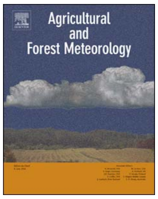
Agricultural and Forest Meteorology 247 (2017) 454–466

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

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



Stomatal and non-stomatal limitations of photosynthesis for four tree species under drought: A comparison of model formulations

J.E. Drake[a,b,*], S.A. Power[a], R.A. Duursma[a], B.E. Medlyn[a], M.J. Aspinwall[a], B. Choat[a], D. Creek[a], D. Eamus[c], C. Maier[a], S. Pfautsch[a], R.A. Smith[a], M.G. Tjoelker[a], D.T. Tissue[a]

[a] *Hawkesbury Institute for the Environment, Western Sydney University, Locked Bag 1797, Penrith, NSW 2751, Australia*
[b] *College of Environmental Science and Forestry, State University of New York, Syracuse, NY 13210, USA*
[c] *School of Life Sciences, University of Technology Sydney, PO Box 123, Broadway, NSW 2007, Australia*

ARTICLE INFO

Keywords:
Photosynthesis
Drought
Model
Eucalyptus sideroxylon
Eucalyptus tereticornis
Casuarina cunninghamiana
Pinus radiata

ABSTRACT

Drought strongly influences terrestrial C cycling via its effects on plant H_2O and CO_2 exchange. However, the treatment of photosynthetic physiology under drought by many ecosystem and earth system models remains poorly constrained by data. We measured the drought response of four tree species and evaluated alternative model formulations for drought effects on photosynthesis (*A*). We implemented a series of soil drying and re-wetting events (i.e. multiple droughts) with four contrasting tree species in large pots (75 L) placed in the field under rainout shelters. We measured leaf-level gas exchange, predawn and midday leaf water potential (Ψ_{pd} and Ψ_{md}), and leaf isotopic composition (δ^{13}C) and calculated discrimination relative to the atmosphere (Δ). We then evaluated eight modeling frameworks that simulate the effects of drought in different ways. With moderate reductions in volumetric soil water content (θ), all species reduced stomatal conductance (g_s), leading to an equivalent increase in water use efficiency across species inferred from both leaf gas exchange and Δ, despite a small reduction in photosynthetic capacity. With severe reductions in θ, all species strongly reduced g_s along with a coincident reduction in photosynthetic capacity, illustrating the joint importance of stomatal and non-stomatal limitations of photosynthesis under strong drought conditions. Simple empirical models as well as complex mechanistic model formulations were equally successful at capturing the measured variation in *A* and g_s, as long as the predictor variables were available from direct measurements (θ, Ψ_{pd}, and Ψ_{md}). However, models based on leaf water potential face an additional challenge, as we found that Ψ_{pd} was substantially different from Ψ_{soil} predicted by standard approaches based on θ. Modeling frameworks that combine gas exchange and hydraulic traits have the advantage of mechanistic realism, but sacrificed parsimony without an improvement in predictive power in this comparison. Model choice depends on the desired balance between simple empiricism and mechanistic realism. We suggest that empirical models implementing stomatal and non-stomatal limitations based on θ are highly predictive simple models. Mechanistic models that incorporate hydraulic traits have excellent potential, but several challenges currently limit their widespread implementation.

1. Introduction

Water availability is among the most important environmental factors limiting primary production across most of the globe (Nemani et al., 2003) and recent droughts have been linked to mortality and growth reductions in many ecosystems (Allen et al., 2010, 2015; Anderegg et al., 2013; Peng et al., 2011; Phillips et al., 2009). Climate change is predicted to increase the frequency and severity of droughts across many regions of the globe (Burke et al., 2006; Sillmann et al., 2013). Thus, there is an increasing need to robustly model and predict the impacts of drought on carbon and water fluxes. However, several recent model evaluations have demonstrated that our ability to model drought effects is currently limited (De Kauwe et al., 2015; Egea et al., 2011; Galbraith et al., 2010; Powell et al., 2013; Smith et al., 2014; Ukkola et al., 2016).

