

# Study on the Photosynthetic Characteristics of Six Varieties (Strains) in Chinese Chestnut

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**Abstract** [Objectives] This study was conducted to investigate the differences of photosynthetic physiological characteristics of different varieties (strains), which will provide a theoretical basis for high photosynthesis efficiency breeding and application in Chinese chestnut. [Methods] Six Chinese chestnut varieties of *Castanea mollissima* ‘Yanbao’, *C. mollissima* ‘Yanqiu’, *C. mollissima* ‘Yanchang’, *C. mollissima* ‘Yanjia’, *C. mollissima* ‘Qianxi 37’, and *C. mollissima* ‘Hybrid 22’ were used as the materials. Using the portable photosynthesis system Li-6400, we measured the photosynthetic characteristics and diurnal variation of leaf samples of six different chestnut varieties or strains. We fitted the light response curves and photosynthetic parameters using the leaf floating model. Additionally, we determined the chlorophyll content in the leaves using a UV-visible spectrophotometer. [Results] Among the six chestnut varieties or strains, ‘Yanqiu’ exhibited a significantly higher photosynthetic light saturation point ( $P_{LSP}$ ) compared to other five varieties, and ‘Hybrid 22’ ranked second, indicating that these two varieties had the strongest adaptation to high light intensity. The photosynthetic light compensation point ( $P_{LCP}$ ) of ‘Yanchang’ was significantly higher than other five varieties, and ‘Qianxi 37’ ranked second, indicating that these two varieties had the strongest adaptation to low light intensity. Additionally, they exhibited higher chlorophyll content and maintained good photosynthetic characteristics even in shaded environments with weak light stress. Varieties ‘Yanbao’ and ‘Yanjia’ showed higher  $P_{LSP}$  and lower  $P_{LCP}$ , indicating that these two varieties have a wider range of adaptation to light intensity. They were capable of efficiently utilizing light across a broader spectrum of intensities. ‘Yanqiu’ had the highest maximum net photosynthetic rate ( $P_{n,max}$ ) and the lowest dark respiration rate ( $R_d$ ), along with the highest chlorophyll content. It indicated that ‘Yanqiu’ has strong photosynthetic capacity and organic matter accumulation ability. It also had the highest  $P_{LSP}$ , enabling it to fully utilize the high light environment of the Yanshan Mountains and possessed high light efficiency characteristics. The  $P_{n,max}$  of ‘Yanqiu’ was significantly higher than other varieties. ‘Hybrid 22’ and ‘Yanbao’ also exhibited significantly higher  $P_{n,max}$  compared with ‘Yanjia’ and ‘Qianxi 37’. ‘Yanchang’ had the lowest  $P_{n,max}$ . The order of  $P_{n,max}$  among the six chestnut varieties or strains was as follows: ‘Yanqiu’ > ‘Hybrid 22’ > ‘Yanbao’ > ‘Yanjia’ > ‘Qianxi 37’ > ‘Yanchang’. [Conclusions]

**Key words** Chinese chestnut; Diurnal variation of photosynthesis; Light response model; Light response curve; Chlorophyll

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It is of great significance to utilize mountains which are forbidden areas for crop production to produce as much food as possible. Chinese chestnut (*Castanea mollissima* BL.) is the world’s most important edible chestnut, with top production, quality, and stress resistance among all edible chestnuts in the world. It is an ideal “woody grain” suitable for cultivation in mountainous areas and sandy wastelands. Photosynthesis is the most important process for fruits to obtain assimilates accumulation. Ninety to ninety-five percent of the dry matter accumulated in fruits originates from photosynthesis, while only five to ten percent comes from mineral elements in soil<sup>[1]</sup>. As an ecologically-oriented woody grain tree species, Chinese chestnut is increasingly receiving attention. But the biggest challenge in Chinese chestnut production lies in its low yield per unit area, and enhancing

photosynthesis is an effective approach to break through the yield limit<sup>[2-8]</sup>. Like other plants, studying the photosynthesis of plants can help explain and speculate on the energy absorption, fixation, allocation, and conversion in the growth, development, and substance accumulation of chestnuts under the influence of internal and external factors.

Currently, research on photosynthetic efficiency in Chinese chestnut is significantly lagging behind. Few studies have been conducted on the photosynthetic characteristics of different chestnut varieties<sup>[9-13]</sup>. Studying the photosynthetic physiological characteristics of different varieties (strains) can provide a theoretical basis for the selection of high photosynthetic efficiency breeding parents for Chinese chestnuts<sup>[14]</sup>. This study used six new Chinese chestnut varieties and excellent strains as test materials: ‘Yanbao’, ‘Yanqiu’, ‘Yanchang’, ‘Yanjia’, ‘Qianxi37’ and ‘Hybrid 22’. By studying their diurnal variation of photosynthesis, photosynthetic parameters, light response curves and leaf chlorophyll content, the photosynthetic characteristics of the six new varieties and strains were revealed. For photosynthetic parameters and light response curves, the leaf gas exchange model<sup>[15]</sup> was used for fitting. The leaf gas exchange model has been widely applied to fit photosynthetic parameters and light response curves

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in various plants such as summer maize, walnut, and bamboo<sup>[16–18]</sup>. The leaf gas exchange model has unique advantages compared to rectangular hyperbola models and non-rectangular hyperbola models because both rectangular hyperbola and non-rectangular hyperbola models lack equations for extreme values, thus they can only fit light response curves of plants in the absence of light inhibition. In contrast, the leaf gas exchange model has extreme values and can directly determine the maximum net photosynthetic rate and light saturation point without making any assumptions based on the equations<sup>[16]</sup>. The differences in photosynthetic characteristics among different Chinese chestnut varieties were studied by analyzing relevant parameters and combining with leaf chlorophyll content analysis, providing a theoretical basis for the breeding and promotion of high photosynthetic efficiency in Chinese chestnut.

