



Physiology

Variability of mesophyll conductance and its relationship with water use efficiency in cotton leaves under drought pretreatment[☆]



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ABSTRACT

Drought slows net photosynthetic rate (A_N) but increases water use efficiency (WUE). Farmers give an artificial drought pretreatment to some crops in the early growth stage and find that yield increases accompanying with the improvement of WUE. We conducted well-watered, non-drought, mild drought and moderate drought pretreatments of potted cotton cultivars. The aims of the present study were to analyse the importance of mesophyll conductance (g_m) as a factor that may simultaneously improve A_N and WUE under drought pretreatment conditions, and to analyse the role of anatomical structure and biochemical mechanism in the variability of g_m . Our results showed that significant variability of g_m estimated by gas exchange and chlorophyll fluorescence was observed between non-drought pretreatment and drought pretreatment associated with change in A_N and WUE. There was great difference in anatomical structure and expression of aquaporins (*GhAQPI*) among all the treatments. In addition, expression of carbonic anhydrase (*CA*) may not be important in the regulation of g_m under drought pretreatment conditions. We concluded that the variability of g_m offers a potential target for improving leaf A_N and WUE simultaneously by the regulation of anatomical structure and *GhAQPI*.

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Abbreviations: A_N , net photosynthetic rate; *CA*, carbonic anhydrase; C_c , CO_2 concentration in the chloroplast carboxylation site; *Chl*, chlorophyll; C_i , intercellular CO_2 concentration; D_a ($m^{-2} s^{-1}$), the diffusion coefficient for CO_2 in the gas phase; f_{ias} , the volume fraction of intercellular air space; F_m' , maximal fluorescence of light-adapted state; F_s , steady state fluorescence of light-adapted state; g_{cyl} , cytosol conductance; g_{ias} , conductance from sub-stomatal cavities to outer surface of cell walls; g_{liq} , the conductance from outer surface of cell walls to chloroplasts; g_m , mesophyll conductance; g_s , stomatal conductance; g_{str} , stroma conductance; g_{wall} , the cell wall conductance; *H*, the Henry's law constant ($Pa\ m^3\ mol^{-1}$); $H/(R^*T_k)$, a parameter that helps to convert g_{liq} to a gas-phase equivalent conductance; J_{flu} , the electron transport rate; ΔL_{ias} , taken as half the mesophyll thickness; *PPFD*, the photosynthetically active photon flux density; *R*, the gas constant ($Pa\ m^3\ K^{-1}\ mol^{-1}$); R_d , day respiration; γ_{fi} , the dimensionless factor which accounts for the decrease of diffusion conductance in the cytosol and in the stroma compared with free diffusion in water; R_n , dark respiration; *Rubisco*, ribulose-1,5-bisphosphate carboxylase/oxygenase; S_c/S , the surface area of mesophyll cells or chloroplasts exposed to the intercellular air spaces; ΣS_s , the sum of the cross-sectional areas of mesophyll cells; T_{cw} , cell wall thickness; t_{mes} , the mesophyll thickness between the two epidermises; T_k , the absolute temperature (K); T_r , transpiration rate; *W*, the width of the section; *WUE*, water use efficiency; α , chlorophyll fluorescence imaging system; β , the partitioning of absorbed quanta between photosystems I and II (PSI and PSII); Γ^* , CO_2 photo-compensation point; ζ , the diffusion path tortuosity ($m\ m^{-1}$); Φ_{PSII} , the actual photochemical efficiency of photosystem II; Ψ_w , leaf water potential.

