Agricultural and Forest Meteorology 213 (2015) 203–216

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

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

Empirical stomatal conductance models reveal that the isohydric behavior of an *Acacia caven* Mediterranean Savannah scales from leaf to ecosystem

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ARTICLE INFO

Article history:
Received 19 August 2014
Received in revised form 12 June 2015
Accepted 24 June 2015
Available online 25 July 2015

Keywords:
Canopy conductance
Mediterranean Savannah
Drought
Empirical models
Acacia caven

ABSTRACT

Canopy conductance (g_c) is the main controller of plant-atmospheric interaction and a key element in understanding how plants cope with drought. Empirical g_c models provide a good inference as to how environmental forcing affects surface water vapor and CO_2 gas exchange. However, when facing water scarcity, soil moisture or plant water availability becomes the primary controller. We studied g_c in an *Acacia caven* (Mol) savannah in Central Chile under Mediterranean-type climate conditions that present distinguishable wet and dry seasons. We calibrated an empirical g_c, in order to account for whole canopy gas exchange with g_c measurements from three different data sets: (1) an inversion of the Penman–Monteith equation in combination with a Shuttleworth and Wallace model (PMSW) for evapotranspiration from sparse canopies; (2) an inversion of the Penman–Monteith (PM) based on the big leaf approach and (3) a set of leaf stomatal conductance (g_s) ground based measurements taken throughout the season and scaled up to the canopy level. Then the semi-empirical Farquhar–Ball–Berry (FBB) g_c model was added to the comparison to evaluate if the inclusion of a mechanistic component for photosynthesis would improve the prediction of g_c. Models performance was assessed with ground based leaf gas exchange measurements during both wet and dry seasons. *Acacia*'s g_c showed a high synchronicity with soil moisture, exhibiting the typical isohydric behavior of this kind of vegetation. The addition of the Shuttleworth and Wallace modifier to the Penman–Monteith equation did not yield a better calibration for the multiplicative model when compared to the one calibrated with the PM g_c data set, however this does not directly certifies that PM itself is a better estimator of g_c in sparse canopies. Furthermore, scaling issues such as ecosystem heterogeneity and patchiness must be considered when applying these estimations to a watershed level for both eco and hydrological reasons. These empirical models demonstrated to be a good tool for predicting stomatal behavior for this kind of vegetation. Nevertheless, the effect of deep soil moisture on plant water status must be integrated in g_c estimations in order to improve model's performance.

1. Introduction

Mediterranean ecosystems represent only around 2 percent of the Earth's surface, yet they play a key role as biodiversity reserves being shelters of about 20 percent of the planet's flora, most of which is highly endemic (Cowling et al., 1998). These ecosystems are in compass with a climate characterized by a strong seasonality. Precipitation and temperature are dichotomous, with tempera-

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http://dx.doi.org/10.1016/j.agrformet.2015.06.018
0168-1923/

ture trends reaching maxima during the summer months and precipitation reaching maxima during winter months. Soil water availability plays a major limiting role in vegetation growth, and secular regional changes in temperatures and precipitation are believed to be already inducing changes in this type of ecosystems (Keenan et al., 2009). Climate models predict further increases in temperature in the future, with changes in rainfall patterns. Furthermore, despite the fact that net ecosystem exchange from arid and semi-arid ecosystem is regarded as low, these ecosystems represent between 42 and 56% of the world's land (Melillo et al., 1993), hence their importance in both global carbon and water balance. Central Chile represents one of the five regions of the world with a Mediterranean-type climate, where drought is a dominant feature. The region is characterized by a long dry season with the complete absence of rainfall from mid spring to mid fall. Vegetation consists mainly of sclerophyllous shrubs, where *Acacia caven* (Mol) is a dominant species. From Africa to Australia the *Acacia* genus has shown a wide range of adaptations to water scarcity (Cleverly et al., 2013; Eamus et al., 2013; Grouzis et al., 1998; Pohlman et al., 2005; Otieno et al., 2005;) allowing it to cope with severe droughts. Therefore *A. caven* can be considered as an archetype plant for understanding a plant canopy behavior when facing drought and to test model performance under scenarios of water scarcity.

Stomatal conductance (g_s) is the main path through which plants control both leaf transpiration and CO_2 intake (e.g.: Reichstein et al., 2002; Krishnan et al., 2006; Kljun et al., 2007; Keenan et al., 2009), and one of the main mechanisms through which plants cope with drought stress (Damour et al., 2010). Farquhar et al. (1980) represented leaf photosynthesis as a process dominated by light and internal CO_2 concentration (C_i), which in turn depends on g_s and net assimilation rate (A_n). Leaf stomatal conductance and photosynthesis can be scaled-up to canopy level by considering several assumptions attempting to represent complex heterogeneities ubiquitously found in plant canopies. Canopy conductance is the main lock of the soil–plant–atmosphere water continuum, driving both nutrient uptake and soil water depletion (Berry et al., 2010; Damour et al., 2010), thus it is considered a key and complex variable in most land-surface models (Medlyn et al., 2011).