## Materials and methods

### Materials

The experimental materials were four new Chinese chestnut varieties, namely ‘Yanbao’, ‘Yanqiu’, ‘Yanchang’ and ‘Hybrid 22’, and two excellent strains: ‘Yanjia’ and ‘Qianxi37’. Each variety or strain consisted of three plants, grafted and grown for six years. The experiment was conducted at the experimental base of Hebei Normal University of Science and Technology in Changli County, Qinhuangdao City, Hebei Province, China (39.55° N, 119.10° E). Plants of *Castanea mollissima* ‘Yanshanduanzhi’ were used as rootstocks, which were five years old at the time of grafting. The cultivation management conditions of each variety or strain were consistent, and their growth was all moderate.

### Methods

**Determination of diurnal variation in gas exchange parameters** The experiment was conducted on July 25, 2023 (with clear weather), and healthy mature leaves from the middle portion of the consistently growing one-year-old shoots were selected. An LI-6400 portable photosynthesis analyzer, produced by LI-COR Company in the United States, was used. The photosynthetic diurnal variation of the leaves was measured from 8:00 AM to 6:00 PM on the same day. A total of five leaves were measured, with three repeated measurements for each leaf. Measurements were taken every 2 h. The main measured parameters included net photosynthetic rate [ $P_n$ ,  $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ ], stomatal conductance [ $G_s$ ,  $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ ], intercellular carbon dioxide concentration ( $C_i$ ,  $\mu\text{mol}/\text{mol}$ ), transpiration rate [ $T_r$ ,  $\text{mmol}/(\text{m}^2 \cdot \text{s})$ ] and photosynthetic active radiation [PAR,  $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ ].

**Measurement of the light response curve** The experiment was conducted on July 26, 2023 (a clear weather) between 9:00 – 11:00 AM. Three healthy and mature leaves from the middle portion of consistent-growing one-year-old shoots were measured for photosynthetic characteristics and after that the leaves were picked for pigment content determination. The light intensity gradients were set as follows: 2 000, 1 500, 1 200, 1 000, 750, 500, 300,

150, 100, 50, 20, 10 and 0  $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ , and the carbon dioxide concentration was set at 400  $\mu\text{mol}/\text{mol}$ , and the air flow rate was set at 500  $\text{mmol}/\text{s}$ . Using the photosynthesis assistant software, the characteristics of the Chinese chestnut light response curve were analyzed. The leaf photosynthesis model was used to fit the curve and obtain the parameter values for Apparent Quantum Yield ( $\eta_{\text{AQY}}$ ,  $\text{mol}/\text{mol}$ ), Light-saturated Point [ $P_{\text{LSP}}$ ,  $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ ], Light Compensation Point [ $P_{\text{LCP}}$ ,  $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ ], Dark Respiration Rate [ $R_d$ ,  $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ ] and Maximum Net Photosynthetic Rate [ $P_{n, \text{max}}$ ,  $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ ].

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

In the equation,  $P_n$  represented net photosynthetic rate;  $I$  represents light intensity;  $\alpha$  represented the initial quantum efficiency of the plant's photosynthetic response curve at  $I=0$ ;  $P_{n, \text{max}}$  represented the maximum net photosynthetic rate;  $R_d$  represented the dark respiration rate;  $\theta$  represented the curvature parameter reflecting the degree of curve of the light response curve, with a value of  $0 < \theta \leq 1$ ;  $\beta$  represented the light inhibition term; and  $\gamma$  represented the light saturation term.

**Measurement of photosynthetic pigment contents** For each variety, ten of healthy and mature leaves from the middle portion of consistent-growing one-year-old shoots from different orientations of the tree were selected to measure photosynthetic pigment contents, ten leaves per variety for each of the five replicates were taken as materials. The 95% ethanol extraction method was used for determination<sup>[19]</sup>. A 0.4 g of fresh sample the surface of which had been cleaned to remove any dirt was cut into small pieces (removing the midrib) and ground into a fine powder, which was then transferred into a stoppered test tube. Next, 10 ml of 95% ethanol was added into the test tube using a pipette. After the leaves turned pale, the chlorophyll extraction solution was poured into a 1 cm cuvette. Next, 95% ethanol was used as a blank control and the absorbance values at wavelengths of 663, 645 and 470 nm were measured using a UV spectrophotometer. The concentrations of chlorophyll a, chlorophyll b, total chlorophyll and carotenoids were calculated.

$$\text{Ca (Chla)} = 12.2A_{663} - 2.81A_{646}$$

$$\text{Cb (Chlb)} = 20.13A_{646} - 5.03A_{663}$$

$$\text{Ct (Chlorophyll)} = \text{Ca} + \text{Cb} = 17.32A_{646} + 7.18A_{663}$$

$$\text{Cx} \cdot \text{c (Carotenoid)} = (1\,000A_{470} - 3.27\text{Ca} - 104\text{Cb})/229$$

Ca, Cb, Ct and Cx · c refer to the concentrations of chlorophyll a, chlorophyll b, total chlorophyll and carotenoids respectively.  $A_{663}$ ,  $A_{646}$  and  $A_{470}$  represents the absorbance values of the chloroplast pigment extraction solution at wavelengths 663, 645 and 470 nm, respectively.

After obtaining the pigment concentrations, the content of each pigment in the leaves was calculated using the following formula:

Pigment content = Pigment concentration (mg/L) × Extraction solution volume (L) × Dilution factor/Sample fresh weight (g)

**Data analysis** Statistical analysis and graphical representation of the experimental data were performed using Excel 2010, SPSS 26.0 and GraphPad Prism8.

## Results and Analysis

### Daily variation of photosynthetic parameters for six Chinese chestnut varieties (or strains)

**Diurnal variation of net photosynthetic rate in different varieties or strains** From Fig. 1, it could be observed that diurnal variation curves of net photosynthetic rate ( $P_n$ ) for the six chestnut varieties (strains) were all bimodal, indicating the presence of a photosynthetic ‘midday depression’ phenomenon. The first peak occurred at 10:00, while the second peak occurred at 14:00. The daily average net photosynthetic rate of the ‘Yanqiu’ was significantly higher than other five varieties (strains). The order of daily average net photosynthetic rate, from the highest to the lowest, was ‘Yanqiu’ > ‘Hybrid22’ > ‘Yanbao’ > ‘Yanjia’ > ‘Qianxi37’ > ‘Yanchang’, with peak values reaching 15.435, 14.910, 14.576, 13.940, 13.940, 12.472, 12.377  $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ , respectively.

