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Lower photosynthetic capacity under higher spectral reflectance? The case of *Actinidia polygama*

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Abstract

The variegated leaves of *Actinidia polygama* exhibit a striking colour change during development. However, little is known whether the photosynthetic capacity of white leaves can be maintained. Therefore, spectrum properties, leaf structure, net photosynthetic rate (P_N), and chlorophyll fluorescence in the green and white leaves were investigated. Although reflectance at 400 - 700 nm in white leaves was higher than that in green leaves, total chlorophyll content of white leaves was similar to that in green leaves. Palisade tissue cells of white leaves contained functional chloroplasts. Large intercellular spaces were observed between the epidermal and mesophyll cells and within the palisade tissue cell layer in white leaves. Both P_N and the actual quantum yield of photosystem II in white leaves were similar to green leaves. At different leaf growth stages, P_N of white leaves was about 88 - 100 % of the P_N of green leaves. The efficiency of electron move beyond Q_A^- (ET/TR) and the quantum yield of electron transport (ET/ABS) in white leaves was higher than in green leaves. In conclusion, photosynthetic capacity in white leaves of *A. polygama* showed two favorable characteristics during the whole sampling period: *1*) despite a higher spectral reflectance in white leaves, P_N of white leaves remained relatively high compared with green leaves; *2*) the higher activity of photosystem II of white leaves enabled photosynthetic capacity maintenance.

Additional key words: anthocyanin, chlorophyll, fluorescence, net photosynthetic rate; photosystem II.

Introduction

In recent years, some studies have focused on functions of variegated leaves (Niu *et al*. 2014, Ranjan *et al*. 2014, Song *et al*. 2018), but only some on their photosynthetic capacity (Hughes *et al*. 2014). Previous studies reported that higher spectral reflectance usually lead to lower photosynthetic capacity, for example, red leaves reflect most of the red radiation (Karageorgou and Manetas 2006, Zhang *et al*. 2016). Furthermore, non-photosynthetic pigments compete with chlorophylls for photon capture, their presence entails a photosynthetic cost equal to the lost photons (Zeliou *et al*. 2009). In some plants, for example *Begonia*, *Schismatoglottis calyptrata*, and *Arum italicum*, a large proportion of leaves became white during development (Tsukaya *et al*. 2004, Zhang *et al*. 2009, Rocca *et al*. 2011). The photosynthesis is important physiological function of variegated leaves, especially of those appearing during juvenile stages (Solovchenko and Chivkunova 2011). However, until now, few studies have paid attention to maintenance of the photosynthetic capacity of the variegated leaves (Rocca *et al*. 2011).

Actinidia polygama is a species of deciduous woody vines of the genus *Actinidia*. It is distributed in cold areas in Asia (such as northeastern China). It is also cultivated widely in mixed forests. The plant is a very long-lived woody scrambling vine and creeper. It ultimately grows to 8 - 10 m. *A. polygama* is the hardiest species in the genus, surviving temperatures of -40 °C in the winter. Some of its leaves exhibit striking white color (Fig. 1). White leaf of *A. polygama* is different from other variegated plants, whose colour of adaxial and abaxial surface in variegated

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Abbreviations: ΦPSII - quantum yield of photosystem II; ChlNDI - chlorophyll normalized difference vegetation index; ET_0/ABS - quantum yield of electron transport; ET_0/TR_0 - efficiency of electron move beyond Q_A^-; P_N - net photosynthetic rate; PPFD - photosynthetic photon flux density; PSII - photosystem II.
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leaves is homogeneous (Aluru *et al*. 2006, Kato *et al*. 2007). In *A. polygama*, variegated leaves are white on the adaxial surface, but the entire abaxial surface is green. Hence, white leaves of *A. polygama* are different from photobleaching and white mutants (for example *Var* - variegation and reticulate mutants), which are mainly due to damage caused by reactive oxygen species (Takahashi *et al*. 2002, Naresh and Bai 2009, Uzarevic *et al*. 2011) and completely defective chloroplast development (Aluru *et al*. 2006, Liu *et al*. 2010, Lundquist *et al*. 2014). These latter kinds of mutation usually belong to lethal genotypes, and the lifespan of such leaves is very short. However, there are long time observations on white leaves of *A. polygama* showing that they can develop normally from Mid-June to September, and are, therefore probably not due to lethal genotypes. However, it is not clear whether photosynthetic function is retained in white leaves of *A. polygama*.

