Stomatal and non-stomatal limitations to photosynthesis of *Populus euphratica* Oliv. leaves in an extremely arid area of northwestern China

Guanlong Gao (✉ guanlong_gao@163.com)

<https://orcid.org/0000-0003-3277-4126>

Qi Feng

Northwest Institute of Eco-Environment and Resources

Xiande Liu

Academy of Water Resources Conservation Forests in Qilian Mountains of Gansu Province

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Abstract

On the basis of successive measurements of leaf gas exchange during the main growing seasons of *Populus euphratica* Oliv. in 2013 and 2014, respectively, we analyzed the stomatal and non-stomatal limitations to photosynthesis under natural conditions in an extremely arid region of northwestern China. Our results showed that (1) the distribution patterns of net photosynthesis (P_n) and stomatal conductance (g_s) were similar, both of which increased in the morning, peaked at around noon, and then decreased. This contrasted with the observed changes in sub-stomatal CO_2 concentrations (C_i). (2) The phenomenon of midday depression of photosynthesis (MDP) was obvious from July to September during the two years. At the beginning of MDP, the stomatal limitation to photosynthesis (L_s) peaked, where its predominance was supported by C_i being at a minimum. Thereafter, L_s decreased and C_i/g_s increased sharply, indicating that the non-stomatal limitation to photosynthesis predominated. (3) Both the L_s and relative stomatal limitation to photosynthesis (RL_s) increased in the morning, and then decreased, whereas C_i/g_s presented contrary changes. (4) The RL_s values were greater than the L_s values, which was mainly due to the nonlinearity of the P_n/C_i curve, which often leads to large overestimations. (5) The L_s values in our study were much greater than those from other studies under natural conditions. The most probable reason was that the extremely high temperature and scarce water resource caused the stomata to close to reduce transpiration, resulting in the stomatal limitation to photosynthesis being more intense.

Background

Arid and semi-arid lands cover approximately 40 % of Earth's terrestrial surface and are expanding globally (Reynolds 2000) and the arid regions are expected to become drier as a result of climate change (Dai 2011, Sheffield et al. 2012, McDowell et al. 2015). The ecosystems in arid and semi-arid lands represent a dynamic but poorly understood component of the global carbon, water, and energy cycles (Naithani et al. 2012). The Ejina oasis, which is located in the lower reaches of the Heihe River Basin of northwestern China, is one of the most arid regions in the world, with annual rainfalls of less than 50 mm (Si et al. 2009). *Populus euphratica* Oliv. is the constructive species of the desert riparian forest in this region, where its regular growth is important for the formation of a natural barrier to support the existence of the Ejina oasis. Owing to the lack of water resources, however, the *P. euphratica* forests have degenerated in this region in the last century.

Drought stress is an important environmental factor inhibiting the growth and reducing the yield of plants worldwide (Li et al. 2000, Li and Wang 2003, Zhang et al. 2005). The limitation of plant growth due to low water availability is mainly caused by reductions in the plant carbon balance, which is largely dependent on photosynthesis (Flexas et al. 2009). Photosynthesis, the basic manufacturing process required for the existence of life on this planet, contributes to more than 90 % of crop biomass (Makino 2011). It can increase the carbon gain of crops and, thus, improve their yield and quality (Xie et al. 2017). Previous studies have shown that photosynthesis is one of the first physiological processes to be affected under drought (Lawlor 1995, Munns 2002). According to Farquhar and Sharkey (1982), there are two aspects to

the restrictions in photosynthesis: (1) the intercellular CO₂ concentration (C_i) cannot meet the needs of photosynthesis owing to the limitation of stomatal conductance (stomatal limitation); and (2) the chloroplast and Rubisco activities and ribulose biphosphate (RuBP) regeneration are decreased (non-stomatal limitation). Thus far, it is still unclear and under debate on whether drought limits photosynthesis mainly through stomatal or non-stomatal limitations (Noormets et al. 2001, Flexas and Medrano 2002).

Previous studies on stomatal and non-stomatal limitations of photosynthesis were conducted mostly under various controlled conditions, such as water stress (Ni and Pallardy 1992, Signarbieux and Feller 2011, Varone et al. 2012, Campos et al. 2014, Anev et al. 2016), saline-alkali stress (Steduto et al. 2000, Centritto et al. 2003, Meloni et al. 2003, Yang et al. 2008, Li et al. 2010), multifactor stress (Correia et al. 2005), and other stressors (Pereira et al. 2013, Maggard et al. 2016), whereas studies conducted under natural conditions were rare. In particular, in the extremely arid regions of northwestern China where the natural environments are harsh, studies on stomatal and non-stomatal limitations to photosynthesis have seldom been carried out. For *P. euphratica* grown in the Ejina oasis, researchers have focused mainly on the aspects of hydraulic redistribution (Yu et al. 2013), measuring and modeling of evapotranspiration and stomatal conductance (Hou et al. 2010, Zhu et al. 2011, Gao et al. 2016a, 2016b, 2017), and so on, whereas little research effort has been devoted to the stomatal and non-stomatal limitations to photosynthesis. Furthermore, drought can decrease the leaf photosynthetic rate (Zhou et al. 2015), which consequently limits the ecosystem productivity of *P. euphratica*. Therefore, the study of stomatal and non-stomatal limitations to photosynthesis of *P. euphratica* leaves in extremely arid areas is of particular importance.