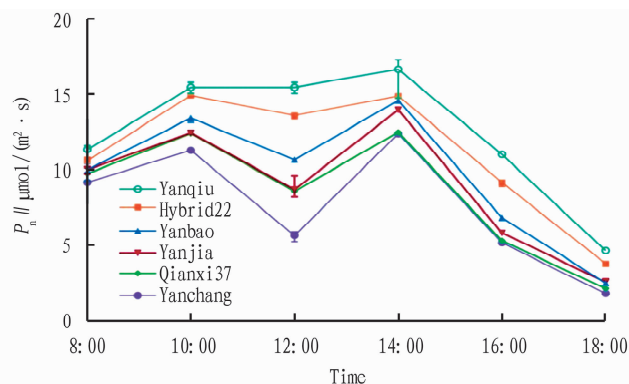


Fig. 1 Diurnal variation of net photosynthetic rate ( $P_n$ ) of the six Chinese chestnut varieties or strains

**Diurnal variation of stomatal conductance in different varieties or strains** From Fig. 2, it could be observed that diurnal variation curves of  $G_s$  for the six chestnut varieties (strains) were all bimodal, the first peak occurred at 10:00, while the second peak occurred at 14:00. All six varieties (strains) reached their maximum stomatal aperture at 14:00, with peak values of 0.426, 0.357, 0.320, 0.295, 0.300 and 0.307  $\text{mol}/(\text{m}^2 \cdot \text{s})$ . The order of daily average stomatal conductance from the highest to the lowest was ‘Yanqiu’ > ‘Hybrid22’ > ‘Yanbao’ > ‘Yanchang’ > ‘Qianxi37’ > ‘Yanjia’.

**Diurnal variation of intercellular carbon dioxide concentration in different varieties or strains** From Fig. 3, it could be observed that the diurnal variation curves of  $C_i$  in the six chestnut varieties (strains) showed lower concentrations in the morning and higher concentrations at noon, exhibiting an upward, downward and upward trend. The occurrence of a low value at 14:00 might indicate a decrease in light intensity after 14:00, triggering the opening of stomata and an increase in  $G_s$ , resulting in the consumption of a large amount of carbon dioxide. The peak values for

‘Yanqiu’ and ‘Hybrid22’ occurred at 12:00, while the peak values for ‘Yanbao’, ‘Yanjia’, ‘Qianxi37’ and ‘Yanchang’ occurred at 10:00. Both ‘Yanqiu’ and ‘Hybrid22’ exhibited a low value at 14:00, while ‘Yanbao’, ‘Yanjia’, ‘Qianxi37’ and ‘Yanchang’ showed a low value at 12:00. The order of daily average  $C_i$  was ‘Yanqiu’ > ‘Hybrid22’ > ‘Yanbao’ > ‘Yanjia’ > ‘Qianxi37’ > ‘Yanchang’.

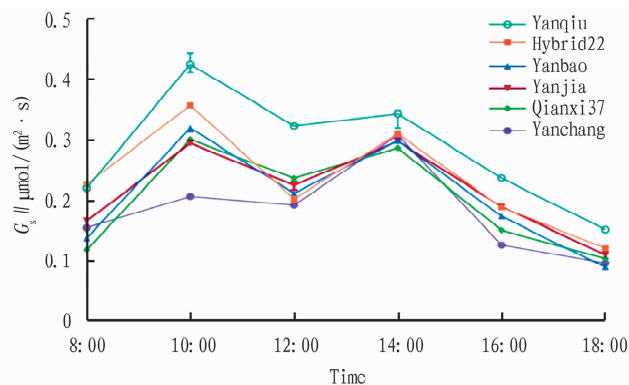


Fig. 2 Diurnal variation of  $G_s$  of the six Chinese chestnut varieties or strains

