Research paper

Differences in leaf physiological and morphological traits between *Camellia japonica* and *Camellia reticulata*

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**Abstract**

Plants of the genus *Camellia* are widely cultivated throughout the world as ornamentals because of their bright and large flowers. The widely cultivated varieties are mainly derived from the mutant lines and hybrid progenies of *Camellia japonica* Linn. and *Camellia reticulata* Lindl. While their geographical distributions and environmental adaptabilities are significantly different, no systematic comparison has been conducted between these two species. To investigate differences in how these plants have adapted to their environments, we measured photosynthesis and 20 leaf functional traits of *C. japonica* and *C. reticulata* grown under the same conditions. Compared with *C. japonica*, *C. reticulata* showed higher values for light saturation point, light-saturated photosynthetic rate, leaf dry mass per unit area and stomatal area, but lower values for apparent quantum efficiency, leaf size, stomatal density and leaf nitrogen content per unit mass. Stomatal area was positively correlated with light-saturated photosynthetic rate and light saturation point, but negatively correlated with stomatal density. The differences between *C. reticulata* and *C. japonica* were mainly reflected in their adaptations to light intensity and leaf morphological traits. *C. reticulata* is better adapted to high light intensity than *C. japonica*. This difference is related to the two species’ differing life forms. Thus, leaf morphological traits have played an important role in the light adaptation of *C. reticulata* and *C. japonica*, and might be first noticed and selected during the breeding process. These findings will contribute to the cultivation of camellia plants.

**Keywords:**

Camellia, Light adaptation, Leaf traits, Ornamental plant, Photosynthesis

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**1. Introduction**

Plants of the genus *Camellia* (family Theaceae) are used throughout the world not only for beverages and oil, but also as important ornamental plants (Ming, 2000; Barman et al., 2008; Yang et al., 2015). As famous ornamental plants bearing large and bright flowers, camellias have been cultivated in China and elsewhere in Asia for thousands of years and are currently widely cultivated worldwide (Yu, 1985; Li et al., 2016a). In particular, the varieties that are crossed or selected from *Camellia japonica* L. and *Camellia reticulata* Lindl. are the most widely cultivated camellias.

Although these two species belong to the genus *Camellia* section camellia, they exhibit significant differences in geographical distribution, environmental adaptability, and growth performance (Ming, 2000; Liu et al., 2003; Yang et al., 2011). For example, *C. japonica* is mostly a shrub, and grows in forests at altitudes of around 300–1100 m in eastern China, southern Korea and southern Japan. More than 10,000 cultivars have been developed from *C. japonica*, with different flower colors and forms (Li et al., 2016a). These cultivars can be grown in most subtropical and warm temperate regions of the world, but should be planted in the shade. In contrast, *C. reticulata* is a small tree, and is native to southwestern China. It has a narrow distribution, with its wild populations restricted to mixed mountain forest at altitudes of 1600–2900 m in western and central Yunnan Province and southwestern Sichuan Province (Yu, 1985; Ming, 2000). This species is very susceptible to cold weather, and therefore has a much narrower cultivation range than *C. japonica*. The differing characteristics of *C. japonica* and *C. reticulata* suggest that they might have
different environmental adaptations. But to date, no studies have compared the environmental adaptations of these two camellias, which limits their cultivation and utilization. The growth and reproduction of plants depend on their physiological adaptabilities to the environments (Aleric and Kirkman, 2005; Wu and Campbell, 2006; Li et al., 2019). Empirical observations suggest that both C. japonica and C. reticulata produce more flowers under high light conditions, but may suffer from leaf burns under strong light, especially C. japonica. A previous study has also found that cultivars of C. japonica are susceptible to high light (Liu et al., 2003), whereas the photosynthetic adaptations of three cultivars of C. reticulata to light intensity differ (Yang et al., 2011). Furthermore, when C. reticulata plants produce new sprouts, even if the soil moisture conditions are good, the leaves and new shoots are prone to wilting; however, in C. japonica this phenomenon is not clearly observed. This indicates that these two species may differ in how they adapt to light and moisture. Differences in plant photosynthesis and functional traits are widely used in explaining carbon gains, plant performance, and physiological tolerances to different environments (Niinemets and Kull, 1994; Hamerlynck and Knapp, 1996; Rozendaal et al. 2006; Niinemets, 2007; Li et al., 2016b). For example, acclimation to light environments (Scoffoni et al., 2015). The effect of light is critical for plant establishment, growth, and survival (Poorer, 1999; Goldstein et al., 2016). Insufficient light may reduce growth of plants by limiting photosynthetic gas exchange, while high light levels may lead to the increased formation of damaging reactive oxygen species as byproducts of photosynthesis, thereby damaging the photosynthetic apparatus and reducing photosynthetic carbon gain (Hjelm and Ogren, 2004; Aleric and Kirkman, 2005). Plants may optimize their photosynthesis under various light environments through regulating leaf nitrogen content, activation of Rubisco, nitrogen allocation among different pools within the photosynthetic apparatus, chlorophyll content, and diffusion conductance (Niinemets and Kull, 1994; Jensen, 2004; Rozendaal et al., 2006; Evans and Clarke, 2019). However, the photosynthetic adaptation to light intensity varies significantly across species. Sun plants often have higher light saturation points than shade plants (Pandey and Kushwaha, 2005; Zhang et al., 2006). But studies of the photosynthetic adaptation to differing light environments are rare for species within the genus Camellia, especially for C. reticulata and C. japonica (Liu et al., 2003; Barman et al., 2008; Yang et al., 2011).