The objectives of this study were to (1) analyze the diurnal changes in the environmental conditions and physiological factors of *P. euphratica* leaves and (2) study the stomatal and non-stomatal limitations to photosynthesis of *P. euphratica* leaves under natural conditions in an extremely arid region. Our research should be of great significance, as the analysis of stomatal and non-stomatal limitations to photosynthesis of *P. euphratica* leaves under natural conditions in the Ejina oasis has not yet been reported.

Methods

2.1. Experimental site

Measurements of leaf gas exchange in *P. euphratica* leaves were recorded at the Qidaoqiao *P. euphratica* Forest Reserve in Ejina County (Inner Mongolia, China) from June to September in 2013 and 2014, respectively (Fig. 1, 42°21'N, 101°15'E, altitude 920.5 m a.s.l.). In the forest reserve, the average tree age is 32 years, with good growth status. The trees have an average height of 10.2 m, an average diameter at breast height of 24.67 cm, and an average crown breadth of 442 cm × 450 cm. The soil is sandy loam of approximately 2 m in depth and has a volumetric water content of 0.35 m³ m⁻³. The bulk density of the soil is 1.53 g cm⁻³.

2.2. Measurements and data processing

We selected three individual *P. euphratica* trees in 2013 and 2014, respectively, and measured the leaf gas exchange in three fully expanded leaves of each tree hourly from the east and west, on four or five sunny days every month. An LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA) was used for the measurements. We measured all the available parameters; namely, net photosynthesis (P_n , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), stomatal conductance (g_s , $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$), sub-stomatal and ambient CO_2 concentrations (C_i and C_a , $\mu\text{mol CO}_2 \text{ mol}^{-1}$), photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{ s}^{-1}$), air temperature (T_a , $^{\circ}\text{C}$), relative humidity (h_s , %), and vapor pressure deficit (VPD, kPa). The measurements were conducted from 8:00 to 20:00, where the observation session was adjusted by advancing or postponing it by 1 h according to the specific circumstances of sunrise and sunset. We also used a sky lift to reach the canopy when measuring the leaves. The sample sizes in 2013 and 2014 were 103 averages based on 927 measurements and 183 averages based on 1647 measurements, respectively.

2.3. Formulae

Stomatal limitation to photosynthesis can be quantified by the parameter L_s , which can be calculated according to the following formula described by Farquhar and Sharkey (1982):

Due to technical limitations, Equation 1 has been placed in the Supplementary Files section.

where G is the CO_2 compensation point of assimilation in the presence of dark respiration. G can always be neglected, whereupon the formula is then expressed as follows:

Due to technical limitations, Equation 2 has been placed in the Supplementary Files section.

Another way to quantify the relative importance of the stomata in controlling the processes of photosynthesis is the resistance-based method described by Jones (Jones 1998), who proposed the relative stomatal limitation to photosynthesis (RL_s). The value can be calculated by the following formula:

Due to technical limitations, Equation 3 has been placed in the Supplementary Files section.

where r_s is the stomatal resistance, r_a is the boundary layer resistance, and r^* is the slope of the tangent to the P_n/C_i curve at the operating point.

r_s and r_a can be calculated by the following formulae:

Due to technical limitations, Equation 4 has been placed in the Supplementary Files section.

where l_w is the leaf width, u_h is the wind speed at the top of the canopy, and h is the mean height of the canopy.

The non-stomatal limitation to photosynthesis can be indicated by C_i/g_s .

Discussion

3.1 Diurnal changes in the environmental factors

Detailed information on the key environmental variables is essential to assess diurnal changes in the stomatal and non-stomatal limitations to photosynthesis. We chose one sunny day per month to analyze the diurnal change patterns of the environmental factors (PAR, T_a , VPD, and h_s) during the main growing seasons of *P. euphratica* in 2013 and 2014, respectively (Fig. 2). Generally, the distribution patterns of PAR, T_a , and VPD all presented single-peak curves. For the most part, PAR, T_a , and VPD increased in the morning, peaked between 13:00 and 15:00, and then decreased. During the study period, the daily average PAR was 941.74 W m^{-2} , varying from 11.62 to 1689.33 W m^{-2} . The daily average T_a was 31.60°C , which was very close to those of the previous years (data not shown). The h_s value decreased gradually after 10:00, mainly due to the increase in T_a , which in turn caused the enhancement of evaporation and water loss to the air. The daily average h_s was 46.63 %, varying from 17.54 % to 75.21 %. It was obvious that the values for all four parameters did not show significant differences between 2013 and 2014.

