Agricultural and Forest Meteorology 250–251 (2018) 24–34

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

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

Diel ecosystem conductance response to vapor pressure deficit is suboptimal and independent of soil moisture

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ARTICLE INFO

Keywords:
Stomatal conductance
Ecosystem conductance
VPD
GPP
Soil moisture

ABSTRACT

Ecosystem conductance, which describes ecosystem regulation of water and carbon exchange and links plant functions with the environment, is a critical component in ecosystem and earth system models. However, the behaviors of ecosystem conductance at the ecosystem level and its responses to environmental conditions are still largely unclear. In this study, half-hourly data of 77 eddy-covariance sites from the FLUXNET2015 dataset were used to compare four ecosystem conductance models at the ecosystem level and determine the most consistent vapor pressure deficit (VPD) dependence across plant functional types for varying soil moisture stress levels at the subdaily time scale. We used leaf-level VPD (VPD_l), a better indicator of atmospheric dryness at the leaf level, for canopy-level analysis instead of measured atmospheric VPD. Detection of the best-fitted exponent of VPD_l indicates that ecosystem conductance responds to VPD between optimality-theory (i.e., $VPD^{-0.5}$ dependence) and Leuning's (i.e., VPD^{-1} dependence) models. Accounting for different soil moisture stress levels only affected minimum ecosystem conductance and did not affect the exponent and factor of VPD_l, indicating limited diurnal soil moisture-VPD_l interactions. These results indicate limited interaction between xylem and stomata at subdaily time scales and that soil moisture effects can be simplified as a regulation of minimum (soil plus canopy) conductance.

1. Introduction

Stomata, at the surface of plant's leaves, control water losses and CO_2 uptake during photosynthesis, so that they play an important role in soil-plant-atmosphere processes (Damour et al., 2010). Stomatal conductance, which describes the efficiency of water and CO_2 flux exchange between stomata and the atmosphere, is a critical parameter in ecosystem and earth system models, linking plant functions and climatic environment. The ability of correctly simulating stomatal conductance and its response to environmental fluctuations is key to successfully model global carbon and water cycles (Kala et al., 2016; Rogers et al., 2017; Schulze et al., 1994).

Plants respond to increasing atmospheric aridity, which is due to low atmospheric humidity (Lange et al., 1971) and high vapor pressure deficit (VPD) (Aphalo and Jarvis, 1991; Berg et al., 2016; Monteith, 1995), by closing their stomata to mitigate water losses through transpiration, thus reducing stomatal conductance. On the other hand, a decline in soil moisture results in more negative soil water potential, which triggers cavitation and embolism, and gives more resistance for water transport within the xylem (Blackman et al., 2009). A continuous decrease of soil moisture will eventually lead to loss of hydraulic conductance and cause plant mortality (Cochard and Delzon, 2013). Stomatal closure occurs during soil water stress to regulate transpiration and avoid increasing losses of hydraulic conductance (Brodribb and Holbrook, 2003; Martínez-Vilalta et al., 2014). Stomatal conductance is also affected by CO_2 concentration (Ball et al., 1987) and leaf temperature (Lloyd, 1991). Understanding how stomatal conductance and productivity is affected by changes in atmospheric dryness, and interacts with soil water deficit, is especially important to understand how the global carbon cycle responds to water stress and aridity (Keenan et al., 2014; Konings et al., 2017; Poulter et al., 2014).

Different stomatal conductance models have been proposed to express the stomatal dependence on environmental conditions. Jarvis (1976) first developed a stomatal conductance model with consideration of stomatal conductance responses to different stress factors, including light density, leaf temperature, VPD, CO_2 concentration and

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https://doi.org/10.1016/j.agrformet.2017.12.078
Received 10 June 2017; Received in revised form 21 November 2017; Accepted 3 December 2017