Leaf morphological traits often adjust in response to different light environments and may affect the photosynthetic gas exchanges of plants (Murphy et al., 2012; Sack and Scoffoni, 2013; Scoffoni et al., 2015). For example, plants growing under shady conditions tend to develop lower leaf mass per unit area, vein density (Dv), and stomatal density (SD) than sun plants, but bigger stoma (Kim et al., 2011; Brodribb and Jordan, 2011; Scoffoni et al., 2015; Stewart et al., 2017). However, SD and Dv are not different in some species under different light intensities (Fetzer et al., 1983; Sack and Scoffoni, 2013). Stomatal density and size primarily dictate maximum stomatal conductance, and therefore potential transpiration demand (Franks et al., 2009; Brodribb and Jordan, 2011). Increased SD enhances the photosynthetic rate by modulating gas diffusion (Tanaka et al., 2013). Meanwhile, Dv is correlated with SD, maximum hydraulic conductance, and maximum photosynthetic rate (Sack and Frolé, 2006; Zhang et al., 2012). However, in rice, an increase in SD does not enhance photosynthetic capacity (Schuler et al., 2018). Thus, the response pattern of leaf traits to the environment is highly species dependent (Yang et al., 2018). But, differences in photosynthesis and functional traits are not well understood in species within the genus Camellia (Cai et al., 2017).

In the present study, the photosynthetic characteristics and leaf functional traits of four varieties of C. japonica and four varieties of C. reticulata were investigated under the same growing conditions. Our goals were to understand (1) the difference in the photosynthetic characteristics and leaf functional traits between C. japonica and C. reticulata; (2) the difference in the photosynthetic responses of C. japonica and C. reticulata to light intensity; and (3) how leaf morphological traits affect physiological traits and the adaptation of photosynthesis to light intensity. The results will be of great significance for guiding the cultivation of camellia plants.

2. Materials and methods

2.1. Plant materials

Four varieties of C. japonica and four varieties of C. reticulata were selected to compare the photosynthetic characteristics and leaf functional traits of these two camellia species. The four varieties of C. reticulata were Shizitou, Zaotaohong, Juban, and Songzilin. They are traditional varieties of C. reticulata and have a long cultivation history in Yunnan Province, China. The four varieties of C. japonica were Royal Velvet, Kramer’s Supreme, Nuccio’s Bella Rossa, and Flowerwood. These are introduced varieties, bred by growers in the United States of America. All materials used in the experiment were four-year old seedlings grown via cutting propagation.