In order to assess the photosynthetic capacity of white leaves of the *A. polygama*, these were compared with green leaves with respect to leaf reflectance, leaf structure, net photosynthetic rate, and chlorophyll fluorescence parameters throughout the sampling period.

Materials and methods

Plants: *Actinidia polygama* (Sieb. *et* Zucc.) Planch. *ex* Maxim. plants were use for these experiments. The plants were grown in the biological garden (N 43˚48´45″ and E 125˚24´15″) of Jilin Agricultural University, Changchun City, Jilin Province. The annual precipitation was 867 mm and the annual temperature range from 35 °C and -40 °C in the region. When the plants in the experimental area were in direct sunlight, they received natural irradiance of 1 300 - 1 400 μmol m^{-2} s^{-1}). Measurements started in mid-June 2019, and the criteria for leaf selection were that the leaves had a similar dimension (about 15 × 9 cm) and a similar exposure to sunlight. Homogenous areas of the same leaves were measured during leaf development in each independent experiment.

Leaf reflectance was measured of five white and green intact leaves of different development stages with a bifurcated fiber optic cable and a leaf-clip of a *Unispec SC Spectrometer* (*PP Systems*, Amesbury, MA, USA). The *Unispec SC* has a nominal spectral range from 350 to 1 130 nm with approximately 3 nm nominal bandwidth (Xue *et al*. 2014). The leaf was irradiated from one side with a tungsten halogen lamp in the spectrometer using bifurcated fiber. The reflectance spectrum over the range 400 - 750 nm was analyzed. The following chlorophyll normalized difference vegetation index (ChlNDI), which can estimate relative chlorophyll content, was derived from spectral reflectance curves (R denotes reflectance and the subscripts refer to specific spectral wavelength): $ChlNDI = (R_{750} - R_{705})/(R_{750} + R_{705})$ (Gitelson and Merzlyak 1994, Blackburn 1998).

Chlorophyll content: Ten leaf discs were excised using a standard hole punch, immediately sealed in pre-labeled aluminum envelopes and placed in liquid nitrogen. Tissues were stored at -80 °C until analysis. Leaf discs were extracted in solvent mixture of acetone, methanol, and water (80:15:5, v/v/v.). The chlorophyll content was measured at 663 and 645 nm using an UV-visible spectrophotometer *UV-1601* (*Shimadzu*, Kyoto, Japan) according to Porra (2002). Total chlorophyll content was calculated by the formula (Total chlorophyll) = $(20.29 \times A_{645}) - (8.05 \times A_{663})$, in which A denotes the absorbance at the chlorophyll peaks (663 nm and 645 nm).

Leaf structure and chloroplast ultrastructure: Sample preparation for semi-thin sections and transmission electron microscopy (TEM) was performed according to previously described methods (Konoplyova *et al*. 2008, Sheue *et al*. 2012). Small pieces of leaf (1.0 × 1.0 mm^2) from both white and green leaves were cut and fixed in 2.5 % (m/v) glutaraldehyde in 0.1 M sodium phosphate buffer (pH 7.3) overnight at 4 °C. Semi-thin sections were stained with 1 % (m/v) toluidine blue (Wang *et al*. 2015) and observed under a light microscope (*ECLIPSE 80i*, *Nikon*, Tokyo, Japan). Photomicrographs were taken using a *Zeiss Axiolab* (Tokyo, Japan) with a digital camera (*Nikon DXM1200*). Ultrathin sections were observed using a transmission electron microscope (TEM; *JEM-1200EX*; *JEOL*, Tokyo, Japan) at 80 kV.

