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Quantification of leaf gas exchange characteristics of dominant C_3/C_4 plants at the Kalahari transect

M. Yu [a,b,*], Q. Gao [c], H.E. Epstein [b], P. Dowty [d]

[a] *Institute for Tropical Ecosystem Studies, University of Puerto Rico, Rio Piedras, San Juan, PR 00931, USA*
[b] *Department of Environmental Sciences, University of Virginia, Charlottesville VA 22904, USA*
[c] *State Key Lab of Earth Surface Processes and Resources Ecology, Beijing Normal University, Beijing 100875, PR China*
[d] *Washington State Department of Natural Resources, Olympia, WA 98504, USA*

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Abstract

Leaf gas exchange characteristics play a key role in carbon sequestration and water balance from site to regional scales, yet show differences among plant species with alternative adaptations to the environment. To investigate the influences of climate regimes on leaf gas exchange characteristics and the underlying mechanisms and adaptations, we analyzed the photosynthesis and stomatal conductance characteristics of dominant C_3 and C_4 species at wet and dry ends of Kalahari transect in southern Africa by fitting empirical and mechanistic models to field measurements of leaf gas exchange rates. Adaptations to different climatic moisture regimes greatly influenced the leaf gas exchange characteristics of the species with different photosynthetic pathways along the Kalahari transect via a variety of mechanisms. We found that the leaf of C_3 species with higher leaf nitrogen concentration at the dry site had higher photosynthesis rates than those at the wet sites. Our analysis also indicated that *Stipagrostis uniplumis* had high sensitivities to both radiation and vapor pressure deficit (*VPD*), indicating that the species may have soft guard cell structure to conserve water. We also found that the relatively high soil-to-leaf conductance allowing efficient water supply from soil to plant leaves might contribute to the small sensitivities of stomatal conductance to *VPD* for the grasses of *S. ciliata* and *S. obtusa*. The results of leaf gas exchange characteristics and underlying mechanisms provide basic but crucial parameters for simulation studies of carbon sequestration and water balance at site to regional scales in the Kalahari region.

Keywords: Arid and semiarid environments; CO_2 assimilation; Ecophysiological models; Kalahari; Leaf gas exchange; Stomatal conductance

1. Introduction

Water has profound influences in regulating leaf gas exchange processes in arid and semiarid ecosystems and thus largely affects net ecosystem production and carbon sequestration. Plants with different photosynthetic pathways show different strategies of adaptation to environmental conditions, such as drought, in order to optimize use of resources and minimize damage from environmental stress. Evidence from *in situ* leaf gas exchange measurements confirmed the differences in carbon assimilation and stomatal conductance characteristics among plants under changing moisture regimes (Comstock and Ehleringer, 1993; Diasfilho and Dawson, 1995; Picon et al., 1996; Wilson et al., 2000; Raftoyannis and Radoglou, 2002; Midgley et al., 2004). A number of empirical (Ball et al., 1987; Dewar, 1995; Leuning, 1995) and mechanistic models (Farquhar et al., 1980; Thornley and Johnson, 1990; Collatz et al., 1992; Gao et al., 2002) have also been developed to further investigate the responses and mechanisms, and to predict photosynthesis and stomatal conductance in a variable environment.

The mechanistic biochemical photosynthesis models developed by Berry and Farquhar (1978) and Farquhar, Von Caemmerer and Berry (1980), hereafter referred to as BF models, have been extensively employed in comparisons of carbon assimilation characteristics among species under

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* Corresponding author. Institute for Tropical Ecosystem Studies, University of Puerto Rico, Rio Piedras, P.O. Box 21910, San Juan, PR 00931-1910, USA.
E-mail address: meiyu@ites.upr.edu (M. Yu).

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changing environmental variables, such as ambient CO_2 concentration (Medlyn et al., 1999) and temperature (Leuning, 2002), as well as at different growth stages (Medlyn et al., 2002; Kosugi et al., 2003). By taking the minimum of the electron-limited and Rubisco-limited carbon assimilation rates, the BF models describe the mechanism of competing biochemical processes and electron transport in photosynthesis. The leaf photosynthesis models by Thornley and Johnson (1990), hereafter referred to as TJ models, simplify the leaf gas exchange processes and focus on the apparent responses of carboxylation and oxygenation to light, and CO_2 and O_2 concentrations. Gao et al. (2004) applied both kinds of photosynthesis models in a study of leaf gas exchange characteristics for 11 C_3/C_4 species in northern China, and concluded that neither the BF models nor the TJ models were absolutely superior.

