



Assessing stomatal and non-stomatal limitations to carbon assimilation under progressive drought in peanut (*Arachis hypogaea* L.)



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ABSTRACT

Drought is known to limit carbon assimilation in plants. However, it has been debated whether photosynthesis is primarily inhibited by stomatal or non-stomatal factors. This research assessed the underlying limitations to photosynthesis in peanuts (*Arachis hypogaea* L.) grown under progressive drought. Specifically, field-grown peanut plants were exposed to either well-watered or drought-stressed conditions during flowering. Measurements included survey measurements of gas exchange, chlorophyll fluorescence, PSII thermotolerance, pigment content, and rapid A-C_i response (RACiR) assessments. Drought significantly decreased stomatal conductance with consequent declines in photosynthesis (A_N), actual quantum yield of PSII, and electron transport rate (ETR). Pigment contents were variable and depended on stress severity. Stomatal closure on stressed plants resulted in higher leaf temperatures, but F_v/F_m and PSII thermotolerance were only slightly affected by drought. A strong, hyperbolic relationship was observed between stomatal conductance, A_N, and ETR. However, when RACiR analysis was conducted, drought significantly decreased A_N at C_i values comparable to drought-stressed plants, indicating non-stomatal limitations to A_N. The maximum rate of carboxylation and maximum electron transport rate were severely limited by drought, and chloroplast CO₂ concentration (C_C) declined substantially under drought along with a comparable increase in partitioning of electron flow to photorespiration. Thus, while stomatal conductance may be a viable reference indicator of water deficit stress in peanut, we conclude that declines in A_N were largely due to non-stomatal (diffusional and metabolic) limitations. Additionally, this is the first study to apply the rapid A-C_i response method to peanut, with comparable results to traditional A-C_i methods.

1. Introduction

One of the mechanisms by which drought limits productivity in field crops is by decreasing source strength, which is the product of leaf area and average photosynthetic efficiency of all leaves in the canopy (Krieg and Sung, 1986). Expectedly, a tremendous amount of research has been aimed at identifying the weak link in the photosynthetic response to water deficit for a number of plant species (Chastain et al., 2014; Snider et al., 2014; Ennahli and Earl, 2005; Lauriano et al., 2000, 2004;

Lawlor, 2002; Medrano et al., 2002; Tezara et al., 1999). Furthermore, there has been a long-running debate on whether photosynthesis is primarily inhibited under drought by stomatal or non-stomatal limitations to carbon assimilation (Reviewed in Flexas and Medrano, 2002; Lawlor, 2002). As a general rule, it has been suggested that under mild to moderate water deficit stress, photosynthesis declines due to stomatal closure and reduced intercellular CO₂ concentration (C_i) or due to decreased mesophyll conductance (g_m), which reduces CO₂ concentration in the chloroplast (C_C), but under more severe stress, metabolic

Abbreviations: A_N, net photosynthesis; C_i, leaf internal CO₂; ETR, photosynthetic electron transport rate; F₀, basal fluorescence; F_v, maximum fluorescence intensity; F_v/F_m, maximum quantum yield of photosystem II; g_s, stomatal conductance; J_{max}, maximum photosynthetic electron transport rate; PSII, Photosystem II; RACiR, rapid A-C_i response curve; R_p, dark respiration rate; T₁₅, 15% decline in F_v/F_m relative to the optimum temperature; T_{air}, air temperature; T_{leaf}, leaf temperature; V_{cmax}, maximum rate of rubisco carboxylation; Φ_{PSII}, actual quantum yield of photosystem II

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(ATP production, Rubisco activity, etc.) impairment dominates (Ennahli and Earl, 2005; Flexas et al., 2006; Galmes et al., 2007). However, caution should be taken in broadly applying these rules across plant species because previous work comparing different species under the same field conditions has demonstrated different strategies for coping with drought. For example, Zhang et al. (2011) found that photosynthetic declines in cotton (*Gossypium hirsutum* L.) were associated with increased photorespiration, whereas soybean (*Glycine max* L.) lowered photosynthetic rates under drought by increasing non-photochemical quenching. Interestingly, Medrano et al. (2002) suggested that stomatal conductance (g_s) could serve as a broadly applicable reference indicator of drought stress. They observed significant relationships between g_s and a number of photosynthetic processes for multiple species under a range of experimental conditions (i.e. potted plants versus field grown). For example, the drought responses for processes that are largely recognized as “non-stomatal” were strongly associated with g_s .

Quantifying the response of net photosynthesis (A_N) to leaf internal CO_2 (C_i) concentration has provided valuable insight into the underlying mechanisms contributing to photosynthetic limitations under a range of experimental conditions (Ennahli and Earl, 2005; Wise et al., 2004; Wullschlegel, 1993). For example, under drought, a decline in A_N at the same C_i value as well-watered plants would indicate a non-stomatal limitation to photosynthesis (Ennahli and Earl, 2005). If one applies the Farquhar et al. (1980) model of photosynthesis to A- C_i response curves, the maximum rate of rubisco carboxylation ($V_{c,max}$), maximum photosynthetic electron transport rate (J_{max}), and dark respiration rate (R_D) can be estimated (Dubois et al., 2007; Sharkey et al., 2007; Long and Bernacchi, 2003), thereby indicating which process or processes are most limited under a given set of conditions. Despite the valuable information that can be obtained using these methods, traditional A- C_i analysis is time consuming (only a few plants can be measured in a given day using the most commonly-available portable photosynthesis systems; Stinziano et al., 2017), which often necessitates that measurements be conducted over a large portion of a given day and across multiple sample dates to ensure sufficient sample size (Gilbert et al., 2012; Wise et al., 2004). This constraint can be particularly problematic when assessing photosynthetic responses to progressive drought stress because plant water status changes with duration of drought and with diurnal sample time (Grimes and Yamada, 1982). This allows only a brief window of time (approximately two or three hours in the afternoon) during which to conduct measurements. A relatively novel method to rapidly assess A- C_i responses (termed RACiR) exploits the short response time and the high frequency data collection of the LI-6800 portable photosynthesis system (LI-COR Inc., Lincoln NE) to generate A- C_i response curves in as little as 5 min (Stinziano et al., 2017) with comparable results to traditional A- C_i methods, thereby increasing the number of samples that can be measured in a given window of time. While the aforementioned approach would lend itself to measurement of water deficit stress responses, there have been no studies published to date that have utilized RACiR analysis to quantify photosynthetic responses to drought in field-grown plants.