Net photosynthetic rate (P_N) was measured between 08:00 and 11:00 h (to avoid midday depression of photosynthesis) with a *CIRAS-2* portable photosynthesis system (*PP-Systems*, Amesbury, USA). Photosynthetic photon flux density (PPFD) was gradually decreased stepwise using an integrated LED light source from 1200 to 0 μmol m^{-2} s^{-1} and P_N at each PPFD was recorded when it was stable (usually 2 - 3 min). The net photosynthetic rate was also measured in the field on intact leaves between 08:00 and 11:00 h on clear days with a *CIRAS-2* (4 cm^2 homogenous areas of the same leaves were measured during leaf development). Measurements were done under natural PPFD at 1 300 - 1 400 μmol m^{-2} s^{-1}, at 360 μmol mol^{-1} CO_2, a leaf temperature about 30 °C, a 70 % relative humidity, and a flow rate of 196 cm^3 min^{-1}. Each measurement was completed within 2 - 3 min when steady-state photosynthesis had been achieved.

Chlorophyll fluorescence was measured with an *FMS-2* pulse-modulated fluorometer *(Hansatech Instruments*, King's Lynn, Norfolk, UK). The fluorescence measurement protocol was as follows: the light-adapted leaves were continuously irradiated by actinic radiation from the *FMS-2* light source. The steady-state fluorescence level (F_s) and the maximum fluorescence in the light-adapted state (F_m') during exposure to different PPFDs were measured (Jiang *et al*. 2005). The PPFDs were set in the order of 2 100, 1 600, 1 200, 900, 600, 400, 300, 200, 150, 100, 70, 50, 25, 15 and 0 μmol m^{-2} s^{-1} to obtain ΦPSII-PPFD response curves. The ΦPSII was calculated as $(F_m' - F_s) / F_m'$, where ΦPSII is quantum yield of photosystem II.

During leaf development, leaves were sampled at pre-dawn (3:00 - 5:00). Chlorophyll *a* fluorescence transience

(OJIP) was measured with a plant efficiency analyzer (*Pocket-PEA*, *Hansatech Instruments*). The saturating red radiation of 3 000 μmol m^{-2} s^{-1} was produced by an array of four light-emitting diodes (LEDs, peak 650 nm). Fluorescent signals were recorded within a time scan from 10 μs to 1 s with a data acquisition rate of 100 readings ms^{-1} for the first 2 ms, and 1 reading ms^{-1} after 2 ms. All measurements were performed on adaxial surface of fully dark-adapted (1 h) leaves. Fluorescent transients were analyzed with the JIP-test (Strasser and Strasser 1995, Strasser 1997, Van Heerden *et al*. 2007). The description and calculation of parameters are given according to Zhang *et al* (2012). The JIP-test defines the maximal (subscript "0") energy fluxes in the energy cascade for the events absorption (ABS), trapping (TR_0), and electron transport (ET_0) (Christen *et al*. 2007). The efficiency of electron move beyond QA^-, $ET_0/TR_0 = 1 - V_J$; quantum yield for electron transport, $ET_0/ABS = \{1 - (F_0/F_m)\} \cdot ET_0/TR_0$.

Statistical analysis was performed with the *SAS* software (*JMP 6.0*, *SAS Institute*, Cary, USA). For data sets with parametric distribution, significant differences among means of green and white were determined using the Student's *t*-test ($P < 0.01$). Leaf reflection spectra were calculated and are presented as the average of five independent measurements. Chlorophyll content was calculated and is presented as the average of three independent measurements. Gas exchange data were calculated as the average of individual measurements of three leaves. The photosynthetic light response curve data and light responses of quantum yield of photosystem II represent the means of individual measurements of three leaves. Chlorophyll *a* fluorescent parameters represent means individual measurements of five leaves.

Fig. 1. An *Actinidia polygama* plant with white leaves (*A*) and a detail of a white leaf (*B*).