A key problem is that the treatment of drought effects on photosynthetic physiology in many ecosystem and earth system models is poorly constrained with data. Medlyn et al. (2016) recently reviewed the drought response of photosynthesis as implemented in seven commonly-used ecosystem models, concluding that there was little empirical basis for the parameterisation of drought sensitivity. Models either used parameter values with no empirical justification (Landsberg

---

* Corresponding author at: Hawkesbury Institute for the Environment, Western Sydney University, Locked Bag 1797, Penrith, NSW, 2751, Australia.
E-mail address: jedrake@esf.edu (J.E. Drake).

http://dx.doi.org/10.1016/j.agrformet.2017.08.026
Received 1 December 2016; Received in revised form 16 August 2017; Accepted 19 August 2017

and Waring, 1997; Oleson et al., 2010; Sitch et al., 2003), or relied on early work with sunflower or corn (Denmead and Shaw, 1962; Gollan et al., 1986, 1992). These models were not directly informed or constrained by data regarding tree responses to drought, which is problematic given the dominant influence of woody species on the terrestrial C cycle (Bonan, 2008; Pan et al., 2011) and the understanding that species differ in drought sensitivity (Condit et al., 1995; McDowell et al., 2008; Bartlett et al., 2016; Klein, 2014; Zhou et al., 2014; De Kauwe et al., 2015). Thus, there is a real need to parameterise and evaluate alternative drought models against empirical datasets for woody species. We recognise that tree and forest responses to drought are complex and are likely not predictable from the drought effect on photosynthesis alone, as growth often ceases earlier than photosynthesis during drought and C starvation is often not predictive of mortality (McDowell, 2011; Hartmann et al., 2013, 2015). However, the photosynthetic impacts of drought are still an important component of tree and forest responses that need to be modelled appropriately (Medlyn et al., 2016; Rogers et al., 2016).

Ecosystem and land-surface models often implement a drought-induced reduction in photosynthetic physiology via an empirical scalar (β) ranging from 0 to 1 that depends on a metric of water availability (Smith et al., 2014). In many cases, this β value is multiplied by stomatal conductance (g_s) or a variable describing the response of g_s to environmental drivers (e.g., Ball et al., 1987; Medlyn et al., 2011) to simulate stomatal closure under drought. Given that drought-related changes to mesophyll conductance and photosynthetic biochemistry can also induce non-stomatal limitations to photosynthesis (Farquhar and Sharkey, 1982; Keenan et al., 2010; Zhou et al., 2013, 2014), other models multiply this β value by the maximum velocity of Rubisco carboxylation (V_{cmax}) to reduce photosynthetic capacity under drought (reviewed by Smith et al., 2014).

These β values can be calculated based on a variety of different metrics of water availability. Common predictors include soil volumetric water content (θ), soil water potential (Ψ_{soil}), and predawn leaf water potential (Ψ_{pd}; e.g., De Kauwe et al., 2015; Egea et al., 2011; Keenan et al., 2010; Smith et al., 2014). An alternative approach is to use leaf water potential itself (Ψ_l) using an iterative approach incorporating plant hydraulics to predict Ψ_l from plant stomatal and hydraulic conductance (Tuzet et al., 2003). Given the central role of Ψ_l in regulating plant function, many authors argue that models should move to formulations based on Ψ_l (e.g. Sperry et al., 2016a; Rogers et al., 2016), and new theories of stomatal regulation focus on hydraulic costs, expressed as a function of Ψ_l (Wolf et al., 2016; Sperry et al., 2016b). However, few studies have constrained these disparate model formulations with data or examined the consequences of these model formulations for the prediction of photosynthesis during drought. There is a need to critically evaluate these alternative formulations against data.