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1. Introduction

Soil drought stress is one of the major environmental factors limiting crop growth and yield in arid and semi-arid areas. Therefore, increasing water use efficiency (WUE) becomes a major priority under the increasing aridity associated with warmer temperatures and change in precipitation (Costa et al., 2007; Morison et al., 2008). In fact, in the agricultural production practice, to increase WUE thereby maintaining yield in drought conditions, farmers give an artificial drought pretreatment to some crops in the early growth stage, e.g. cotton (Shi et al., 2004), maize (Zhang et al., 2008), and wheat (Wang et al., 2008; Wang et al., 2010) in the hope of making crops more tolerant to a subsequent drought that may occur in the later period of growth and development. Subsequently, WUE is improved under drought pretreatment conditions. WUE can be expressed as the ratio of net photosynthetic rate (A_N) to transpiration rate (T_r) ($WUE = A_N/T_r$). Generally, the improvement of WUE occurs at the expense of A_N (Aranda et al., 2007). Efforts have been made to clarify the underlying mechanisms of the responses of A_N to drought stress in many plants (Flexas and Medrano, 2002; Lawlor and Cornic, 2002; Chaves et al., 2003). However, few studies, from the view of the agriculture practice, focus on the physiological response mechanism of A_N and WUE on drought pretreatment.

Photosynthesis requires diffusion of CO₂ from the atmosphere into the leaf and finally to the site of carboxylation in the chloroplast stroma (Flexas et al., 2007). Some researchers have suggested that drought stress strongly reduces CO₂ availability in the chloroplasts by limiting CO₂ diffusion paths, and thus photosynthetic capacity is progressively decreased under drought conditions (Chaves et al., 2002; Flexas et al., 2002, 2004; Galmés et al., 2007). Most commonly, the diffusion pathway of CO₂ is simplified into three main components: boundary layer conductance, stomatal conductance (g_s), and mesophyll conductance (g_m). Boundary layer conductance depends on several leaf physical and environmental properties (Bernacchi et al., 2002), therefore some researchers cannot take it into account within the same species and climate zone. Stomatal closure is one of the first responses to soil drought accompanying decreased g_s and A_N (Medrano et al., 1997). There is evidence that g_m , as well as g_s , is also an important leaf characteristic for influencing plant photosynthetic responses to environmental stresses, since g_m determines the drawdown of CO₂ from sub-stomatal cavities to chloroplasts (Flexas et al., 2007, 2008; Niinemets et al., 2009). Many researchers have reported that g_m decreases in response to drought (Flexas et al., 2009; Galmés et al., 2011). Other studies have focused on the limiting role of mesophyll diffusion conductance to CO₂ to photosynthesis under water stress (Warren and Adams, 2006; Flexas et al., 2008).

Under drought treatments, the change in g_m is influenced by multiple factors, such as the effect of leaf anatomical structure on g_m . CO₂ molecules passing from sub-stomatal cavities to chloroplasts diffuse through the gas phase and the liquid phase. Gas phase diffusion mainly occurs in leaf intercellular air spaces, and liquid phase diffusion occurs in cell walls, plasma-lemma, the cytosol, chloroplast envelope membranes, and chloroplast stroma (Evans et al., 2009; Flexas et al., 2013). Many authors have reported that gas phase resistance is very low and can be ignored (Evans et al., 2009). Therefore, liquid phase conductance determines the main composite segments of diffusion. Flexas et al. (2012) considered that the rate of CO₂ diffusion depends on the effective thickness and diffusivity of each component section. Perhaps drought decreases $g_{m\text{and}}$ then reduces A_N by means of thickening the cell wall (Miyazawa and Terashima, 2001) and shrinking the surface area of mesophyll cells or chloroplasts exposed to the intercellular air spaces (S_c/S) (Evans et al., 1994). Some reviews and reports (Patakas et al., 2003; Tholen et al., 2008; Hassiotou et al., 2010; Scafaro et al., 2011) also suggested that leaf anatomical characteristics affect g_m . A quantitative one-dimensional gas diffusion model proposed by Niinemets and Reichstein (2003a) further improved by Tomás et al. (2013) has facilitated understanding of the effect of different leaf anatomical characteristics on g_m .