2.2. Experimental site and design

The experiments were conducted in the Dachunhe Experimental Station of Flower Research Institute of Yunnan Academy of Agricultural Sciences in southwestern China. The study site is at an altitude of 2050 m a.s.l. It has a mean annual temperature of 14.8 °C, a mean annual sunshine duration of 2291.2 h, and a mean annual precipitation of 900 mm, with 80% of this rainfall occurring between May and October. All seedlings were planted in plastic pots (30 cm in diameter) filled with peat moss. Before the emergence of new leaves, 30 seedlings of each variety were exposed to about 70% sunlight provided by shade nets applied on March 15, 2017. During the experiment, the seedlings were given slow-release fertilizer (N: P: K, 15:15:15) every two weeks, and watered every 1–3 days as needed. From July 3 to July 25 in 2017, the seedling’s mature leaves that had formed in the current year were used for the observations on photosynthesis and leaf traits.

2.3. Measurements of photosynthesis and functional traits

The photosynthetic responses to light intensity were measured on the fully expanded leaves using a Li-Cor 6400 portable photosynthesis system with a 6400–40 fluorescence chamber (Lincoln, NE, USA). After leaves were illuminated by an actinic light of 1200 µmol m−2 s−1 (10% blue light, 90% red light) for 15 min to induce the maximum stomatal aperture, the recordings of photosynthetic rate in response to incident photosynthetic photon flux density (PPFD) were made between 1800 and 0 µmol m−2 s−1 using an automated protocol built into the Li-Cor 6400 system. The program was configured to advance to the next step if the sum of three coefficients of variation (i.e. CO2, water vapor, and flow rate) was less than 0.3%, with a minimum waiting time of 3 min. Each leaf was equilibrated to initial conditions by waiting at least 15 min before executing the automated protocol. Photosynthetic light response curves of 3 individual leaves were measured at 11 light intensities under controlled levels of CO2 (400 µmol mol−1), flow rate (500 mmol s−1), leaf temperature (25 °C), and leaf-to-air vapor pressure deficit (1.0–1.5 kPa). The values for light saturated
photosynthetic rate \((P_{\text{max}})\), apparent quantum efficiency (AQE), respiration rate \((R_e)\), light compensation point (LCP), and light saturation point (LSP) were determined from digital images via the IMAGEJ program (http://rsb.info.nih.gov/ij). The value for Dv was expressed as vein length per unit leaf area, mounted on a Leica DM2500 microscope (Leica Microsystems, Wetzlar, Germany). Vein length was determined at 10× magnification with a Vario MAX CN Elemental Analyzer (Elementar Analysensysteme GmbH, Germany). The leaf samples were then digested with \(\text{HNO}_3-\text{HClO}_4\) and dissolved in HCl, and the phosphorus content was determined by an ICAP 7400 inductively coupled plasma atomic-emission spectrometer (Thermo Fisher Scientific USA, USA).

The section excised from the leaf was stained with 1% safranin and mounted in glycerol to obtain vein density \((D_v)\). The sample was photographed at 10× magnification with a digital camera mounted on a Leica DM2500 microscope (Leica Microsystems, Wetzlar, Germany). Vein length was determined from digital images via the IMAGEJ program (http://rsb.info.nih.gov/ij/). The value for \(D_v\) was expressed as vein length per unit leaf area. For stomatal observations, the lower and upper epidermis were peeled from the middle portions of fresh leaves, and the images were captured under the Leica DM2500 microscope. Stomata areas \((SA)\) were observed in 30 randomly selected fields. Stomatal density \((SD)\) was calculated as the number of per unit leaf area, and stomatal length \((SL)\) was represented as the length of the guard cell.

