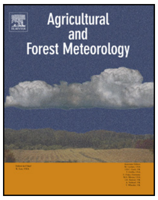
Agricultural and Forest Meteorology xxx (2013) xxx–xxx

Contents lists available at SciVerse ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet



How should we model plant responses to drought? An analysis of stomatal and non-stomatal responses to water stress

Shuangxi Zhou[a,*], Remko A. Duursma[b], Belinda E. Medlyn[a], Jeff W.G. Kelly[a], I. Colin Prentice[a,c]

[a] Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia
[b] Hawkesbury Institute for the Environment, University of Western Sydney, Locked Bag 1797, Penrith, NSW 2751, Australia
[c] Grantham Institute and Division of Ecology and Evolution, Imperial College, Silwood Park Campus, Ascot SL5 7PY, UK

ARTICLE INFO

Article history:
Received 15 November 2012
Received in revised form 19 February 2013
Accepted 16 May 2013

Keywords:
Photosynthetic limitation
Stomatal conductance
V_{cmax}
Mesophyll conductance
Drought
Model

ABSTRACT

Models disagree on how to represent effects of drought stress on plant gas exchange. Some models assume drought stress affects the marginal water use efficiency of plants (marginal WUE = $\partial A/\partial E$; i.e. the change in photosynthesis per unit of change in transpiration) whereas others assume drought stress acts directly on photosynthetic capacity. We investigated drought stress in an analysis of results from 22 experimental data sets where photosynthesis, stomatal conductance and predawn leaf water potential were measured at increasing levels of water stress.

Our analysis was framed by a recently developed stomatal model that reconciles the empirical and optimal approaches to predicting stomatal conductance. The model has single parameter g_1, a decreasing function of marginal WUE. Species differed greatly in their estimated g_1 values under moist conditions, and in the rate at which g_1 declined with water stress. In some species, particularly the sclerophyll trees, g_1 remained nearly constant or even increased.

Photosynthesis was found almost universally to decrease more than could be explained by the reduction in g_1, implying a decline in apparent carboxylation capacity (V_{cmax}). Species differed in the predawn water potential at which apparent V_{cmax} declined most steeply, and in the steepness of this decline. Principal components analysis revealed a gradient in water relation strategies from trees to herbs. Herbs had higher apparent V_{cmax} under moist conditions but trees tended to maintain more open stomata and higher apparent V_{cmax} under dry conditions. There was also a gradient from malacophylls to sclerophylls, with sclerophylls having lower g_1 values under well-watered conditions and a lower sensitivity of apparent V_{cmax} to drought.

Despite the limited amount of data available for this analysis, it is possible to draw some firm conclusions for modeling: (1) stomatal and non-stomatal limitations to photosynthesis must both be considered for the short-term response to drought and (2) plants adapted to arid climate respond very differently from others.

1. Introduction

Soil water deficit or “ecological drought” is considered to be the main environmental factor limiting global plant photosynthesis (Nemani et al., 2003). Modeling the effect of drought on photosynthesis (A) and stomatal conductance (g_s) is crucial to understand and project the consequences of global environmental change for plants and ecosystems. However, there is disagreement among models in how to represent drought effects. Many models simply reduce the slope of the g_s/A relationship (e.g. Battaglia et al., 2004; Kirschbaum, 1999; Friend and Kiang, 2005; Medlyn, 2004; Sala and Tenhunen, 1996; Wang and Leuning, 1998), whereas others assume drought affects A directly by reducing V_{cmax} (maximum rate of carboxylation) and/or J_{max} (maximum rate of electron transport) in the Farquhar et al. (1980) C_3 photosynthesis model (e.g. Calvet et al., 2004; Keenan et al., 2009; Krinner et al., 2005; Moorcroft et al., 2001; Sellers et al., 1996). Only a few models include both effects (e.g. the Sheffield Dynamic Global Vegetation Model, SDGVM) (Woodward and Lomas, 2004). Recent studies have suggested that both effects ought to be included (Egea et al., 2011), but it is not known which approach best captures the drought response, nor is it known how drought responses vary among species and plant functional types (PFTs). The goal of this paper is to investigate drought responses in a range of species. Datasets of photosynthesis, stomatal conductance and pre-dawn leaf water

---

* Corresponding author.
E-mail addresses: shuangxi.zhou@students.mq.edu.au, shuangxi.zhou2014@gmail.com (S. Zhou).

0168-1923/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.agrformet.2013.05.009

Please cite this article in press as: Zhou, S., et al., How should we model plant responses to drought? An analysis of stomatal and non-stomatal responses to water stress. Agric. Forest Meteorol. (2013), http://dx.doi.org/10.1016/j.agrformet.2013.05.009