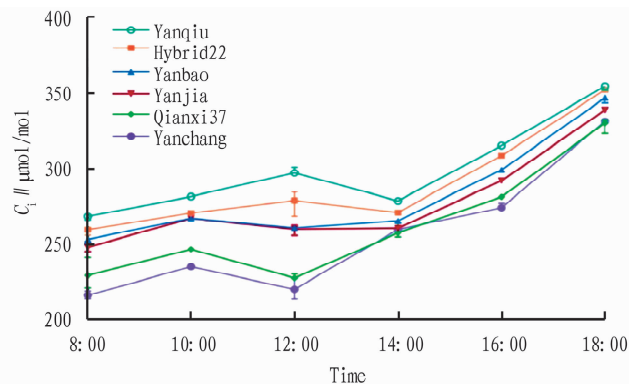


Fig. 3 Diurnal variation of  $C_i$  of six Chinese chestnut varieties or strains

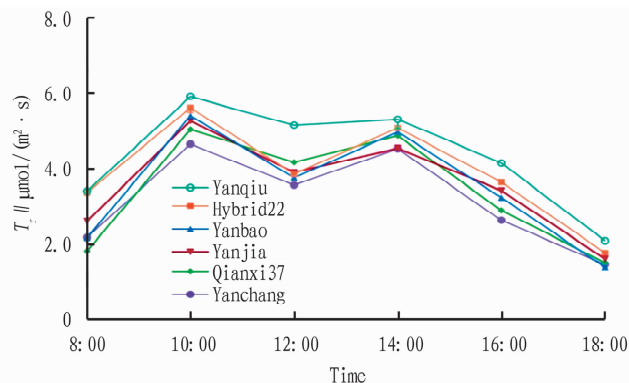


Fig. 4 Diurnal variation of  $T_r$  of the six chestnut varieties or strains

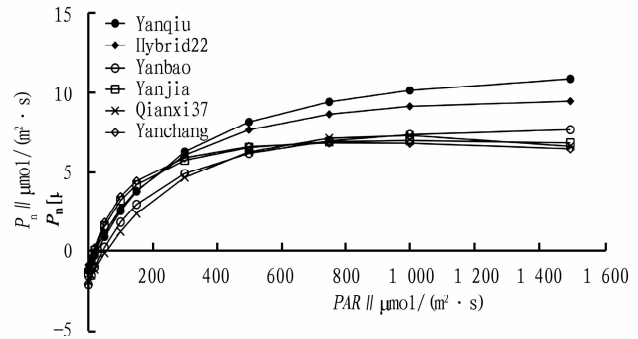
**Diurnal variation of transpiration rate in different varieties or strains** From Fig. 4, it could be observed that the diurnal variation curves of transpiration rate ( $T_r$ ) in the six chestnut varieties (strains) were all bimodal, with the first peak occurring at 10:00

and the second peak occurring at 14:00. The peak values of transpiration rate ( $T_r$ ) coincided with  $P_n$  and  $G_s$ , with higher transpiration rates in the morning compared to the evening. The peak value in the morning was higher than the peak value at noon, as the plants experience increased water loss due to intense sunlight during midday. ‘Yanqiu’ had the highest daily average  $T_r$ , while ‘Yanchang’ had the lowest. The order of daily average transpiration rate was ‘Yanqiu’ > ‘Hybrid22’ > ‘Yanbao’ > ‘Yanjia’ > ‘Qianxi37’ > ‘Yanchang’.

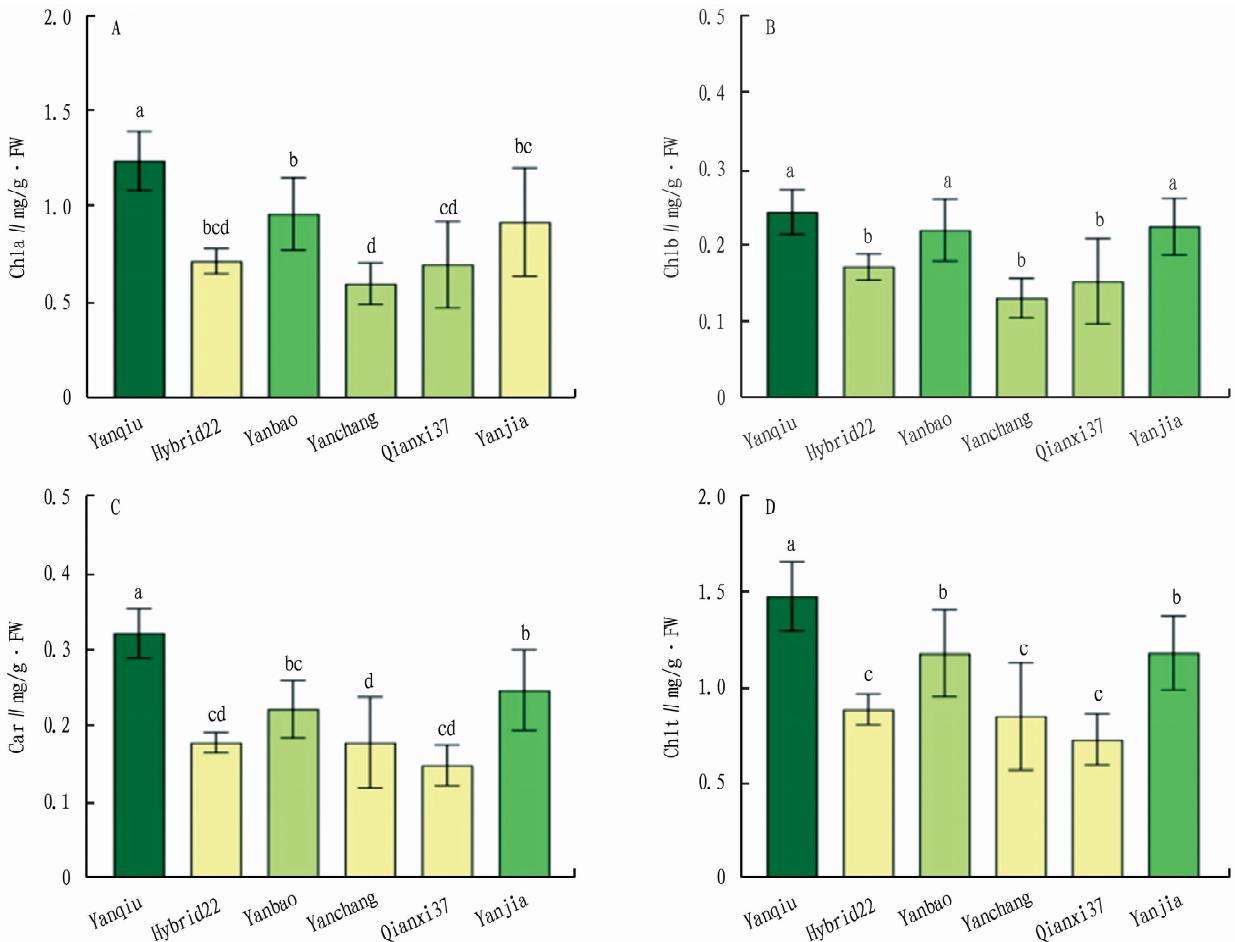
#### Comparison of light response curves and characteristic parameters among the six Chinese chestnut varieties or strains