Stomatal control is vital for regulating leaf gas exchange, especially for plants in semiarid and arid areas. Hence stomatal conductance models are often coupled with photosynthesis models to investigate leaf gas exchanges and their responses to environmental factors (Katul et al., 2003; Tuzet et al., 2003; Gao et al., 2004). The empirical stomatal conductance model by Ball et al. (1987) was widely used and modified by Leuning (1990) to include a CO_2 compensation point for improving model behavior under low ambient CO_2 concentrations. The Leuning (1995) model further replaced relative humidity with vapor pressure deficit (*VPD*) to better conform to the observed relationship between stomatal conductance and *VPD*, as well as that between the ratio of intracellular to ambient CO_2 concentration and *VPD*. While stomatal conductance and net photosynthesis rates are explicitly related in the above models, the empirical model by Jarvis (1976) and mechanistic model by Gao et al. (2002) simulate stomatal conductance solely from external environmental variables, such as radiation, *VPD*, and soil water potential.

Photosynthesis and stomatal conductance models are also the key modules in the simulation studies of carbon sequestration and water balance at the site to regional scales (Running and Coughlan, 1988; Foley et al., 1996; Friend et al., 1997; Gao et al., 2007). These studies showed that the leaf-level carbon assimilation and water exchange estimated using the above photosynthesis and stomatal conductance models can be successfully scaled to regional ecosystem level. Therefore, the leaf-level characteristics in gas exchanges estimated by the photosynthesis and stomatal conductance models, such as the maximum carboxylation rate and the sensitivity to moisture change, will greatly affect ecosystem behaviors in carbon sequestration, water balance, as well as responses to global change at larger scales.

The Kalahari transect, with a strong moisture gradient and almost uniform soil substrate, provides an ideal platform to analyze responses of ecosystem functioning and structures (competition between trees and grasses in particular) to soil moisture in the context of global change (Scholes and Archer, 1997; Scholes et al., 2002; Shugart et al., 2004; Swap et al., 2004; Scanlon et al., 2005). However, leaf gas exchange studies are very limited in this area (Midgley et al., 2004), therefore insightful modeling analysis on different plant life forms and different moisture regimes, will enhance simulation studies of carbon sequestration, water balance, and ecosystem responses to global change at landscape and regional scales.

Our objectives were: 1) to analyze photosynthesis characteristics of dominant C_3 and C_4 species at the dry and wet ends of the Kalahari transect by inverting both BF and TJ models; 2) to analyze the stomatal conductance characteristics by inverting stomatal conductance models by Ball et al. (1987), Leuning (1995) and Gao et al. (2002); and 3) to interpret leaf gas exchange characteristics and underlying mechanisms based on the above analyses. The analysis provided basic but crucial parameters for ecosystem simulation at coarser scales, and may contribute to studies of leaf traits in this region (Wright et al., 2005).

2. Methods and materials

2.1. Photosynthesis models

We inverted two sets of photosynthesis models from the field gas exchange data using nonlinear least square techniques. The two sets of models are the well known biochemical models or BF models, and the modified Thornley and Johnson's leaf models or TJ models. Each set contains two models, one for C_3 and the other for C_4 species. Detailed model descriptions can be found in Gao et al. (2004). For both sets of models, data variables are incident photon flux density, Q, measured stomatal conductance, g_s, leaf temperature, T_l, and partial CO_2 pressure on leaf surface, C_a. The response variable is the measured net photosynthesis rate A, in other words, A is regard as a function of the above input variables.

For the BF model for C_3 species, the parameters to be obtained from the model inversion are the maximum carboxylation rate V_{cmax25}, the maximum electron transport rate J_{max25}, the dark respiration rate R_{d25}, and a curvature parameter 2 (Subscript '25' denotes the corresponding value at 25 °C, detailed information in the online Appendix). For the BF model for C_4 species, the parameters to be obtained are the maximum carboxylation rate in the bundle sheath V_{4cmax25}, the intrinsic quantum efficiency for RuBP regeneration in the bundle sheath α_{r25} and that for PEP carboxylation in the mesophyll cells α_{p25}, the first-order reaction constant for carboxylation in the mesophyll cells g_{p25}, and R_{d25}. The parameters to be obtained for the TJ models are the apparent photon efficiency R_{25}, the carboxylation conductance g_{x25} for C_3 species model or the transporting conductance of CO_2 from the mesophyll to the bundle sheath cells g_{t25} for C_4 species model, the photorespiration conductance g_{r25}, and R_{d25}.

2.2. Stomatal conductance models

We used two empirical models of stomatal conductance, the Ball's model (Ball et al., 1987) and the Leuning's model (Leuning, 1990, 1995), and a mechanistic model of stomatal conductance by Gao et al. (2002). The three models have g_s (mol m^{-2} s^{-1}) as the common response variable but the independent variables are different.