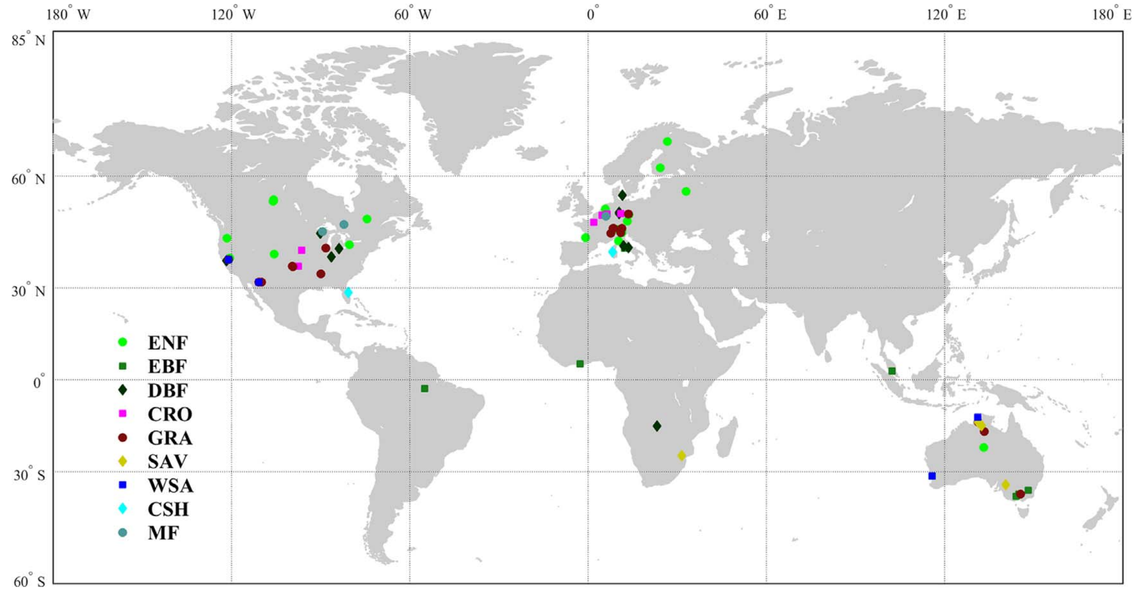

Fig. 1. Locations of the 77 flux sites from FLUXNET2015 dataset used in this study. Nine plant functional types were included. ENF is evergreen needleleaf forests, EBF is evergreen broadleaf forests, DBF is deciduous broadleaf forests, CRO is croplands, GRA is grasslands, SAV is savannas, WSA is woody savannas, CSH is closed shrublands and MF is mixed forests.

leaf water potential. Several follow-up studies found that stomatal conductance strongly responds to air humidity and especially to VPD at the leaf surface, and most stomatal conductance models now use leaf-surface VPD regulation on stomata (Granier and Loustau, 1994; Lindroth and Halldin, 1986; Lohammar et al., 1980; Oren et al., 1999). Based on a linear relationship between stomatal conductance and photosynthesis (Wong et al., 1979), Ball et al. (1987) proposed an empirical model accounting for the positive impact of both assimilation rate and relative humidity, and Leuning (1995) later replaced the relative humidity term by a negative influence of leaf-scale VPD (more precisely a VPD^{-1} dependence).

In parallel with empirical models, an optimal theory was developed explaining stomatal responses to the environment, as an optimal balance of maximizing CO_2 uptake and minimizing water losses, and this model was then applied in process-based models (Cowan and Farquhar, 1977; Hari et al., 1986; Katul et al., 2010; Lloyd and Farquhar, 1994; Schymanski et al., 2007). Starting from the optimal theory, Medlyn et al. (2011) showed that optimal stomatal conductance models are consistent with empirical models based on reasonable assumptions, and they also pointed out that stomatal conductance exhibits a -0.5 dependence on VPD (i.e. $\mathrm{VPD}^{-0.5}$) rather than the VPD^{-1} dependence in Leuning's model. There are models accounting for impacts of both leaf or guard cell water potential and soil water potential, which have been applied as well (Buckley et al., 2003; Gao et al., 2002; Oren et al., 1999). However, it is difficult to decouple regulations of both soil water stress and atmospheric aridity on stomatal behaviors on different time scales (Sulman et al., 2016). Mechanisms of stomatal conductance responses and adaptation to the surrounding environment are still not fully understood and strongly debated (Galmés et al., 2007; Miner et al., 2016).

Most stomatal conductance models focus on behaviors of stomata at the leaf scale, and under idealized conditions (e.g. well-watered), and have been tested on both leaf-scale and canopy-scale data (Hari et al., 1999; Kolari et al., 2007; Mercado et al., 2009). For global biosphere modeling, stomatal conductance models based on global datasets, which are mainly measured at the leaf-scale level, are integrated into earth system models (Lin et al., 2015). The problem of scaling up stomatal behavior from leaf to the ecosystem scale (Jarvis and McNaughton, 1986; Rambal et al., 2003) still exists in the applications of stomatal conductance models in land surface and earth system models. When studying the ecosystem-scale response to environmental changes, ecosystem-level measurements are used instead of leaf-level measurements, e.g. using latent heat flux and VPD measured at a reference height instead of leaf-scale transpiration and VPD respectively (Beer et al., 2009; Novick et al., 2016a; Zhou et al., 2014). A better representation of stomatal conductance can benefit global land surface and earth system models (Bonan et al., 2014; De Kauwe et al., 2015). Therefore, to improve biosphere modeling, analysis of terrestrial systems needs better predictions of ecosystem stomatal conductance (i.e. canopy conductance) accounting for real environmental conditions, with combined soil water stress and atmospheric aridity in particular.

Here, we investigated the relative contributions of VPD and soil water stress on stomatal conductance and their impact on the ecosystem conductance. We used subdaily (half-hourly) eddy-covariance flux data during growing seasons at 77 sites filtered from the FLUXNET2015 dataset (http://fluxnet.fluxdata.org). The main objectives of this study were to: 1) determine the most consistent VPD dependence model across plant functional types for varying soil moisture stress levels and 2) understand the diurnal interactions between atmospheric drying, stomatal conductance and xylem water transport. Under changing environmental conditions, addressing these goals can provide better understanding of ecosystem-level conductance behaviors and can improve global ecosystem conductance predictions and terrestrial biosphere process modeling.

2. Materials and methods

2.1. Data

We used half-hourly data of 77 eddy-covariance sites from the FLUXNET2015 dataset (Table S1), which is publicly available online (http://fluxnet.fluxdata.org). Sites were chosen when their data records covered at least 4 years, and most of the chosen sites have much longer data record. The selected sites also had to have meteorological data, including radiation, precipitation, air humidity and other necessary data to compute aerodynamic resistance applied in the Penman-Monteith framework, and soil moisture data. The locations of the 77 flux sites are shown in Fig. 1 and most sites lie in North America, Europe and Australia. We grouped the sites into nine plant functional types based on IGBP (International Geosphere–Biosphere Programme) vegetation classification scheme (Loveland et al., 1999): evergreen needleleaf forests (ENF), evergreen broadleaf forests (EBF), deciduous