From Fig. 5, it could be observed that the light response curves of the six varieties (strains) exhibited similar patterns. The net photosynthetic rate increased with increasing light intensity, but reached a plateau after reaching a certain value, indicating that it no longer increased with further increase in light intensity. When the photosynthetically active radiation (PAR) reached  $50 \mu\text{mol}/(\text{m}^2 \cdot \text{s})$ , ‘Yanchang’, ‘Qianxi37’, ‘Yanjia’ and ‘Yanbao’ exhibited negative values for net photosynthetic rate, while ‘Yanqiu’ and ‘Hybrid 22’ had positive values for net photosynthetic rate. When PAR reached  $200 \mu\text{mol}/(\text{m}^2 \cdot \text{s})$ , the net photosynthetic differences between each variety or strain started to increase. As PAR increased to  $800 \mu\text{mol}/(\text{m}^2 \cdot \text{s})$ , the net

photosynthetic rate of the ‘Yanchang’ variety tended to saturate. When PAR reached  $1000 \mu\text{mol}/(\text{m}^2 \cdot \text{s})$ , the net photosynthetic rates of ‘Qianxi 37’, ‘Yanjia’ and ‘Yanbao’ tended to saturate. However, the net photosynthetic rate of ‘Yanqiu’ and ‘Hybrid 22’ still showed an upward trend. When the net photosynthetic rate was positive, the order of the net photosynthetic rates with increasing photosynthetically active radiation was always ‘Yanqiu’ > ‘Hybrid22’ > ‘Yanbao’ > ‘Yanjia’ > ‘Qianxi37’ > ‘Yanchang’.



**Fig. 5** Optical response curves of different Chinese chestnut varieties (strains)



**Fig. 6** Chlorophyll contents of different Chinese chestnut varieties (strains)

**Table 1** Characteristic parameters of optical response curve of 6 chestnut varieties (strains)

Varieties (strains)	$\eta_{AQY}$ // mol/mol	$P_{LSP}$ // $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$	$P_{LCP}$ // $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$	$P_{n, \max}$ // $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$	$R_d$ // $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$
Yanqiu	0.037 ± 0.001 b	1 380.18 ± 117.738 a	54.235 ± 1.461 b	15.402 ± 0.926 a	1.058 ± 0.298 c
Hyrid 22	0.031 ± 0.000 c	1 158.803 ± 12.726 b	58.797 ± 0.434 a	8.976 ± 0.030 b	1.724 ± 0.047 a
Yanbao	0.038 ± 0.000 a	1 078.603 ± 10.078 bc	19.144 ± 0.025 c	8.326 ± 0.016 b	1.212 ± 0.004 bc
Yanjia	0.038 ± 0.001 a	1 012.915 ± 57.687 cd	18.895 ± 1.150 c	6.980 ± 0.062 c	1.336 ± 0.016 b
Qianxi 37	0.038 ± 0.000 a	921.458 ± 23.958 de	17.844 ± 0.036 cd	6.857 ± 0.012 c	1.325 ± 0.003 b
Yanchang	0.038 ± 0.000 a	879.665 ± 29.162 e	16.637 ± 0.029 d	6.159 ± 0.023 d	1.442 ± 0.001 b

$\eta_{AQY}$  is Apparent Quantum Yield;  $P_{LSP}$  is Photoinhibition Light Saturation;  $P_{LCP}$  is Photocompensation Point;  $P_{n, \max}$  is Maximum Net Photosynthetic Rate; and  $R_d$  is Dark Rrespiration Rate.

### Chlorophyll contents of the six Chinese chestnut varieties (strains)

Fig. 6A showed the chlorophyll a content, with ‘Yanqiu’ having significantly higher content compared to other five cultivars, followed by ‘Yanbao’. The average chlorophyll a content among the six Chinese chestnut varieties was ranked as follows: ‘Yanqiu’ > ‘Hybrid22’ > ‘Yanbao’ > ‘Yanchang’ > ‘Qianxi37’ > ‘Yanjia’, with values of 1.235, 0.956, 0.917, 0.712, 0.696, 0.597 mg/g · FW. Fig. 6B showed that the chlorophyll b contents of ‘Yanqiu’, ‘Yanbao’ and ‘Yanchang’ were significantly higher than those of ‘Hybrid 22’, ‘Yanjia’ and ‘Qianxi 37’. In Fig. 6C, the carotenoid content of ‘Yanqiu’ was significantly higher than other five varieties, followed by ‘Yanchang’. In Fig. 6D, the total chlorophyll content of ‘Yanqiu’ was significantly higher than other five varieties, and ‘Yanbao’ and ‘Yanchang’ had significantly higher contents than ‘Hybrid 22’, ‘Qianxi 37’ and ‘Yanjia’. Therefore, among the six Chinese chestnut varieties (strains), ‘Yanqiu’ had the highest contents of chlorophyll a, chlorophyll b, carotenoids and total chlorophyll, reaching 1.235, 0.244, 0.321 and 1.478 mg/g · FW, respectively.

### Discussion

The diurnal variation of net photosynthetic rate can reflect the ability of plants to sustain photosynthesis throughout the day. Due to the constant changes in physiological and ecological factors that influence the net photosynthetic rate of plants, the net photosynthetic rate can also exhibits different variations<sup>[20]</sup>. Stomata are the main channels through which gas exchange occurs between the internal leaf tissues and the external environment, facilitating the exchange of oxygen and carbon dioxide. Stomatal conductance ( $G_s$ ) reflects the intensity of photosynthesis in plants<sup>[21]</sup>. Transpiration rate reflects the strength of transpiration in plants. It is influenced by the combination of plant characteristics and external factors. When the transpiration rate increases, stomatal conductance and net photosynthetic rate also increase simultaneously<sup>[22]</sup>. The diurnal variation of photosynthesis in Chinese chestnut had been reported to exhibit both single-peak and double-peak patterns. During the dry season and the peak growth period (June – August), sunny days display a double-peak pattern. The phenomenon of ‘midday depression’ occurs at noon due to increased light intensity and temperature, leading to a decrease in photosynthetic efficiency<sup>[23]</sup>. During the early growth stage in May and the late stage in October, sunny days exhibit a single-peak pattern. In the morning and

evening, insufficient light intensity and temperature result in lower photosynthetic efficiency. However, at midday, when light intensity and temperature are optimal, photosynthetic efficiency is higher. It indicates that light and temperature stress lead to decreased photosynthetic efficiency<sup>[24]</sup>. In this study, the diurnal variation of photosynthesis was measured on July 25, with clear weather conditions. Measurements were conducted from 8:00 AM to 6:00 PM to capture the diurnal pattern of leaf photosynthesis. The diurnal variation of  $P_n$ ,  $G_s$  and  $T_r$  in all six Chinese chestnut varieties (strains) exhibited a double-peak pattern, indicating the presence of a midday depression phenomenon. The first peak occurred at 10:00 AM, followed by a second peak at 2:00 PM.