3.2 Diurnal changes in the physiological factors

We selected the same days to analyze the diurnal change patterns of the physiological factors (P_n , g_s , and C_i) during the main growing seasons of *P. euphratica* in 2013 and 2014, respectively (Fig. 3). We can see from Figure 3 that the distribution patterns of P_n and g_s were similar. P_n increased in the morning, peaked at around 14:00, and then decreased. In August and September, the values of P_n were much greater than those in June and July. The g_s value increased rapidly in the morning, peaked between 10:00 and 12:00, and then decreased gradually in the afternoon. The peak values of g_s in the different months

were fairly close to one another ($0.40\text{--}0.46\text{ mol H}_2\text{O m}^{-2}\text{ s}^{-1}$). We can also see that there were fluctuations in P_n and g_s between 11:00 and 14:00 from July to September, which indicated the obvious phenomenon of midday depression of photosynthesis (MDP) (e.g., July and September 2013 and August 2014, respectively). C_i presented a contrasting pattern of diurnal changes to those of P_n and g_s (Fig. 3), where the **minimums** appeared between 14:00 and 16:00. The ranges of g_s and C_i values in the different months were similar, where g_s ranged from 0.02 to $0.47\text{ mol H}_2\text{O m}^{-2}\text{ s}^{-1}$ and C_i ranged from 126.78 to $401.21\text{ }\mu\text{mol CO}_2\text{ mol}^{-1}$.

3.3 Diurnal changes in L_s , RL_s , and C_i/g_s

The diurnal changes in L_s , RL_s , and C_i/g_s during the main growing seasons of *P. euphratica* in 2013 and 2014 are shown in Figure 4. We can see that both L_s and RL_s increased in the morning and then decreased. The L_s values in the afternoon were significantly greater than those in the morning. Generally, the RL_s values were greater than the L_s values. C_i/g_s presented a contrasting pattern of diurnal changes to those of L_s and RL_s . The C_i/g_s values were generally low in the morning and increased sharply after 17:00. The highest values of these parameters in 2013 and 2014 were 0.51 and 0.70 for L_s , 0.44 and 0.58 for RL_s , and 7.30 and 4.83 for C_i/g_s , respectively.

Conclusions

The Ejn oasis is one of the most arid regions in the world, and less precipitation can be expected to be available for plants there. Drought can be considered as one of the main environmental factors limiting photosynthesis and plant productivity. Nevertheless, whether water deficit affects plant photosynthesis via stomatal or non-stomatal limitation is still unclear and under debate. In order to clarify this question, we analyzed stomatal and non-stomatal limitations to photosynthesis under natural conditions in an extremely arid region of northwestern China through successive measurements of leaf gas exchange in *P. euphratica* during its main growing seasons in 2013 and 2014, respectively.

The diurnal changes in C_i presented “V-shaped” curves (greater C_i values in the morning and evening, and lower values at noon), which was basically consistent with the conclusions made in studies of Wheat (Jiang et al. 2001) and *Haloxylon ammodendron* (Yang et al. 2015) in arid regions. The similarity in the distribution patterns of P_n and g_s indicated that g_s was to some extent the main factor influencing P_n under extremely arid conditions.

During the study periods, especially from July to September, the MDP phenomenon was evident. This was mainly owing to the high transpiration rates caused by the high VPD values, which led to an intense water deficit in the leaves. On the one hand, g_s decreased and limited the entry of C_a ; on the other hand, the water deficit caused a decrease in mesophyll conductance (g_m), which decreased the CO_2 concentration in the chloroplast to a very low level, resulting in the decrease in P_n . For *P. euphratica*

growing in extremely arid regions from July to September, where the T_a at around noon is the highest and the transpiration rate is the fastest, MDP can protect the tree from losing too much water.