Mechanistic and empirical model approaches have been used to represent g_c. Mechanistic models rely upon g_c response to internal physiological processes that drive stomatal behavior, whereas empirical models have simplified the representation of g_c by relating observed canopy responses to changes in environmental conditions based on a purely statistical parameterization without any specific physiological meaning. Multiplicative models based on an empirical approach establish a set of penalty functions modifying a maximal g_c while accounting for environmental covariates (Jarvis, 1976). On the other hand, semi-empirical models are based on g_s behavior but can be later scaled up to the canopy level, aiming to mix both mechanistic and empirical approaches. After Wong et al. (1979) showed that stomatal movement not only responds to plant water status but also on leaf A_n, Ball et al. (1987) aimed to couple g_s to A_n through Farquhar et al. (1980) mechanistic model for leaf carbon exchange and performing a statistical fitting between A_n and g_s, which resulted in the Farquhar–Ball–Berry (FBB) semi-empirical model (Dewar, 2002).

Empirical models have been largely used at the field level (e.g.: Stewart, 1988; Grace et al., 1995; Van Wijk et al., 2000; Harris et al., 2004). However, when facing drought conditions, it is necessary to introduce some modifications. Models based on photosynthesis depend on a linear relationship between g_s and A_n that could change depending on plant water status (Tenhunen et al., 1990). Empirical multiplicative models can add the effect of soil water availability or plant water status as another environmental factor regulating g_c. Similar water status restrictions can be applied in semi-empirical models, thus accounting for isohydric behavior (Tardieu and Simonneau, 1998). However, since empirical approaches have been developed under a constrained range of environmental variables, extreme conditions such as high vapor pressure deficit, low water availability or extreme temperatures, challenge the ability of these models to accurately estimate g_c (Gao et al., 2002).

We aim to use a combination of observational and modeling techniques in order to account for the effect of drought stress on gas exchange. Accordingly, we first evaluate different methodologies to obtain *Acacia*'s g_c linking latent heat (λE) to canopy's resistance to water loss. We assessed the inversion of the Penman–Monteith (PM) equation based on the big leaf approach, thus obtaining hourly g_c measurements. Furthermore, in order to consider the nature of a sparse canopy such as the Savannah in this study, a combination of PM with the Shuttleworth and Wallace (PMSW) was evaluated. Ecosystem λE was obtained from Eddy Covariance measurements for both the PM and PMSW approaches. Secondly, both g_c measurements were used to calibrate a multiplicative model integrating soil moisture as an environmental covariate, additionally, a third calibration was performed with ground-based measurements of g_s, scaled up to canopy level (g_c). Finally, a semi-empirical model based on the FBB approach was added to the comparison in order to evaluate how a mechanistic approach could improve g_c estimations. All models outputs were compared against ground-based measurements in order to evaluate their performance in the field. By comparing g_c models which use different approaches and have different calibrations, we aim to select the best model that allows us to (a) have a good estimate of water and CO_2 fluxes through g_c behavior and (b) help us understand plants' strategy for regulating water loss (i.e. iso or anisohydric behavior) influences the seasonality of Mediterranean ecosystem fluxes.

2. Materials and methods

2.1. Site and data description

The study site corresponds to a 24Ha shrubland Savannah in Central Chile (33°02′S, 70°44′W), located at 660 m above the sea level with an average slope of less than 5%. The climate can be regarded as Mediterranean, with a mean annual temperature of 15.6 °C and a total mean annual precipitation of 245 mm. The site is characterized by wet and dry seasons when the majority of rainfall is concentrated between May and September, and a long dry summer extending from October to April. This type of climate shows particularly high values of water vapor deficit during spring and summer, as relative humidity is usually below 50% and daily temperatures exceed 30 °C.

The Savannah is dominated by *A. caven* trees sparsely distributed throughout the field. The soil corresponds to a Mollisol with a bulk density of 1.4 g cm^{-3} and a clay–loam texture. During late winter and early spring a herbaceous layer mainly consisting of *Anoda* sp., *Erodium moschatum*, *Trifolium* sp., *Oxalis* sp., *Urtica hurens* and *Helenium aromanticum* is observed, however during the dry season the field is completely dominated by *A. caven*. *Acacia* trees on the study site show clear signs of re-sprouting given the fact that most parts of central Chile's shrublands were logged for charcoal production during the last two centuries. Nevertheless, the field was acquired seven years ago by a third party and has since been used for conservation purposes thus eradicating logging and human fire risks, although the sporadic presence of cattle (herbivory) was observed.

Canopy coverage fraction (f_c) is 0.25. Trees coverage was determined by satellite images obtained from Google Earth during the dry season and later analyzed through a self-made Matlab script (Mathworks, MA, USA). Because *Acacia* crowns in grey scale images