Carbon dioxide is the substrate for photosynthesis and the production of organic compounds in plants. The magnitude of diurnal variation in intercellular carbon dioxide concentration ( $C_i$ ) directly affects the rate of photosynthesis in plants<sup>[25]</sup>. The average and peak values of  $P_n$ ,  $G_s$ ,  $C_i$  and  $T_r$  were consistently higher in ‘Yanqiu’ compared to other varieties (strains), with ‘Hybrid 22’ following closely. It indicated that ‘Yanqiu’ had the highest photosynthetic capacity among the examined varieties. The peak values of net photosynthetic rate reached levels of 15.435, 14.910, 14.576, 13.940, 13.940, 12.472 and 12.377  $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$  for the respective varieties.  $C_i$  continued to increase after noon, indicating that the photosynthetic capacity of these six Chinese chestnut varieties did not increase. It suggested that these varieties were less affected by the midday depression phenomenon and maintained their photosynthetic efficiency during the afternoon period. When  $P_n$  decreased,  $G_s$  followed a similar trend, while  $C_i$  increased. It indicated that the occurrence of the midday depression phenomenon in these six Chinese chestnut varieties was primarily limited by non-stomatal factors<sup>[25]</sup>. At 14:00,  $C_i$  reached a lower value, which might be attributed to a reduction in light intensity and the subsequent opening of stomata, leading to an increase in  $G_s$ . This increase in  $G_s$  resulted in the consumption of a significant amount of carbon dioxide. The  $T_r$  changed with the variations of  $P_n$  and  $G_s$ . As  $P_n$  increased and  $G_s$  increased, the stomata opened, leading to a significant loss of water in Chinese chestnut. Excessive transpiration could cause water deficiency, resulting in a decrease in stomatal conductivity and even stomatal closure. Therefore, in summer production practice, maintaining a certain transpiration rate and stomatal conductivity through measures like timely irrigation could provide crucial protection for Chinese chestnut to achieve their optimal photosynthetic performance.

Light response curves reflect the relationship between the net

photosynthetic rate of plants and the photosynthetically active radiation<sup>[26]</sup>. The light response curve of plants is an analysis of the relationship between PAR and  $P_n$  during photosynthesis. The characteristic parameters of the light response curve are indicators used to study the photosynthetic physiological characteristics and adaptability of plants<sup>[27]</sup>. Using the leaf drift model, it is possible to calculate the corresponding characteristic parameters such as  $\eta_{AQY}$ ,  $P_{LSP}$ ,  $P_{LCP}$ ,  $P_{n, \max}$  and  $R_d$ . These parameters can be used to describe the light response curve characteristics of chestnut varieties.  $\eta_{AQY}$  reflects the photosynthetic capacity of plant leaves under weak light conditions<sup>[28]</sup>. The  $\eta_{AQY}$  values of ‘Yanbao’, ‘Yanjia’, ‘Qianxi 37’ and ‘Yanchang’ were larger than those of other varieties. Among them, ‘Yanjia’ had the highest  $\eta_{AQY}$  value, indicating the strongest ability to utilize weak light.  $R_d$  represented the rate of gas exchange in plants under dark conditions. A lower  $R_d$  indicated that plants consumed less photosynthetic products, resulting in a higher carbon gain for the leaves<sup>[29]</sup>. The  $R_d$  of ‘Yanqiu’ was significantly lower than that of other varieties. The Maximum Net Photosynthetic Rate ( $P_{n, \max}$ ) reflects the photosynthetic potential of plants. A higher  $P_{n, \max}$  value indicates a higher photosynthetic potential of plant leaves and a greater synthesis of photosynthetic products under effective light<sup>[30]</sup>. The  $P_{n, \max}$  of ‘Yanqiu’ was significantly higher than that of other varieties. ‘Hybrid 22’ and ‘Yanbao’ were significantly higher than ‘Yanjia’ and ‘Qianxi 37’, while ‘Yanchang’ had the lowest  $P_{n, \max}$ . Furthermore, the order was ‘Yanqiu’ > ‘Hybrid 22’ > ‘Yanbao’ > ‘Yanjia’ > ‘Qianxi 37’ > ‘Yanchang’.  $P_{LSP}$  and  $P_{LCP}$  reflect the range of light utilization by plants. A higher  $P_{LSP}$  indicates a stronger adaptation to high light intensity, while a lower  $P_{LCP}$  indicates a stronger adaptation to low light intensity<sup>[28]</sup>. The  $P_{LSP}$  of ‘Yanqiu’ was significantly higher than other five varieties, with ‘Hybrid 22’ coming next, indicating that these two varieties had the strongest adaptation to high light intensity. The  $P_{LCP}$  of ‘Yanchang’ was significantly higher than other five varieties or strains, followed by ‘Qianxi 37’, indicating that these two varieties had the strongest adaptation to low light intensity and maintained good photosynthetic characteristics even in shaded environments. ‘Yanbao’ and ‘Yanjia’ had relatively higher  $P_{LSP}$  and lower  $P_{LCP}$ , indicating that these two varieties had a wider range of light utilization.

