynthetic capacity, superior stem and leaf structure, that enhances the plants' stress resistance. These seedlings exhibited larger SW and SS, and moderate SD which is advantageous for gas exchange. Collectively, these traits were observed to promote photosynthesis, increase organic matter accumulation, enhance overall properties, and improve competitiveness compared with the seedlings from other provenances (Table 9). Leaf PT, P/S, CTR, and chlorophyll content were the critical determinants of the photosynthetic capacity of *C. camphora* seedlings across the four provenances. Though variations were observed in the adaptability of *C. camphora* seedlings from different provenances to the same environment, the differences in leaf structure among the seedlings from provenances with similar climatic conditions were not significantly influenced by the environmental factors of their original provenance. This suggested a potential relationship with their intrinsic adaptability. Our findings provided a vital theoretical foundation for the introduction and cultivation of *C. camphora* in various regions and provided insights for the selection of provenances and conservation of genetic resources in the future.

Acknowledgments

My deepest gratitude goes first and foremost to Professor You, for constant encouragement and guidance. Without supporting of his project, this thesis could not have reached its present form. Second, I would like to express my heartfelt gratitude to my fellow classmates, Ji Yu, Guo Yanmeng and Zou Ruobing, who gave me their help in my experiment.

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