2.4. Data analysis

All statistical analyses were conducted using SPSS 16.0 for windows (SPSS Inc., Chicago, Illinois, USA). The differences in leaf functional traits between \(C.\ reticulata\) and \(C.\ japonica\) were tested by the Independent Samples \(t\) Test, while the differences among varieties were examined by one-way ANOVA with means discriminated by LSD multiple comparison tests. Relationships among variables were evaluated by a pair-wise Pearson correlation.

3. Results

We compared 20 leaf physiological and morphological traits of \(C.\ japonica\) and \(C.\ reticulata\) and found that half of the traits differed between the two species (Table 1). The varieties of \(C.\ reticulata\) had higher values for LSP, LCP, \(P_{\text{max}},\ LMA,\) ratio of Chl a to Chl b and SA than those of \(C.\ japonica\), but lower values for AQE, SD and leaf nitrogen content per unit mass. However, the values for \(R_e,\) leaf size, LT, chlorophyll content, leaf phosphorus content, \(N_m,\) Chl/Na ratio, and \(D_v\) were not significantly different between the two species. The value for LSP was 1149.0 ± 24.9 \(\mu\text{mol m}^{-2}\text{s}^{-1}\) in \(C.\ reticulata\) and 972.9 ± 33.7 \(\mu\text{mol m}^{-2}\text{s}^{-1}\) in \(C.\ japonica\). This indicates the difference between \(C.\ japonica\) and \(C.\ reticulata\) was mainly reflected in the photosynthetic adaptation of light intensity and leaf morphological traits (Table 1; Fig. 1).

There were differences in leaf functional traits among the varieties of both \(C.\ japonica\) and \(C.\ reticulata\). For \(C.\ japonica\), the values for \(P_{\text{max}},\) leaf size, SD, SA, and \(D_v\) differed among varieties. However, the differences in leaf morphological traits were more obvious than the other traits (Figs. 2–4). For \(C.\ reticulata\), there were differences in \(P_{\text{max}},\) LMA, leaf size, SD, SA, and \(D_v\) among varieties, especially leaf size (Figs. 2–4). This indicates that leaf morphological traits were the main difference among the varieties of \(C.\ japonica\) or the varieties of \(C.\ reticulata\).

Stomatal area \((SA)\) was positively correlated with light-saturated photosynthetic rate and light saturation point in the camellias used in the experiment but was negatively correlated with stomatal density. Leaf area per leaf was also positively correlated with vein density (Fig. 5). However, the correlations between \(P_{\text{max}}\) and SD, \(D_v\) and LMA were very low.

4. Discussion

The present study found that the light levels at which the varieties of \(C.\ reticulata\) achieved their maximal photosynthetic rates were higher than those of the \(C.\ japonica\) varieties. This was

Table 1 Comparison of leaf physiological and morphological traits of Camellia japonica and C. reticulata.