Apart from leaf anatomical characteristics, the resistance to CO₂ diffusion also has a biochemical component (Terashima et al., 2005). Evidence has suggested two promising candidates to play this biochemical role: carbonic anhydrase (CA), and aquaporins (AQPs). Concerning the involvement of CA in the regulation of g_m , less evidence has been found. The role of CA in regulating g_m is more controversial than the evidence found for AQPs which is the most abundant protein in plant plasma membranes (Flexas et al., 2012). AQP1 is a member of the plasma membrane aquaporin1 family (PIP1). Uehlein et al. (2003) showed that tobacco aquaporin NtAQP1 facilitates transmembrane CO₂ transport by expression in *Xenopus* oocytes and suggested that NtAQP1 expression could be affecting g_m . Research has also demonstrated that aquaporin NtAQP1 is involved in g_m and plays a key role in the transport of water, as well as CO₂, through cell membranes (Flexas et al., 2006).

Despite all of the negative response to drought stress, the fact remains that WUE increases as A_N and CO₂ diffusion conductance decreases under drought stress conditions (Pou et al., 2008). The increased WUE is mainly caused by decreasing g_s (Flexas et al.,

2004). It is also highly useful to increase A_N under drought stress, because a decline of A_N decreases production of food and fuel. Therefore, to improve the A_N and WUE simultaneously has been an important goal for a long time. Theoretically, increasing g_m could increase A_N and WUE simultaneously (Flexas et al., 2010, 2013; Xu et al., 2013). Increasing g_m increases the CO₂ concentration at the carboxylation site in the chloroplast without increasing water loss; therefore, A_N and WUE are increased (Flexas et al., 2010). However, research has indicated that WUE should correlate with the ratio g_m/g_s , not g_m itself (Flexas et al., 2013) and in Eucalyptus, higher g_m/g_s also contributes to higher A_N (Cano et al., 2014). Therefore, g_m or g_m/g_s plays a key role in increasing A_N and WUE simultaneously.

Cotton (*Gossypium hirsutum* L.) is a common cash crop in Central Asia which mainly is an arid and semi-arid region, where water deficit severely limits the yield of cottons in the long term. Thus, improved water use efficiency by drought will be a target to improve production and agricultural water-saving irrigation. Our previous studies found that A_N and WUE increased simultaneously under drought pretreatment conditions compared with non-drought pretreatment conditions. Based on the above discussion, we conducted an experiment in an artificial climate chamber to simulate this phenomenon that drought pretreatment can improve A_N and WUE simultaneously and test the following hypotheses in an upland cotton (*G. hirsutum* L. cv. Xinluzao 45):

- (1) Drought pretreatment may improve A_N and WUE simultaneously.
- (2) Perhaps g_m (or g_m/g_s) plays an important role in improving A_N and WUE simultaneously.
- (3) Under drought pretreatment, mechanisms regulating g_m may be related to anatomical structure and biochemical mechanism.

2. Material and methods

2.1. Plant material

Cotton (*G. hirsutum* L. cv. Xinluzao 45) plants were germinated and grown environmentally in a controlled artificial climate chamber located at the University of Shihezi (China). The 24 cultivars were sown in 10 L pots filled with a mixture of clay soil and organic substrate. Artificial climate chamber air temperatures were set to 28 °C for the 12–14 h photoperiod and 25 °C at night. Growth light was supplied by sodium lamps to maintain a minimum photon flux of 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at plant height (we measured and fitted some light response curves of cotton leaves in an environmentally controlled artificial climate chamber and concluded that the light saturation point is about 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$).

2.2. Water drought treatments

All plants (24 pots) were irrigated daily to water saturation (40% soil absolute water content). The water treatment was conducted when the fifth leaves of all cotton plants were fully expanded. Plants were divided in four groups of 6 individuals of each treatment and arranged in a randomized plot. These four groups include well-watered, non-drought pretreatment, mild, and moderate drought pretreatment, respectively. The first group was kept under well-watered conditions (40% soil absolute water content) throughout the entire experimental period. The second group was also kept at 40% soil absolute water content for the first eleven days, and then subjected to moderate drought (22% soil absolute water content). The third group was kept under mild drought conditions (30% soil absolute water content), this level of absolute water content was reached 1 d after stopping irrigation. Once the desired water stress was obtained, plants were maintained at constant water stress for

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