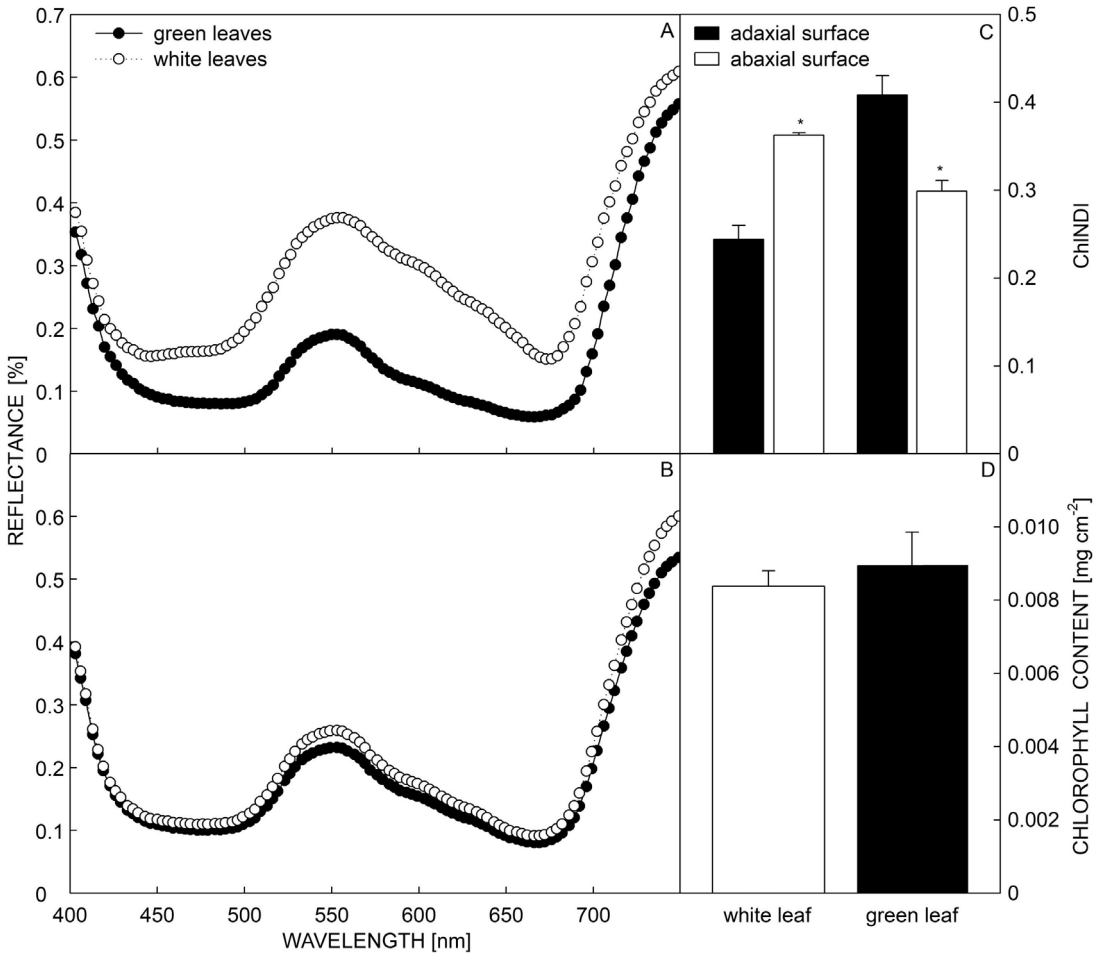

Fig. 2. Different reflectance spectra of *Actinidia polygama* white and green leaves on the adaxial (*A*) and abaxial (*B*) surfaces, chlorophyll normalized difference vegetation index (ChlNDI) (*C*), and total chlorophyll content (*D*). Means ± SEs, $n = 5$ (*A*-*C*) or 3 (*D*); *Asterisks* indicate significant differences ($P < 0.05$) between adaxial and abaxial surfaces.

Results

The reflectance spectra over the range 400 - 750 nm in leaves of different colour were analyzed (Fig. 2). Reflectance was more pronounced in white leaves than in green leaves. On adaxial surfaces, the reflectance of