Although the L_s increased gradually in the morning and then decreased, it still remained at high levels and was the main reason for the decrease in P_n in the afternoon. During the MDP periods, L_s peaked, and C_i was at a minimum, showing the apparent stomatal limitation to photosynthesis. This was consistent with the viewpoint of Farquhar and Sharkey (1982), who proposed the simultaneous increase in L_s and decrease in C_i as being the criterion for determining stomatal limitation. The low soil moisture content limited the water uptake by *P. euphratica*, and the intense solar radiation and high VPD values increased the water loss from the trees. Owing to a combination of transpiration and photosynthesis, the stomata closed to maintain water balance inside the plant and limit CO_2 entry into the leaves. Therefore, stomatal limitation to photosynthesis was predominant. Afterward, L_s decreased and C_i/g_s increased sharply, and the non-stomatal limitation to photosynthesis predominated. Several studies have shown g_m to be the main factor controlling non-stomatal limitation to photosynthesis, especially under stress (Grassi and Magnani 2005, Niinemets et al. 2005, Warren 2008). The structure of leaves determined the maximum value of g_m (Nobel 1977), and g_m also changed rapidly according to the environment conditions (Flexas et al. 2008). In extremely arid regions (like our study area, Ejin oasis), the soil moisture content is very low, and water stress is the main factor limiting g_m (Scartazza et al. 1998, Delfine et al. 2001, Monti et al. 2006). Because a greater VPD usually leads to lower g_m (Bongi and Loreto, 1989), we can infer that the g_m values in the morning were greater than those in the afternoon, as the VPD changed inversely (Fig. 2). It was much easier for C_i to enter into the chloroplast through the cytomembrane and cytoplasm and supply the CO_2 that would be consumed by photosynthesis, leading subsequently to low C_i/g_s values in the morning. In the afternoon, g_m decreased and hindered the diffusion of CO_2 into the chloroplast, and C_i/g_s subsequently increased.

We can also see from Figure 4 that the values of RL_s were greater than those of L_s , and this was mainly due to the nonlinearity of the P_n/C_i curve. Such occurrence often leads to a large overestimation of the importance of the stomata in controlling photosynthesis (Jones 1998). Consequently, L_s is more applicable than RL_s for representing stomatal limitation to photosynthesis. We have summarized the maximum L_s values of different species from previous research studies and this study in Table 1. We can see that the maximum L_s values from Yang et al. (2015) (0.64) and this study (0.70 in 2013 and 0.51 in 2014, respectively) were much greater than those from other studies, probably because both experiments were conducted under conditions of extremely intense water stress in northwestern China. At our study site specifically, *P. euphratica* grew in an environment with high temperatures (mean T_a values at 31.6 °C in 2013 and 29.9 °C in 2014, respectively) and scarce water resources (annual precipitation of 25.6 mm and 27.0 mm, and mean h_s values of 54.2 % and 43.0 % in 2013 and 2014, respectively) during the study periods, and therefore, the stomata closed to reduce transpiration, resulting in the predominance of stomatal limitation to photosynthesis.

As our data were obtained using the LI-6400 portable photosynthesis system, there was a lack of parameters (chloroplast structure, photosynthetic pigment content, Rubisco activity, RuBP regeneration capacity) measured to represent the non-stomatal limitation to photosynthesis. We will make up for this in our future work.

Declarations

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Authors' contributions

X.L. and Q.F. designed and G.G. performed the experiments; all authors analyzed the data; G.G. wrote the manuscript; Q.F. provided the guidance on the whole manuscript and all authors read and approved the final manuscript.

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Availability of data and materials

All data generated or analyzed during this study are included in this published article.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors have no conflict of interest to declare.

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Tables

Table 1 Maximum values of stomatal limitation to photosynthesis (L_s) under natural conditions for different species from previous research studies and this study

Species	Maximum L_s	Location	Literature resources
<i>Dacrydium cupressinum</i> Lamb.	0.29	New Zealand	Tissue et al. (2005)
<i>Meterosideros umbellate</i> Cav.	0.41		
<i>Weinmannia racemosa</i> L.f.	0.42		
<i>Quintinia acutifolia</i> Kirk.	0.41		
<i>Quercus robur</i> L.	0.17	Italy	Grassi and Magnani (2005)
<i>Fraxinus oxyphylla</i> Bieb.	0.21		
Spring wheat	0.64	China	Yang et al. (2015)
<i>Populus euphratica</i> Oliv.	0.70 (2013)	China	This study
	0.51 (2014)		

Figures

Figure 1

Location map of the study area. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 2

Diurnal change patterns of photosynthetically active radiation (PAR), vapor pressure deficit (VPD), air temperature (T_a) and relative humidity (h_s) during the main growing seasons of *Populus euphratica* in 2013 and 2014, respectively.

Figure 3

Diurnal change patterns of the net photosynthetic rate (P_n), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) during the main growing seasons of *Populus euphratica* in 2013 and 2014, respectively.

Figure 4

Diurnal change patterns of (relative) stomatal and non-stomatal limitations to photosynthesis of *Populus euphratica* leaves during the main growing seasons in 2013 and 2014, respectively. RLs, relative stomatal limitation to photosynthesis; Ls, stomatal limitation to photosynthesis; Ci/gs, non-stomatal limitation to photosynthesis.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Equation4.png](#)
- [Equation3.png](#)
- [Equation1.png](#)
- [Equation2.png](#)