Chlorophyll was the primary pigment involved in photosynthesis in plant leaves. It plays a crucial role in the absorption, transfer, and conversion of light energy during photosynthesis. Chlorophyll a was the main pigment responsible for the plant’s photosynthetic capacity, while chlorophyll b acts as an accessory pigment. Carotenoids are responsible for photoprotection and light energy capture. The chlorophyll content of leaves was positively correlated with the photosynthetic rate during the same period<sup>[31–32]</sup>. In this study, the content of chlorophyll b in ‘Yanqiu’, ‘Yanbao’ and ‘Yanchang’ was significantly higher than that in ‘Hybrid 22’, ‘Yanjia’ and ‘Qianxi 37’. The carotenoid content in ‘Yanqiu’ was significantly higher than that in other five varieties (strains), with ‘Yanchang’ being the second highest. The total chlorophyll content in ‘Yanqiu’ was significantly higher than in other five va-

rieties (strains), while ‘Yanbao’ and ‘Yanchang’ were significantly higher than ‘Hybrid 22’, ‘Qianxi 37’ and ‘Yanjia’. The contents of chlorophyll a, chlorophyll b, carotenoids and total chlorophyll in ‘Yanqiu’ were all the highest, reaching 1.235, 0.244, 0.321 and 1.478 mg/g · FW, respectively. The  $P_{n, \max}$  was also the highest in ‘Yanqiu’. It reflected a certain degree of correlation between the photosynthetic rate and chlorophyll content in ‘Yanqiu’.

Based on the above, among the six varieties (strains), ‘Yanqiu’ had the highest  $P_{n, \max}$  and the lowest  $R_d$ , and also had the highest chlorophyll content, indicating its strong photosynthetic capacity and organic matter accumulation ability. ‘Hybrid 22’ had the second-highest  $P_{n, \max}$  and was also suitable for high mountain high-light environments. ‘Yanbao’ and ‘Yanjia’ had a wide range of adaptation to light and could adapt well to both weak and strong light stresses. The  $P_{LCP}$  of ‘Yanchang’ was significantly higher than other five varieties (strains), with ‘Qianxi 37’ being the second highest. It indicated that these two varieties (strains) had the strongest adaptation ability to low light conditions. Additionally, they had higher chlorophyll content, which meant they still exhibited good photosynthetic characteristics under weak light stress. Conducting research on Chinese chestnut photosynthetic physiology is of great significance for Chinese chestnut production, cultivation and breeding.

## References

- [1] WU JK, XIAO X, LIU H, *et al.* Research progress on photosynthesis in fruit trees[J]. *Hebei Fruit Trees*, 2022(3): 1–2, 6. (in Chinese).
- [2] GUO SJ, XIE P. Study on the photosynthetic characteristics of different types of branches during the flowering and early fruiting stages of chestnut [J]. *Journal of Northeast Agricultural University*, 2013, 44(10): 76–81. (in Chinese).
- [3] YOU X, GONG JR. The significance and examples of chlorophyll fluorescence kinetic parameters in D[J]. *Western Forestry Science*, 2012, 41(5): 90–94. (in Chinese).
- [4] PENG FR, YANG XH, HUANG BL, *et al.* Preliminary research on the physiological and ecological characteristics of net photosynthesis in densely planted chestnut trees[J]. *Journal of Nanjing Forestry University*, 1998, 22(3): 9–13. (in Chinese).
- [5] SUN S, ZHANG LT, YANG XH, *et al.* Reflectance spectra and chlorophyll fluorescence kinetics during the leaf unfolding process of young chestnut leaves[J]. *Forestry Science*, 2009, 45(4): 162–166. (in Chinese).
- [6] PENG FR, HUANG BL. Study on the photosynthetic characteristics of densely planted chestnut trees[J]. *Journal of Zhejiang Forestry College*, 1997, 14(2): 43–46. (in Chinese).
- [7] FORCE L, CRITCHLEY C, VAN RENSEN J. New fluorescence parameters for monitoring photosynthesis in leaves[J]. *Photosynthesis Research*, 2003, 78(1): 17–33.
- [8] HENRIQUES FS. Leaf chlorophyll fluorescence: Background and fundamentals for plant biologists[J]. *Botanical Review*, 2009, 75(3): 249–270.
- [9] MA YL, GUO SJ. Study on the spatial heterogeneity of photosynthetic characteristics in the canopy of chestnut trees[J]. *Journal of Beijing Forestry University*, 2020, 42(10): 71–83. (in Chinese).

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- [18] XU X, CHEN J, HU R, *et al.* A dual-modality immunosensor for simple and reliable detection of nitrated alpha-synuclein in serum based on silver-coated MOF[J]. *Microchim. Acta*, 2023(190): 196.
- [19] LI D, LV Y, XIA H, *et al.* Target-activated multivalent sensing platform for improving the sensitivity and selectivity of Hg<sup>2+</sup> detection[J]. *Anal. Chim. Acta*, 2023(1256): 341123.
- [20] HE W, QIAO B, LI F, *et al.* A novel electrochemical biosensor for ultrasensitive Hg<sup>2+</sup> detection via a triple signal amplification strategy[J]. *Chem. Commun.*, 2021(57): 619–622.
- [21] HE YQ, CHEN Y, MENG XZ, *et al.* A versatile and smartphone-integrated detection platform based on Exo III-assisted recycling and DNAzyme amplification[J]. *Sensor. Actuat. B: Chem.*, 2023(376): 132976.
- [22] ZHANG D, WANG Y, JIN X, *et al.* A label-free and ultrasensitive electrochemical biosensor for oral cancer overexpressed I gene via exonuclease III-assisted target recycling and dual enzyme-assisted signal amplification strategies[J]. *Analyst*, 2022(147): 2412–2424.
- [23] YANG DK, KUO CJ, CHEN LC. Synthetic multivalent DNAzymes for enhanced hydrogen peroxide catalysis and sensitive colorimetric glucose detection[J]. *Anal. Chim. Acta*, 2015(856): 96–102.
- [24] TAN H, NAN Z. The high peroxidase-like activity of pyrite FS<sub>2</sub>/SiO<sub>2</sub> hollow spheres for ascorbic acid detection[J]. *Mater. Lett.*, 2022(320): 132280.
- [25] CAO Y, LI W, PEI R. Exploring the catalytic mechanism of multivalent G-quadruplex/hemin DNAzymes by modulating the position and spatial orientation of connected G-quadruplexes[J]. *Anal. Chim. Acta*, 2022(1221): 340105.
- [26] LI W, YANG X, HE L, *et al.* Self-assembled DNA nanocentipede as multivalent drug carrier for targeted delivery[J]. *ACS Appl. Mater. Inter.*, 2016(8): 25733–25740.