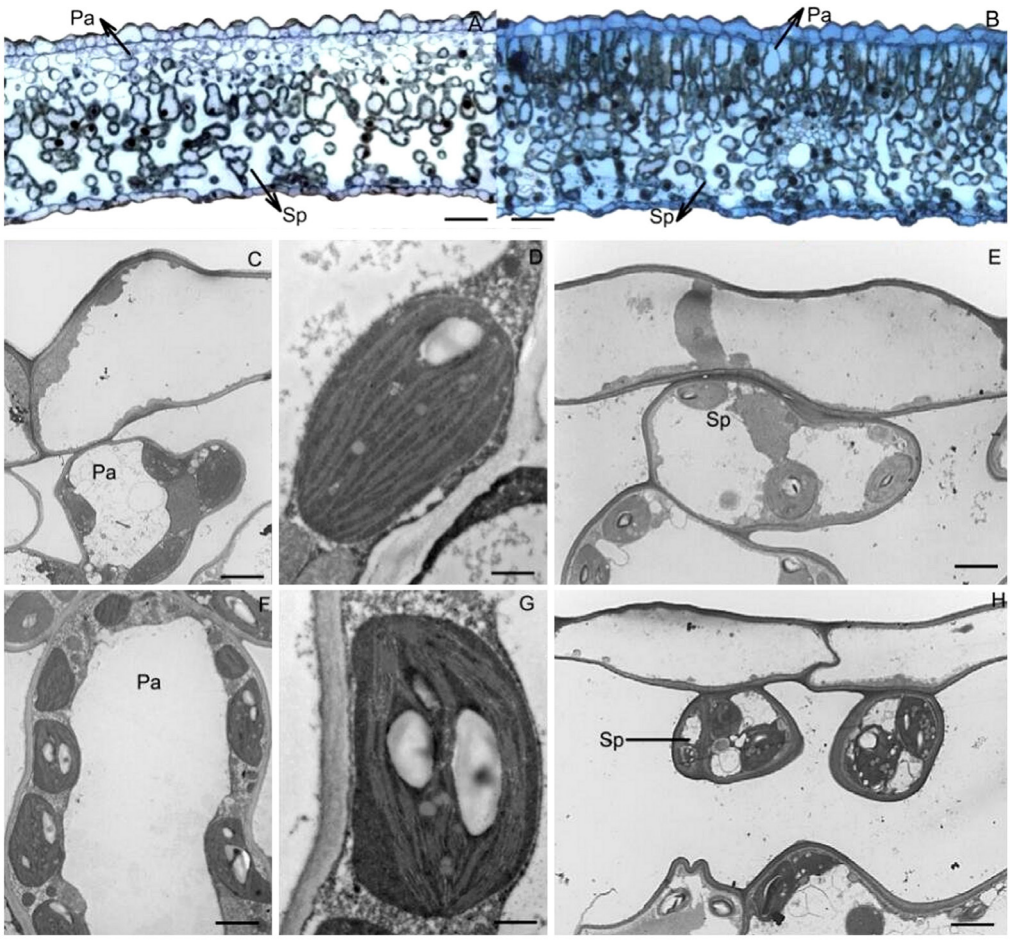

Fig. 3. Anatomical and ultrastructural features of green and white leaves of *Actinidia polygama*. Transverse sections from variegated (*A*) and green (*B*) leaves. Ultrastructure of white leaves: palisade tissue cell (*C*), chloroplast (*D*), spongy tissue cell (*E*). Ultrastructure of green leaves: palisade tissue cell (*F*), chloroplast (*G*), spongy tissue cell (*H*). Pa - palisade tissue; Sp - spongy tissue. *Scale bars*: 50 µm in *A*,*B*, 500 nm in *D*,*G*, 2 µm in *C*,*E*,*F*,*H*.