| Traits                                | \(C.\ japonica\)         | \(C.\ reticulata\)       | P-value   |
|---------------------------------------|--------------------------|--------------------------|-----------|
| Light saturation point (LSP, \(\mu\text{mol m}^{-2}\text{s}^{-1}\)) | \(972.9 ± 33.7\)        | \(11490 ± 24.9\)         | \(<0.001^{***}\) |
| Light compensation point (LCP, \(\mu\text{mol m}^{-2}\text{s}^{-1}\)) | \(16.87 ± 1.08\)        | \(22.50 ± 1.78\)         | \(0.013^*\) |
| Apparent quantum efficiency (AQE, mol CO₂ mol⁻¹ photon) | \(0.078 ± 0.004\)       | \(0.065 ± 0.002\)        | \(0.005^{**}\) |
| Dark respiration rate \((R_e, \mu\text{mol m}^{-2}\text{s}^{-1})\) | \(1.26 ± 0.09\)         | \(1.34 ± 0.10\)          | \(0.432^N\) |
| Light-saturated photosynthetic rate \((A_{\text{max}}, \mu\text{mol m}^{-2}\text{s}^{-1})\) | \(11.21 ± 0.21\)       | \(12.09 ± 0.19\)         | \(0.003^{**}\) |
| Leaf area per leaf \((LA, \text{cm}^2)\) | \(32.38 ± 1.63\)        | \(30.07 ± 1.61\)         | \(0.468^N\) |
| Leaf dry mass per unit area \((LMA, \text{g m}^{-2})\) | \(149.9 ± 3.6\)        | \(166.9 ± 4.9\)          | \(0.006^{**}\) |
| Leaf thickness \((LT, \mu\text{m})\) | \(438.1 ± 9.6\)         | \(440.5 ± 14.9\)         | \(0.892^N\) |
| Chlorophyll a content per unit area \((\text{Chl}, \mu\text{g cm}^{-2})\) | \(42.13 ± 1.22\)       | \(45.58 ± 1.47\)         | \(0.079^N\) |
| Chlorophyll b content per unit area \((\text{Chlb}, \mu\text{g cm}^{-2})\) | \(19.77 ± 0.60\)       | \(19.43 ± 0.55\)         | \(0.674^N\) |
| Total chlorophyll content per unit area \((\text{Chl}, \mu\text{g cm}^{-2})\) | \(61.90 ± 1.42\)       | \(65.01 ± 1.98\)         | \(0.215^N\) |
| Ratio of Chl a to Chlb | \(2.171 ± 0.071\)       | \(2.345 ± 0.036\)        | \(0.029^*\) |
| Leaf nitrogen content per unit mass \((N_m, \text{g kg}^{-1})\) | \(14.28 ± 0.28\)       | \(12.85 ± 0.35\)         | \(0.003^{**}\) |
| Leaf phosphorus content per unit area \((P_n, \text{g kg}^{-1})\) | \(0.912 ± 0.029\)      | \(0.862 ± 0.058\)        | \(0.429^N\) |
| Leaf nitrogen content per unit area \((N_m, \text{g m}^{-2})\) | \(2.140 ± 0.074\)      | \(2.135 ± 0.104\)        | \(0.967^N\) |
| Leaf phosphorus content per unit area \((P_n, \text{g kg}^{-1})\) | \(0.141 ± 0.005\)      | \(0.143 ± 0.009\)        | \(0.818^N\) |
| Chl/Na ratio | \(0.288 ± 0.010\)       | \(0.306 ± 0.014\)        | \(0.345^N\) |
| Stomatal density \((SD, \text{number mm}^{-2})\) | \(252.4 ± 18.4\)       | \(158.3 ± 4.2\)          | \(<0.001^{***}\) |
| Stomatal area \((SA, \mu\text{m}^2)\) | \(745.9 ± 34.8\)        | \(1012.1 ± 18.3\)        | \(<0.001^{***}\) |

The data in the table are means ± 1 SE. *** \(P < 0.001; \)** \(P < 0.01; \)* \(P < 0.05;\) NS, \(P > 0.05.\)
Fig. 1. Responses of photosynthetic rates (Pn) and electron transport rates of photosystem II (ETR) to photosynthetic photon flux density (PPFD) for different varieties of *Camellia japonica* (left) and *C. reticulata* (right). Each point represents the mean ± 1 SE of 3 measurements from different plants.

