



# Photosynthetic characteristics explain the high growth rate for *Eucalyptus camaldulensis*: Implications for breeding strategy

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## ABSTRACT

Eucalypt wood is a valuable raw material for pulping worldwide. Because of its high growth rate, *Eucalyptus camaldulensis* has been introduced for plantation production in many tropical and subtropical areas in China. However, photosynthetic mechanisms underlying the rapid growth rate of *E. camaldulensis* are not well known. Furthermore, little is known about the relative photosynthetic limitations that complicate breeding strategies for this species. In the present study, we examined the photosynthetic characteristics for leaves of *E. camaldulensis* and observed stomata on both adaxial and abaxial surfaces, with their density being higher on the latter. Regardless of which surface was exposed to sunlight, the actual whole-leaf photosynthesis of *E. camaldulensis* reached  $42.00 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , which is much higher than that reported for other C3 plants. Although both surfaces showed high photosynthetic rates, photosynthesis and intrinsic water-use efficiency were always greater on the abaxial surface, mainly because of differences in mesophyll conductance ( $g_m$ ). Analysis of quantitative limitations revealed that  $g_m$  was the most constraining factor for photosynthesis while stomatal conductance was much less important. Taken together, our results imply that  $g_m$  is a potential target for simultaneous improvement of photosynthesis and photosynthetic water-use efficiency in *E. camaldulensis*, and we propose that increased  $g_m$  is an important trait for breeding of that species.

## 1. Introduction

Eucalypt wood is known worldwide as an important source of raw material for pulping. Members of *Eucalyptus* are now among the most valuable and widely planted hardwoods (Rockwood et al., 2008). Most species are native to Australia and Tasmania (Boland et al., 1992). In China, *Eucalyptus camaldulensis* Dehnh. has been introduced for plantation production in many tropical and subtropical areas, primarily to supply the pulp and paper industries. When sufficient water is available, those plants show higher growth rates than many other woody plants (Grotkopp et al., 2010). The rapid growth rate of *E. camaldulensis* is assumed to be caused by its high rate of carbon gain in dependence on photosynthesis. However, the photosynthetic characteristics of this species are not well-known. Furthermore, the relative photosynthetic limitations in *E. camaldulensis* have not yet been clarified, thereby complicating efforts toward its breeding and domestication.

Generally, plants with greater rates of  $\text{CO}_2$  assimilation have high levels of enzymes that are involved in electron transfer and the Calvin-Benson cycle, including cytochrome *f*, ATP synthase, and Rubisco (Evans, 1987; Terashima and Evans, 1988; Hikosaka, 1996; Hikosaka and Terashima, 1996; Yamori et al., 2010, 2011). Furthermore, a high rate of photosynthesis is usually correlated with greater stomatal conductance ( $g_s$ ) and mesophyll conductance ( $g_m$ ), which increase  $\text{CO}_2$  diffusion into the chloroplasts (Yamori et al., 2010, 2011). This phenomenon is beneficial for herbaceous plants such as tobacco (*Nicotiana tabacum*), rice (*Oryza sativa*), wheat (*Triticum aestivum*), and *Spinacia oleracea* (Yamori et al., 2010, 2011). Specifically,  $g_m$  plays a crucial role in determining the photosynthetic rate in C<sub>3</sub> plants (Flexas et al., 2008; Carriqui et al., 2015). Herbaceous annuals, including tobacco, wheat, and rice, that have high photosynthetic rates usually have thinner cell walls that lead to strong  $g_m$  values (Terashima et al., 2006). By comparison, leaves of sclerophyllous plants have thicker cell walls and

**Abbreviations:**  $A_N$ , net assimilation rate;  $C_c$ , chloroplastic  $\text{CO}_2$  concentration;  $C_i$ , sub-stomatal  $\text{CO}_2$  concentration;  $g_m$ , mesophyll conductance;  $g_s$ , stomatal conductance;  $J_{\text{max}}$ , maximum rate of RuBP regeneration calculated from gas exchange on a  $C_i$  basis;  $l_b$ , biochemical limitation;  $l_m$ , mesophyll conductance limitation;  $l_s$ , stomatal limitation;  $V_{\text{cmax}}$ , maximum rate of RuBP carboxylation calculated from gas exchange on a  $C_i$  basis; WUE, water use efficiency

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lower values of  $g_m$  (Terashima et al., 2006; Hassiotou et al., 2009). A reduction in  $g_m$  increases the resistance of CO<sub>2</sub> conductance to the chloroplasts, causing a decline in the chloroplast CO<sub>2</sub> concentration ( $C_c$ ) and, thus, restricted CO<sub>2</sub> assimilation (Lloyd et al., 1992; Hanba et al., 2002; Flexas et al., 2012; Gago et al., 2013; Carriqui et al., 2015). Therefore, sclerophyllous plants usually have low rates of photosynthesis (Lloyd et al., 1992).