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(Continued from page 14)

- [10] ZHANG JJ, CHEN ZY, HAN Y, *et al.* Effects of different rootstocks on the growth and photosynthetic characteristics of ‘Guiliyi’ large-fruited Chinese chestnut seedlings[J]. *China Agricultural Science and Technology Tribune*, 2018, 20(03):10–19. (in Chinese).
- [11] TIAN SL, SUN XL, SHEN GN, *et al.* Effects of urea and potassium dihydrogen phosphate co-application on photosynthetic characteristics, growth, and fruiting of chestnut trees[J]. *Journal of Applied Ecology*, 2015, 26(3): 747–754. (in Chinese).
- [12] CHEN JP. Effects of manganese on the photosynthetic characteristics and mineral nutrition of ‘Shimen Zao Shuo’ chestnut[D]. Tai’an: Shandong Agricultural University, 2013. (in Chinese).
- [13] FANG R, HUANG BL. Study on the photosynthetic characteristics of densely planted chestnut trees[J]. *Journal of Zhejiang Forestry College*, 1997(2): 43–46. (in Chinese).
- [14] LI PF. Research and application of high-light efficiency breeding technology in crops[J]. *Seed Science and Technology*, 2006(6): 41–44. (in Chinese).
- [15] YE ZP. A new model for relationship between irradiance and the rate of photosynthesis in *Oryza sativa*[J]. *Photosynthetica*, 2007(45): 637–640.
- [16] LI L, ZHANG XX, ZHENG R, *et al.* Photosynthetic characteristics and fitting of light response curves in summer maize[J]. *Acta Phytocologica Sinica*, 2016, 40(12): 1310–1318. (in Chinese).
- [17] TIAN MY, DOU QQ, XIE YF, *et al.* Study on the photosynthetic characteristics of four thin-shell walnut varieties[J]. *Journal of Nanjing Forestry University: Natural Sciences Edition*, 2022, 46(5): 67–74. (in Chinese).
- [18] LI D, HU DY, ZHAO HX, *et al.* Study on the photosynthetic characteristics and chlorophyll fluorescence characteristics of six ornamental bamboo species[J]. *Shandong Agricultural Sciences*, 2023, 55(7): 34–41. (in Chinese).
- [19] ZONG SJ. Study on flowering, fruiting, and photosynthetic characteristics of six superior Chinese chestnut varieties[D]. Central South University of Forestry and Technology, 2022. (in Chinese).
- [20] ZHANG H. Study on the photosynthetic characteristics of two hawthorn varieties[J]. *Journal of Fruit Resources*, 2023, 4(3): 47–51. (in Chinese).
- [21] ZHANG Y, HAN LQ, ZHAO Y, *et al.* Comparison of leaf structure and photosynthetic characteristics of two main walnut varieties in Xijiang[J]. *Economic Forest Research*, 2022, 40(2): 153–163, 182. (in Chinese).
- [22] YANG W, YU ZY, LI XG. Study on the photosynthetic characteristics of three strawberry varieties[J]. *Northern Horticulture*, 2015(10): 50–53. (in Chinese).
- [23] LIU QZ, DONG HM, LIU P, *et al.* Study on the photosynthetic characteristics of chestnut trees[J]. *Journal of Fruit Science*, 2005, 22(4): 335–338. (in Chinese).
- [24] ZHANG Y, SHAO JZ, LIU XJ, *et al.* Research progress on photosynthesis in Chinese chestnut[J]. *Journal of Northwest Forestry University*, 2007, 22(5): 53–56. (in Chinese).
- [25] XIAO NJ, SHI YC, WEI X, *et al.* Fitting of light response models and study on photosynthetic characteristics of three vine medicinal and edible plants[J]. *Tropical Agricultural Sciences*, 2023, 43(9): 13–21.
- [26] LU B, ZHENG YQ, WEI B, *et al.* Comparative study on diurnal variations of photosynthesis in three Hakeleirei holly varieties[J]. *Forestry and Environmental Science*, 2023, 39(2): 59–66. (in Chinese).
- [27] WU AJ, XU WZ, GUO YL, *et al.* Characteristics of photosynthesis-light response curves of Daurian buckthorn under different water and fertilizer conditions[J]. *Acta Prataculturae Sinica*, 2015, 23(4): 785–792. (in Chinese).
- [28] WANG M, NING DL, LI XZ, *et al.* Research overview on thin-shell walnuts[J]. *China Forestry Science and Technology*, 2010(2): 84–86. (in Chinese).
- [29] WANG J, MO HR, *et al.* Analysis of light response curve characteristics of 10 *Plantago* species[J]. *Anhui Agricultural Sciences*, 2015, 43(33): 23–26, 39. (in Chinese).
- [30] ZHANG YH. Light response curve characteristics of three introduced ornamental tree species[J]. *Forestry Survey and Design*, 2019, 39(1): 1–4. (in Chinese).
- [31] TANG XL, JIANG J, JIN HP, *et al.* Effects of shading on chlorophyll content and photosynthetic characteristics of *Machilus minuta*[J]. *Chinese Journal of Applied Ecology*, 2019, 30(9): 2941–2948. (in Chinese).
- [32] HE HY, PENG FR, ZHANG R, *et al.* Comparative study on photosynthetic characteristics of grafted seedlings of different varieties of *Juglans nigra*[J]. *Journal of Nanjing Forestry University: Natural Sciences Edition*, 2015, 39(4): 19–25. (in Chinese).

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