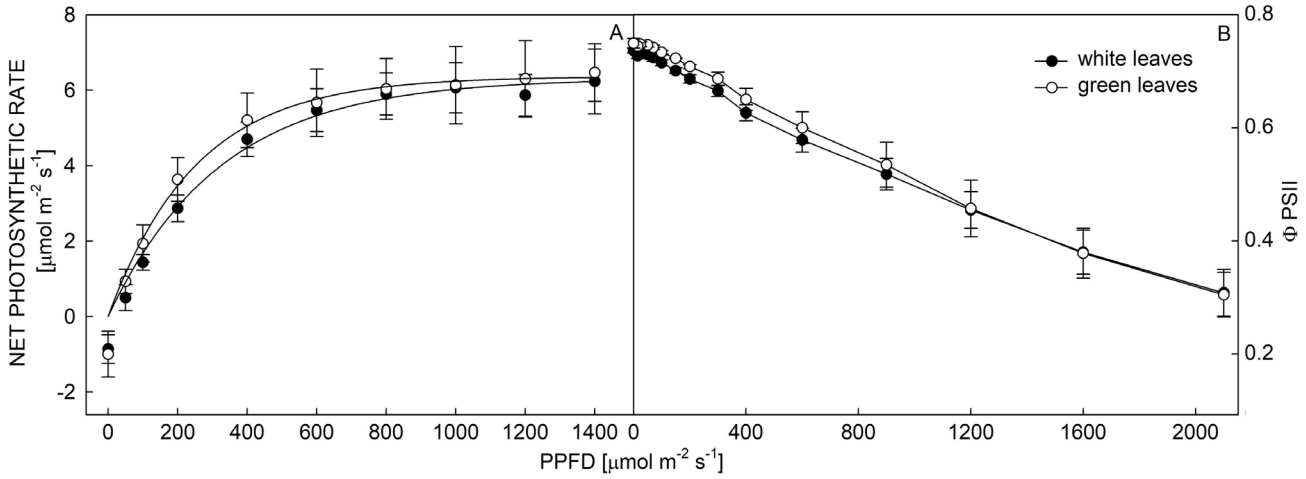

Fig. 4. Responses of net photosynthetic rate and the actual quantum yield of photosystem II (ΦPSII) to photosynthetic photon flux density (PPFD) in white and green leaves of *Actinidia polygama* seedlings. Means ± SEs, $n = 3$.

white leaves was higher than that of green leaves, nearly 15 - 61 % of the incident radiation was reflected (Fig. 2*A*). However, reflectance on abaxial surfaces of white leaves was similar to that of green leaves (Fig. 2*B*). Although ChlNDI of white leaves was lower than of green leaves on the adaxial surface, the trend was contrary on the abaxial surface (Fig. 2*C*). Total chlorophyll content of white and green leaves was similar (Fig. 2*D*).

The anatomy of green and white leaves was significantly different (Fig. 3). In white leaves, 1 - 3 layers of irregular cells were observed (Fig. 3*A*), rather than the typical palisade tissue. However, palisade tissue of green leaf consisted of 2 - 3 layers of packed and elongated cylindrical cells (Fig. 3*B*) that were in tight contact with the adaxial epidermis. Intercellular spaces were observed between the epidermal and the mesophyll cells or within the mesophyll cell layer in white leaves (Fig. 3*A*). In cross-section, spongy tissue in white leaves was thicker than in green leaves (Fig. 3*A*,*B*). In addition, chloroplast development in palisade and spongy parenchyma cells in white (Fig. 3*C*-*E*) and green (Fig. 3*F*-*H*) leaves was normal, starch grain and abundant thylakoid membranes were observed in chloroplasts.