Nevertheless, the sclerophyllous species *E. camaldulensis* shows a relatively high rate of photosynthesis, similar to that of tobacco (Huang et al., 2016), and this eucalypt carries stomata on both the adaxial and abaxial surfaces of its leaves (James and Bell, 1995). Accordingly, we hypothesized that the adaxial surface is responsible for significant CO<sub>2</sub> uptake in addition to the high rate of photosynthesis on the abaxial surface, which, together, might explain the high growth rate for this species. Leaf photosynthesis is mainly dependent on CO<sub>2</sub> uptake along the abaxial surface, and that uptake rate is higher there than on the adaxial surface (Driscoll et al., 2006). In *E. camaldulensis* leaves,  $g_m$  is the main constraint on photosynthesis on the abaxial surface (Huang et al., 2016). Therefore, we also hypothesized that the abaxial surface would show higher values of  $g_m$  and, consequently, a higher rate of assimilation when compared with the adaxial surface.

A key objective for sustainable agriculture and forestry is to breed plants with both high carbon gain and water-use efficiency (WUE), as reflected by the ratio of net photosynthesis ( $A_N$ ) to  $g_s$ . With regard to leaf physiology, achieving this goal would entail increasing  $A_N$  relative to  $g_s$ . Both  $g_s$  and  $g_m$  limit  $A_N$  in crop plants and wild species (Flexas et al., 2013). However, the relative importance of each of those two types of conductance depends upon species and growing conditions. Based on Fick's law of diffusion, intrinsic WUE should be correlated with the ratio  $g_m/g_s$  rather than with  $g_m$  itself (Flexas et al., 2013). Furthermore, if  $A_N$  and WUE are to be improved simultaneously, then any genetic manipulation of  $g_m$  should avoid parallel changes in  $g_s$  (Flexas et al., 2013). For *E. camaldulensis* leaves, the most limiting factor for photosynthesis on the abaxial surface is not known and it is also unclear whether the intrinsic WUE of that species is correlated with  $g_m/g_s$ . Therefore, if researchers are to select the most appropriate trait and develop a means for enhancing  $A_N$  and intrinsic WUE for *E. camaldulensis* leaves, then those relative photosynthetic limitations should be clarified.

Based on previous studies and our observations, we hypothesized that, for *E. camaldulensis* leaves, the abaxial surface shows a higher  $g_m$  and, thus, higher photosynthesis and intrinsic WUE than the adaxial surface. To test this, we measured gas exchange and chlorophyll fluorescence in light-response curves and CO<sub>2</sub>-response curves for both leaf surfaces. All measurements were made in mid-Summer, during a period of moderate temperatures and in the absence of water stress. Our specific objectives were to 1) determine whether *E. camaldulensis* leaves show relatively more significant CO<sub>2</sub> uptake on the adaxial surface; 2) investigate whether  $g_m$  is the main factor limiting photosynthesis for both leaf surfaces; and 3) clarify whether the differences in  $A_N$  and intrinsic WUE between the two surfaces are influenced by changes in  $g_m$ .

## 2. Materials and methods

### 2.1. Plant materials and growing conditions

We examined the photosynthetic characteristics from both the abaxial and adaxial surfaces of leaves from *Eucalyptus camaldulensis*. The plants were grown in an open field at an elevation of 700 m in Dongchuan County, Kunming City, Yunnan Province, China. Photosynthetic parameters were evaluated in June of 2014, using five mature leaves from five individual three-year-old plants that were not exposed to water stress. The gas-exchange measurements were performed at 8:00–11:00 (solar time) on several clear days.