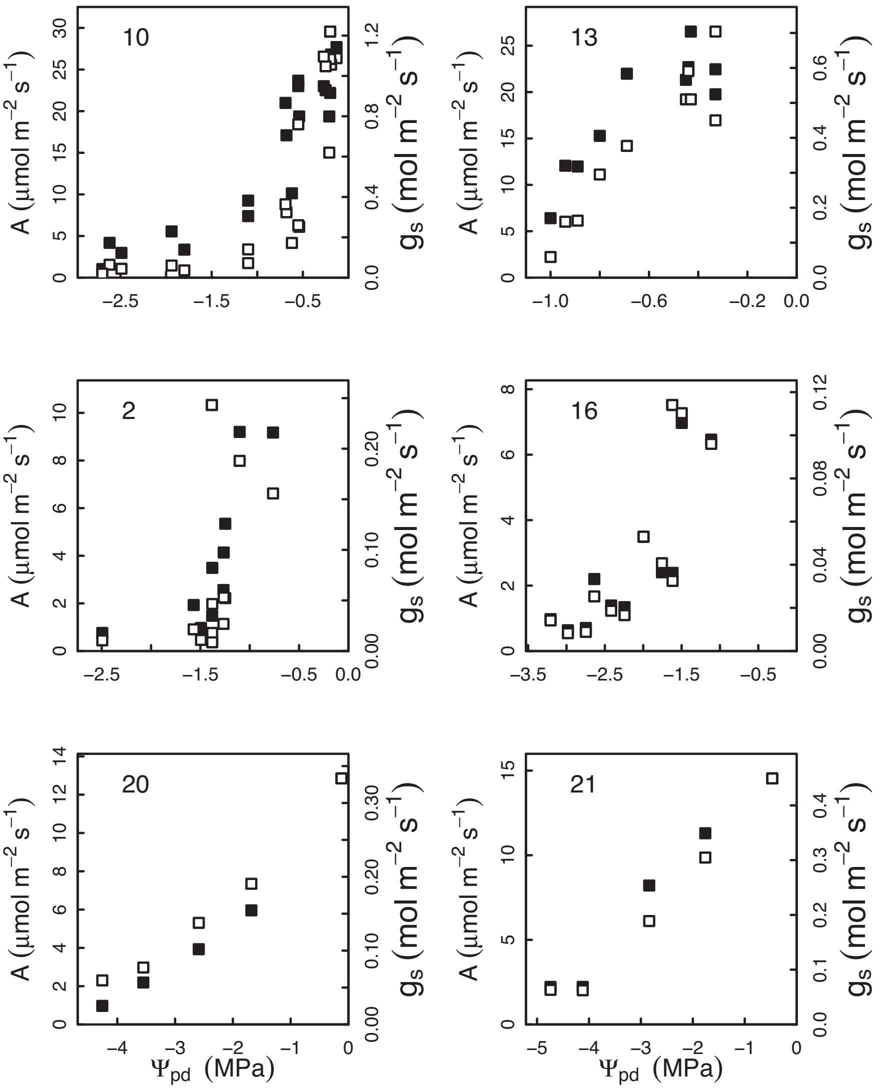


Fig. 1. A (filled squares) and g_s (open squares) responses to Ψ_{pd}, from two data sets representative for each of three PFTs. Herbs: (10) *Helianthus annuus* and (13) *Mediterranean Herbs*; Malacophyll angiosperm tree: (2) *Broussonetia papyrifera* and (16) *Platycarya longipes*; Sclerophyll angiosperm tree: (20) *Quercus ilex* and (21) *Quercus suber*.

potential during drying cycles were obtained from the literature (Fig. 1.) and were analyzed in the framework of a model of optimal stomatal conductance.

The theory of optimal stomatal behavior has been influential in explaining how carbon gain and water loss are balanced. Optimality theory hypothesizes that plants regulate stomatal opening and closing in such a way as to maximize ($A - \lambda E$) where A is photosynthesis, E is transpiration, and λ is the marginal carbon cost of water to the plant (Cowan, 1977; Cowan and Farquhar, 1977). When water availability decreases, it is hypothesized that λ increases, due to the risk of damage from hydraulic failure if plants maintain high transpiration rate, and/or the increased cost of building structures that are more hydraulically efficient (Berninger and Hari, 1993). Theoretical analysis by Mäkelä et al. (1996) indicated that $1/\lambda$ should be expected to decline exponentially with decreasing soil moisture availability, and the rate of decline with soil moisture should increase with the probability of rain.

We use the term stomatal limitation to refer to this idea that the optimal stomatal conductance declines in response to drought causing a decline in photosynthesis. There can also be non-stomatal limitation of photosynthesis, which involves a reduction in apparent V_{cmax}. If A declines with drought more steeply than can be explained by the observed stomatal limitation, this indicates the presence of non-stomatal limitation. Thus we interpret stomatal limitation as involving a change in the leaf-internal concentration of CO$_2$ (C_i) and non-stomatal limitation as a change in the A–C_i curve (Fig. 2). Note that our approach differs from one traditional way of analysing the drought effect on photosynthesis in terms of stomatal and non-stomatal limitations, using the equations from Jones (1985) (e.g. Grassi and Magnani, 2005; Keenan et al., 2009; Kubiske and Abrams, 1993; Ni and Pallardy, 1992; Wilson et al., 2000). Our method differs from that of Jones (1985) because the evidence for stomatal limitation is considered to be reduced C_i and not just reduced g_s, which could also arise a response to biochemical limitation. The difference is important because, in the optimal stomatal model and similar empirical models (e.g. Ball et al., 1987; Leuning, 1995), any reduction in apparent V_{cmax} will drive a reduction in stomatal conductance. Our approach partitions drought effects on stomatal conductance into changes that are an optimal response to a reduction in V_{cmax}, and reductions that are driven by an increase in the marginal cost of water. This way of thinking about stomatal conductance has the advantage of being able to be translated directly into modeling terms.

There has been controversy – perhaps fueled by this ambiguity over definitions – over the extent to which photosynthesis

Please cite this article in press as: Zhou, S., et al., How should we model plant responses to drought? An analysis of stomatal and non-stomatal responses to water stress. Agric. Forest Meteorol. (2013), http://dx.doi.org/10.1016/j.agrformet.2013.05.009