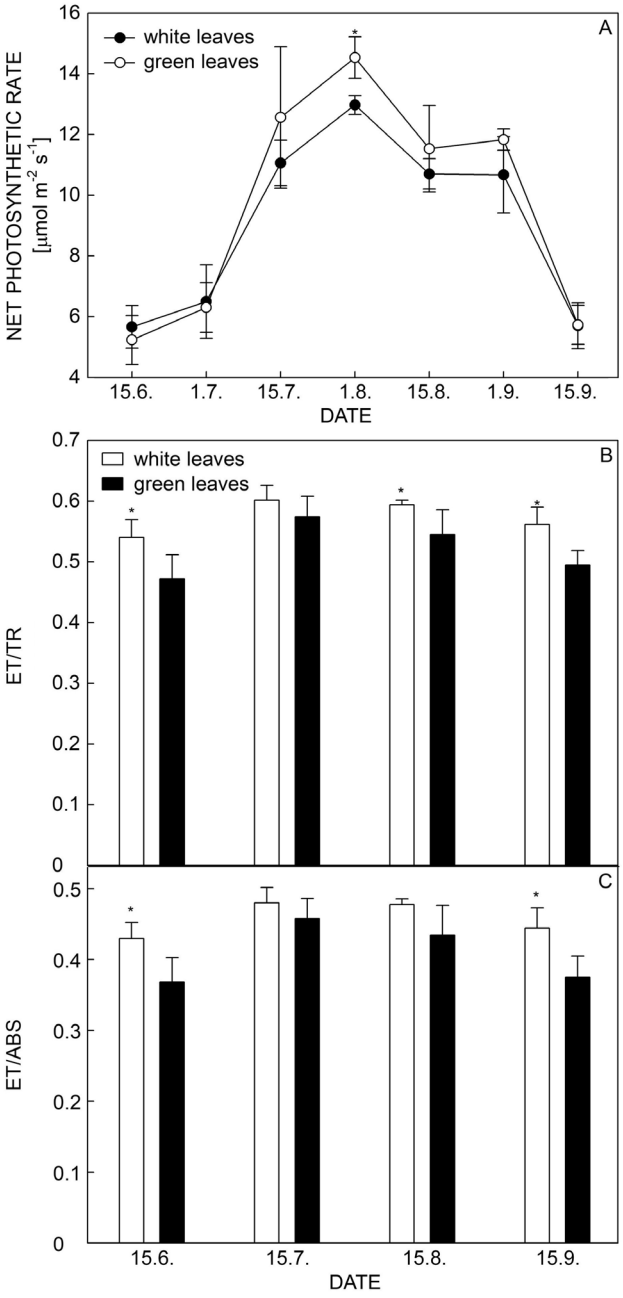

Fig. 5. Net photosynthetic rate (*A*) and chlorophyll fluorescence parameters ET_0/TR_0 (*B*) and ET_0/ABS (*C*) in green and white leaves of *Actinidia polygama* at different dates during a vegetation season. For abbreviations - see Materials and methods. Means ± SEs, $n = 5$. *Asterisks* indicate significant differences ($P < 0.05$) between white and green leaves.

As shown in Fig. 4*A*, the light-saturated P_N of white and green leaves had no significant differences. As shown in Fig. 4*B*, ΦPSII decreased gradually with irradiance increase and ΦPSII of white leaves was similar to that of green leaves. For total P_N during the whole sampling period, the light-saturated P_N of green and white leaves increased gradually with leaf development and P_N of white leaves was about 88 - 100 % of that in green leaves; there were no statistically significant difference (Fig. 5*A*), and P_N of white leaves was equal to 93 % P_N of green leaves.

Much more pronounced differences were found between white and green leaves in the parameters derived from analysis of the fluorescence transient curves according to the JIP-test. During leaf development, ET/TR and ET/ABS of white leaves were higher than those of green leaves (Fig. 5*B*,*C*).

Discussion

Generally speaking, variegated leaves usually have lower photosynthetic rate than green leaves (Burger and Edwards 1996, Hughes *et al*. 2005, Song *et al*. 2018). Photosynthetic capacity of variegated leaves in *Arabidopsis* mutant is almost completely lost, which was due to chlorophyll absence (Yu *et al*. 2011, Sheue *et al*. 2012, Lundquist *et al*. 2014, Song *et al*. 2018). In natural variegated plants, for example *Ficus pumila* cv. Sonny and *Saururus chinensis*, photosynthetic capacity decreased by 50 % even more. However, our study showed that P_N and ΦPSII of white leaves in *A. polygama* was similar to green leaves, although spectral reflectance from adaxial surface of white leaves was two-fold higher than that of green leaves. Why variegated leaves can maintain a rather high P_N? White leaves of *A. polygama* may utilizes two mechanisms for maintaining photosynthetic capacity. First, functional chloroplasts were observed in palisade tissue cells of white leaves. In previous studies, photosynthetic capacity decrease in variegated leaves was mainly due to chlorophyll deficiency (Sheue *et al*. 2012, Song *et al* 2018). For example, palisade tissue cells of variegated leaves do not contain functional chloroplasts in *S. chinensis* (Song *et al* 2018). However, our results show that the total chlorophyll content had no significant difference although the relative chlorophyll content of white leaves was lower than of green leaves at the adaxial surface. Moreover,

the higher photosynthetic activity in white leaves might further maintain photosynthetic capacity.

The parameters derived from JIP-testing can be useful indicators for evaluation of photosynthetic capacity of leaves (Wen *et al*. 2005, Mathur *et al*. 2011). During leaf development, ET_0/TR_0 and ET_0/ABS in white leaves was higher than in green leaves (Fig. 5). The higher efficiency of electron transport (ET_0/ABS and ET_0/TR_0) maximized the photosynthetic ability of white leaves.

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