### 2.2. Measurements of gas exchange and chlorophyll fluorescence

Gas exchange and chlorophyll fluorescence were monitored with an open gas exchange system that incorporated infrared CO<sub>2</sub> and water vapor analyzers (LI-6400XT; Li-Cor Biosciences, Lincoln, NE, USA) and a 2-cm<sup>2</sup> measuring head (6400-40 Leaf Chamber Fluorometer; Li-Cor Biosciences). The rates of CO<sub>2</sub> assimilation were measured separately for the abaxial and adaxial surfaces. When the adaxial surface was exposed to light, the rate of CO<sub>2</sub> uptake on the abaxial surface was measured by the LI-6400XT, which indicated the photosynthetic rate for that abaxial surface (Driscoll et al., 2006). Under such conditions, all photosynthetic parameters were referenced to the abaxial surface. When the abaxial surface was exposed to light, the rate of CO<sub>2</sub> uptake and other photosynthetic parameters were determined for the adaxial surface.

During the period of measurements for light-response curves, the atmospheric CO<sub>2</sub> concentration was maintained at 400  $\mu\text{mol mol}^{-1}$ , and data were recorded at  $27 \pm 1^\circ\text{C}$  and a relative air humidity of 60–70%. After the leaves were exposed to saturating light (2000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) for 20 min to activate photosynthesis, light curves were evaluated at 2-min intervals at different light intensities (2000, 1600, 1200, 1000, 800, 500, 300, 150, 100, 50, and 0  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ). The response of net CO<sub>2</sub> assimilation rate to CO<sub>2</sub> concentration was examined at 2000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  and  $27 \pm 1^\circ\text{C}$ . Before the  $A/C_i$  measurements were made, the designated leaves were light-adapted for at least 20 min at 2000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  and a 400  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> concentration to obtain stable values for  $g_s$  and  $A_n$ . Afterward, the CO<sub>2</sub> concentration was set to 50  $\mu\text{mol mol}^{-1}$  and increased stepwise for  $A/C_i$  measurements made at 50, 100, 150, 200, 300, 400, 600, 800, 1000, and 1200  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub>. Each stepwise measurement was completed within 2–3 min. Using the  $A/C_i$  curves, we calculated the maximum rates of RuBP regeneration ( $J_{\text{max}}$ ) and RuBP carboxylation ( $V_{\text{cmax}}$ ) according to the method of Long and Bernacchi (2003).

The fluorescence parameters  $F_m'$  and  $F_s$  were evaluated as previously described (Baker and Rosenqvist, 2004), with  $F_m'$  representing the maximum fluorescence after light-adaptation and  $F_s$  being the light-adapted steady-state fluorescence. The effective quantum yield of photosystem II (PSII) was calculated as  $\Phi_{\text{PSII}} = (F_m' - F_s)/F_m'$  (Genty et al., 1989). Using the data of  $\Phi_{\text{PSII}}$ , we calculated total photosynthetic electron flow ( $J_T$ ) through PSII as follows (Krall and Edwards, 1992):  $J_T = \Phi_{\text{PSII}} \times \text{PPFD} \times L_{\text{abs}} \times 0.5$ , where PPFD was the photosynthetic photon flux density and  $L_{\text{abs}}$  (leaf absorbance) was assumed to be 0.84. We applied the constant of 0.5 based on the assumption that photons were equally distributed between PSI and PSII.

### 2.3. Estimates of mesophyll conductance and chloroplast CO<sub>2</sub> concentration

Values for mesophyll conductance were estimated through a combination analysis of gas exchange and chlorophyll fluorescence, and according to the following equation (Harley et al., 1992):

$$g_m = \frac{A_N}{C_i - \Gamma^* (J_T + 8(A_N + R_d)) / (J_T - 4(A_N + R_d))}$$

Where  $A_N$  represented the net rate of CO<sub>2</sub> assimilation,  $C_i$  was the intercellular CO<sub>2</sub> concentration,  $\Gamma^*$  was the CO<sub>2</sub> compensation point in the absence of daytime respiration (Farquhar et al., 1980; Brooks and Farquhar, 1985), and  $R_d$  was the rate of mitochondrial respiration as measured after 10 min of dark-adaptation.

Using the estimated  $g_m$ , we then calculated the chloroplast CO<sub>2</sub> concentration ( $C_c$ ) according to the following equation (Long and Bernacchi, 2003; Warren and Dreyer, 2006; Yamori et al., 2010, 2011):

$$C_c = C_i - \frac{A_n}{g_m}$$

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