Fig. 2. Values for light-saturated photosynthetic rate (Pmax), light-saturation point (LSP) and chlorophyll content per unit area (Chl) in different varieties of *Camellia reticulata* (left) and *C. japonica* (right). Each data point represents the average of three independent samples ± 1 SE. Different letters above bars in each graph indicate statistically different mean values (P < 0.05), as determined by LSD multiple comparison tests.
consistent with the empirical observation that *C. reticulata* had a higher light demand than *C. japonica*. The difference in photosynthetic adaptation is both genetically determined and environmentally induced (Hamerlynck and Knapp, 1996). In fact, *C. reticulata* is a small tree, while *C. japonica* is a shrub. This allows *C. reticulata* to grow higher into the forest canopy than *C. japonica*. Within forests, light intensity and humidity change significantly along vertical gradients. The upper canopy has a higher light intensity and is more xeromorphic than the lower canopy (Chazdon, 1988; Niinemets, 2007). Taller species make larger ontogenetic shifts in crown exposure than smaller species (Poorter et al., 2005). The most efficient way to acclimate for light is by adjusting leaf characteristics, such as leaf physiology, morphology, and anatomy (Mantovani, 1999; Rozendaal et al., 2006). A close association is often found between plasticity in leaf traits and maximum height of species (Thomas and Bazzaz, 1999; Cai et al., 2005). Shrub species are shade-adapted and can effectively utilize sun-flecks, while tree species are more likely to experience high light during their lifespans. After transferring to high light environment, the maximum photosynthetic rate of tree species increases considerably, but not in shrub species. Thus, tree species have a greater potential for light acclimation than shrub species (Cai et al., 2005). This indicates that species at different forest canopy layers have divergent light adaptation characteristics due to differences in the light environment experienced throughout their lifespans (Niinemets, 2007). Therefore, *C. reticulata* has a greater potential to adapt to high light environment than *C. japonica*.

Trees growing in gaps or in the upper canopy may experience higher light intensities and suffer more frequent photoinhibition, and rely strongly on biochemical mechanisms to dissipate excess energy and avoid damage to the light reaction centers (Niinemets, 2007; Goldstein et al., 2016). A high photochemical quenching coefficient is advantageous for the separation of electric charges in the reaction center and is beneficial to electron transport and photosystem II yield (Mao et al., 2007). The plastic changes in hydraulic architecture may play an important role in the adaptation of trees to growth irradiance (Goldstein et al., 2016). When plants are exposed to high light, the temperatures of their leaves may increase (Zhang et al., 2005; Li et al., 2013). To avoid overheating and leaf burns, plants may increase their transpiration to lower leaf temperatures. Here, we found that the varieties of *C. reticulata* had higher LMA and SA than *C. japonica*, but a smaller leaf size. Meanwhile, SA was positively correlated with LSP. A previous study has suggested that leaf weight per area increases with relative light availability and species’ light demand, while leaf size decreases with species’ light demand and increasing plant height (Niinemets and Kull, 1994). A large leaf can increase the capture of light energy, but it also increases the heat load, water vapor interface layer, and water demand. In contrast, a small leaf has a thin interface layer which is beneficial for heat dissipation, ensuring the leaf is not easily damaged due to overheating (Rozendaal et al., 2006; Vogel, 2009; Li et al., 2013). Plasticity in leaf size may provide an efficient way for plants to acclimate hydraulic conductance and stomatal conductance to the contrasting evaporative conditions of sun.
and shade (Murphy et al., 2012). Plants exposed to high light may decrease their leaf sizes and increase transpiration rates (Dai et al., 2009; Sack and Scoffoni, 2013). Thus, leaf morphology is an important factor causing the difference in the light adaptation between *C. reticulata* and *C. japonica*.

In this study, whether between the two camellia species, or among the different varieties of the same species, the variation in leaf morphological traits were greater than the physiological traits. For example, although the light-saturated photosynthetic rate of *C. reticulata* was slightly higher than that of *C. japonica*, the light-saturated photosynthetic rate was not significantly different in many cases. However, the leaf morphological traits such as leaf size and LMA varied significantly in many cases. A previous study has also found there are differential responses between ecotypes of *Arabidopsis thaliana* (Stewart et al., 2017). This seems to imply that morphological traits may be first noticed and selected during the breeding process of camellia.