Here, we implement a drought experiment that controlled a single driving variable – soil volumetric water content (θ) – in an attempt to isolate the photosynthetic response to θ without the emergent complexity and feedbacks that characterize drought in intact ecosystems. There is a long history of drought research using a variety of methodologies, including observational gradients in space and time (Babst et al., 2013; Phillips et al., 2009; Sala and Tenhunen, 1996), rainfall manipulation of ecosystems (Volder et al., 2013; West et al., 2012; Limousin et al., 2013; Rowland et al., 2015) or individual trees (Duursma et al., 2011), and studies with potted trees in controlled environments (Zhao et al., 2013; Zhou et al., 2013; Mitchell et al., 2013; Obrien et al., 2014). Photosynthetic and growth responses to drought are highly variable across these methodologies given variation in drought intensity and duration (e.g., Bonal et al., 2016), and because changes in plant functional traits or community composition can mediate the drought response (e.g., Debinski et al., 2010; Jung et al., 2014). This variation makes modeling drought responses challenging. Focusing on the photosynthetic responses to a carefully controlled drought allows us to more clearly evaluate model formulations against data.

We performed a drought experiment with four tree species of divergent form and drought tolerance planted in large (75 L) pots in the field under 8-m-tall rainout shelters. We monitored and carefully controlled the θ of each pot across two soil drying and rewetting events followed by a long and extreme soil drying event. We report measurements of photosynthesis, g_s, leaf water potential (Ψ_{pd} and Ψ_{md}), and leaf ^{13}C discrimination (Δ) as an integrative measure of long-term plant *WUE* (Farquhar et al., 1989). We use these data to parameterise and compare alternative model formulations for photosynthetic responses to drought.

2. Materials and methods

2.1. Site

Rainout shelters (ROS) were used to implement drought treatments at a site near Richmond, NSW, Australia (33.61° S, 150.74° E). The climate is warm-temperate, with a mean annual temperature of 17 °C and a mean annual precipitation (MAP) of 800 mm. Six large aluminum-framed ROS were constructed with dimensions of 12 m long × 8 m wide × 8 m tall with a roof pitch of 30°. The shelters had retractable roofs and side panels that were open during rain-free periods but automatically closed during rain events. An open space was maintained to a height of 1 m to allow air circulation. The site and ROS are described in detail by Dijkstra et al. (2016).

2.2. Study species

We examined leaf-scale responses to drought in four tree species originating from contrasting hydrological environments. *Casuarina cunninghamiana* (river oak) is an evergreen tree found in riparian areas in eastern and northern Australia, and used in agroforestry on sites with high water availability (Reid et al., 2013; Woolfrey and Ladd, 2001). Given its high water use and presence only in habitats with high water availability, we anticipated *C. cunninghamiana* would be a profligate water-user. *Eucalyptus tereticornis* (forest red gum) is one of the most widespread eucalypts, occurring along the coast of eastern Australia from southern Victoria to northern Queensland. It is restricted to locations with MAP $>$ 600 mm, but nonetheless experiences periodic drought. *E. sideroxylon* (red ironbark) occurs further inland in south-eastern Australia, in sites with MAP $>$ 400 mm. *E. sideroxylon* is typically slower-growing and was expected to be more drought-tolerant than either *E. tereticornis* or *C. cunninghamiana*. The fourth species, *Pinus radiata* (Monterey pine), is widely used in plantation forestry in southern Australia. This exotic gymnosperm was chosen to provide a contrast to the three Australian native angiosperms because its stomatal behaviour and high drought tolerance have been firmly established in previous experiments (Brodribb and McAdam, 2013; Mitchell et al., 2013), although a MAP of 650 mm is considered minimal for forest production in Australia (Ivković et al., 2010). Species are hereafter referenced by a four-letter contraction of their genus and species names; *Casuarina cunninghamiana* (Cacu), *Eucalyptus sideroxylon* (Eusi), *Eucalyptus tereticornis* (Eute), and *Pinus radiata* (Pira).

The four study species have divergent leaf morphology. Cacu has highly reduced leaves arranged in tiny whorls around green branchlets (cladodes); these branchlets are the primary photosynthetic organ (Torrey and Berg, 1988). Eusi and Eute have lanceolate and petiolate leaves typical of *Eucalyptus*; the leaves of Eusi tend to be narrower than Eute. Pira is a gymnosperm with needle-leaves arranged in clusters of three.