Another consequence of drought stress is an increase in leaf temperatures due to low stomatal conductance and limited transpirational cooling (Bennett et al., 1984). Thus, the ability of plants to tolerate high temperature should be an important factor influencing plant performance under drought. Chlorophyll fluorescence-based methods have been used successfully to quantify thermotolerance of multiple plant species under field conditions. These approaches typically involve collecting leaf samples from the field, exposing them to increasing incubation temperature in the laboratory, and quantifying high temperature thresholds for fluorescence-based responses (F_v/F_m , F_0 , F_v/F_0 ; Chastain et al., 2016; Snider et al., 2010, 2013, 2015; Froux et al., 2004; Burke, 1990). These methods have been used to document acclimation to growth temperature in crop and forest species (Snider et al., 2013; Froux et al., 2004) and more recently, have been used to document

strong relationships between plant water status and photosystem II thermotolerance in cotton (Chastain et al., 2016). It is possible that this is a factor contributing to the broad tolerance and stability of PSII to water deficit stress reported previously (Medrano et al., 2002). The impact of water deficit on PSII thermostability has not been addressed previously in peanut (*Arachis hypogaea* L.).

Peanut is an oilseed crop of great importance worldwide, generally cultivated in tropical, subtropical, and warm temperate weather (Hammons et al., 2016). Peanut kernels are primarily composed of proteins, unsaturated fats, and fiber, which make this crop an important protein food source, mainly in underdeveloped countries (Davis and Dean, 2016).

Drought conditions often limit peanut production and impair the plant's defense mechanisms, favoring aflatoxin contamination, mainly when drought stress occurs during reproductive development (Jeyaramraja et al., 2018; Wright et al., 1991). Although a short drought period does not always result in a reduction in peanut yield due to its indeterminate growth habit, decreased productivity under drought results from declines in whole-canopy photosynthesis due to decreased leaf area and photosynthetic efficiency per unit leaf area (Reddy et al., 2003). Declines in net photosynthesis have been widely reported in peanuts under mild drought, and a number of authors have attempted to address the physiological basis of drought-induced photosynthetic inhibition or the underlying mechanisms contributing to drought tolerance in peanut (Clifford et al., 2000; Lauriano et al., 1997, 2004; Kottapalli et al., 2009; Qin et al., 2011; Reddy et al., 2003). For example, Clifford et al. (2000) documented extensive declines in photosynthesis and stomatal conductance with progressive drought, and Reddy et al. (2003) reviewed several reports on drought stress effects in peanut and suggested that decreased stomatal conductance was the primary limitation to photosynthesis under drought largely based on the observation that stomatal conductance declines concomitantly with net photosynthetic rate. Lauriano et al. (1997, 2004) used a combination of *in situ* gas exchange measurements coupled with *in vitro* laboratory assessments of electron transport processes and Rubisco activity in isolated chloroplast fractions to delineate the factors limiting photosynthesis under drought in peanut. These authors suggested that drought primarily limited photosynthesis by inhibiting the efficiency of the thylakoid reactions (especially those occurring at photosystem II). By comparison, they found no effect of drought stress on rubisco activity (measured under laboratory conditions). Finally, Kottapalli et al. (2009) screened diverse peanut germplasm for tolerance to drought and identified proteomic responses associated with enhanced drought tolerance. While the aforementioned studies have been important for advancing our understanding of physiological responses of peanut to drought, none utilized simultaneous gas exchange and fluorescence to assess the impact of progressive drought on photochemistry and gas exchange in field-grown peanut. Furthermore, none of the studies noted above have evaluated the responses of A_N to leaf C_i or the parameters derived from the A- C_i curve, such as $V_{c,max}$ and J_{max} , in US runner cultivars (the dominant peanut market type in the US) under drought.

We hypothesized that (i) drought-induced inhibition of photosynthesis in peanut plants would be driven by stomatal and non-stomatal limitations, and as drought progresses, non-stomatal limitations such as electron transport would play a more relevant role in reducing photosynthesis, (ii) g_s will serve as a broadly applicable indicator of water deficit in peanut, regardless of the underlying processes actually limiting A_N , and (iii) that RACiR analysis under severe, photosynthesis-limiting stress will allow us to delineate between RuBP regeneration (J_{max}) and rubisco activity ($V_{c,max}$) as the primary non-stomatal limitation to photosynthesis. Therefore, the first objective of this study was to assess the underlying limitations to photosynthesis in peanuts grown under progressive drought using survey measures of gas exchange and fluorescence, PSII thermotolerance assessments, and pigment analysis. The second objective was to utilize rapid A- C_i response analysis to assess the impact of severe, photosynthesis-limiting drought on $V_{c,max}$ and

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