Plants may enhance their adaptations to the environments or optimize their growth performance via shifts in trait-combinations (Mantovani, 1999; Fonseca et al., 2000; Zhang et al., 2012). Here, we found close associations among traits in camellias. For example, SA was positively correlated with light-saturated photosynthetic rate, but was negatively correlated with SD. Stomata are an important mechanism for regulating the entry of CO2 into the leaves and the loss of water from the leaves. The potential transpiration demand of a leaf is mainly determined by stomatal aperture and density (Franks et al., 2009; Brodribb and Jordan, 2011). The efficiency with which CO2 is absorbed and water loss is restricted appears to be partially a function of stomatal size (Aasamaa et al., 2001; Drake et al., 2012). Thus, stomatal aperture is linked to leaf conductance and photosynthetic rate (Büssis et al., 2006). The negative correlation between SD and SL has been previously observed (Sack et al., 2003; Beaulieu et al., 2008). This negative correlation may increase plasticity in maximum stomatal conductance to water vapor and CO2, with minimal alterations in the balance of water loss and epidermal allocations to the stomata (Sack et al., 2003; Franks et al., 2009). Thus, SA might affect the photosynthetic rate through regulating stomatal conductance in camellias.

The balance between leaf vein and stomatal investments is important in supplying water to evaporative sites so that stomatal openings are maintained (Zhang et al., 2012; Brodribb et al., 2013). However, we did not find significant correlations between the Pmax and SD, or Dv and LMA in camellias. A previous study has also found that the various structural parameters in camellia leaves undergo modifications that differ in both their extent and degree of elasticity (Krüger et al., 1997). Such differences in plasticity of different traits may change the correlation among traits. Thus, the lack of correlation among different traits is a common phenomenon (Zhang et al., 2012). For example, a previous study found that leaf mechanical resistance and photosynthetic capacity are often unrelated (He et al., 2019). The increase in SD does not enhance photosynthetic capacity in rice because the increased numbers can be offset by the decreased functional stomatal aperture (Schuler et al., 2018). Meanwhile, locally stored water can buffer the transpiration stream, decreasing the dependence upon water uptake from the soil (Ogburn and Edwards, 2013). The lack of correlation
among traits may also be due to the difference in selection pressure on different traits, and adaptive strategies to stress (Zhang et al., 2012; He et al., 2019). Thus, *C. reticulata* and *C. japonica* might have different strategies to adapt to their habitats.

Plants may improve their adaptations to light availability through physiological and biochemical regulation (Niinemets, 2007; Zhang et al., 2017). For example, shade plants often enhance their light capture by increasing chlorophyll content, whereas sun plants have higher leaf nitrogen content than shade plants (Niinemets, 2007). Nitrogen is preferentially allocated to chlorophyll related to light harvesting in the acclimation to low light and to CO2 fixation in the acclimation to high light (Hikosaka and Terashima, 1995; Niinemets, 2007). A higher Chl/N ratio indicates that a greater proportion of leaf N is invested in chlorophyll for light capture at the expense of investment in Rubisco in shade leaves (Hikosaka and Terashima, 1995; Zhang et al., 2017). Here, leaf nitrogen content per unit mass (N_{m}) in *C. japonica* was higher than *C. reticulata*, but chlorophyll content (Chl), leaf nitrogen content per unit area (N_{a}), and Chl/N_{a} ratio were not different between the two species. This indicates that leaf nitrogen investment in light harvesting is not different between the two species. Thus, the difference in physiology between *C. japonica* and *C. reticulata* is relatively small. Leaf morphological traits in these two species should have a greater adaptive significance than physiological traits.

In conclusion, *C. reticulata* can adapt to higher light intensity than *C. japonica*. This difference in light demand is related to two species’ differing life forms. The variations in leaf morphological traits between *C. reticulata* and *C. japonica* were larger than physiological traits. Leaf morphological traits is an important factor responsible for differences in the light adaptation between *C. reticulata* and *C. japonica*, and might be first noticed and selected during the breeding process of camellia plants. Although further research is needed to focus on more intrinsic plant functional traits (such as flower trait and shoot trait) of *C. reticulata* and *C. japonica* and how these traits change under different environmental stresses, our findings will contribute to the cultivation of camellia plants.

**Author contributions**

JHW and SBZ conceived and designed the experiments. YFC and SFL performed the experiments. JHW and YFC analyzed and interpreted the data. JHW and SBZ wrote the manuscript. All authors reviewed and approved the manuscript.

**Declaration of Competing Interest**

The authors declare that there are no conflicts of interest.

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