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Applicability of common stomatal conductance models in maize under varying soil moisture conditions

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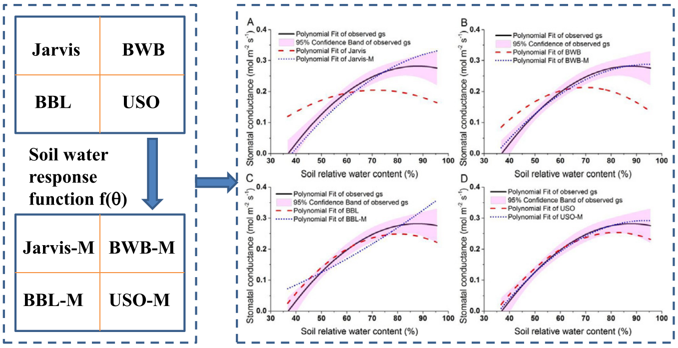
HIGHLIGHTS

- The effects of soil moisture made a difference in the relative performance among the models under varying conditions.
- Introducing a soil water response function improved the performance of the Jarvis, BWB, and USO models.
- The Jarvis, BWB, BBL and USO models were applicable within different ranges of soil moisture.
- The USO model performed best and was applicable under varying soil moisture conditions.

GRAPHICAL ABSTRACT



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ABSTRACT

In the context of climate warming, the varying soil moisture caused by precipitation pattern change will affect the applicability of stomatal conductance models, thereby affecting the simulation accuracy of carbon–nitrogen–water cycles in ecosystems. We studied the applicability of four common stomatal conductance models including Jarvis, Ball-Woodrow-Berry (BWB), Ball-Berry-Leuning (BBL) and unified stomatal optimization (USO) models based on summer maize leaf gas exchange data from a soil moisture consecutive decrease manipulation experiment. The results showed that the USO model performed best, followed by the BBL model, BWB model, and the Jarvis model performed worst under varying soil moisture conditions. The effects of soil moisture made a difference in the relative performance among the models. By introducing a water response function, the performance of the Jarvis, BWB, and USO models improved, which decreased the normalized root mean square error (NRMSE) by 15.7%, 16.6% and 3.9%, respectively; however, the performance of the BBL model was negative, which increased the NRMSE by 5.3%. It was observed that the models of Jarvis, BWB, BBL and USO were applicable within different ranges of soil relative water content (i.e., 55%–65%, 56%–67%, 37%–79% and 37%–95%, respectively) based on the 95% confidence limits. Moreover, introducing a water response function, the applicability of the Jarvis and BWB models improved. The USO model performed best with or without introducing the water response function and was applicable under varying soil moisture conditions. Our results provide a basis for selecting appropriate stomatal conductance models under drought conditions.

Abbreviations: A_n, net photosynthetic rate; g_s, stomatal conductance; SRWC, soil relative water content.

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1. Introduction

Stomata control the transport of water (H_2O) and carbon dioxide (CO_2) between leaves and the atmosphere (Buckley and Mott, 2013), limit CO_2 uptake during photosynthesis and water loss via transpiration, and ultimately affect plant productivity and water use efficiency (Srm et al., 2017). Leaf stomatal conductance is very sensitive to environmental factors such as radiation, temperature and vapor pressure deficit (Bunce, 2010; Tuzet et al., 2003). It has been proposed that both abscisic acid (ABA) in the xylem sap and leaf water status participate in stomatal control at a whole-plant level, with a different balance between these effects in different species (Sharp and Davies, 2009; Tardieu and Davies, 1993). Models that simulate stomatal conductance have become the most effective and appropriate tools for studying this important plant activity (Foley et al., 1996; Hetherington and Woodward, 2003).

A variety of stomatal conductance models at leaf level have been developed so far (Damour et al., 2010), including models based on the relationship between stomatal conductance and environmental factors (Jarvis, 1976), the relationship between stomatal conductance and photosynthesis (Ball et al., 1987; Leuning, 1995; Medlyn et al., 2011), the hydraulic control (Cochard et al., 1996; Tuzet et al., 2003) and the turgor regulation of guard cell (Buckley et al., 2003; Buckley et al., 2012; Dewar, 2002; Tardieu and Davies, 1993). Stomatal conductance models have not only been widely used as part of global climate models (Best et al., 2011; Bonan et al., 2014; De Kauwe et al., 2015; Egea et al., 2011), but also been applied to investigate specific plants and ecosystems, including wheat (Hanan et al., 2005), rice (Ono et al., 2013; Shimono et al., 2010), maize (Ji et al., 2017; Yu et al., 2001), forest (Gao et al., 2016b; Gimeno et al., 2016; Heroult et al., 2013; Medlyn et al., 2011; Wang et al., 2016; Zhou et al., 2013), grassland (Wever et al., 2002; Wolf et al., 2006) and other ecosystems.

Studies have revealed that the accuracy of stomatal conductance models is affected by the plant species, test regions, environmental conditions and time scales (Gao et al., 2016a). Thus, selecting an appropriate stomatal conductance model based on the existing research data can be problematic (Wang et al., 2014). Additionally, when simulating drought effects, it is difficult to accurately reflect the ability of vegetation to respond to water deficit without considering the applicability of stomatal conductance models (Damour et al., 2010). Many studies have modified the stomatal conductance models by considering the impact of water stress on stomatal conductance (Liu et al., 2009; Müller et al., 2014; Misson et al., 2004; Sala and Tenhunen, 1996; Tuzet et al., 2003; Uddling et al., 2005; Wijk et al., 2000). Whether empirical models (Jarvis, 1976; Misson et al., 2004) or semi-empirical models (Misson et al., 2004; Tuzet et al., 2003; Wijk et al., 2000), water stress has been accounted for by expressing the slope of the relationship between photosynthetic rate and stomatal conductance as empirical functions of predawn leaf water potential (Misson et al., 2004; Sala and Tenhunen, 1996), or of leaf water potential (Nikolov et al., 1995; Tuzet et al., 2003; Vico and Porporato, 2008), or soil water content (Egea et al., 2011; Li et al., 2012; Verhoef and Allen, 2000; Wijk et al., 2000).

The consequences of global warming likely include an increase in the frequency and intensity of drought conditions (Stocker et al., 2013). Drought will become one of the most important factors limiting plant production worldwide (Gholipoor et al., 2013; Lobell et al., 2014), bring destructive impacts on crop yields (Yao et al., 2018), and influence the global carbon cycle (Wang et al., 2018). Accurately simulating stomatal behavior under varying soil moisture conditions is important for characterizing the responses and adaptive mechanisms of vegetation ecosystems to climate change and for predicting the carbon and water cycles between plants and the atmosphere in the context of climate change (Berry et al., 2010; Buckley and Mott, 2013; Medlyn et al., 2011).

Globally, maize is an important source of raw materials for food, feedstuffs and products for fermentation and the chemical industry (Zhang et al., 2017b) and is affected seriously by water stress throughout the entire growing season (Anjum et al., 2011; Tayyib, 2013). Based on summer maize leaf gas exchange data observed from a soil moisture consecutive decrease manipulation experiment, the objectives of this study are to: (1) evaluate the performance of four common stomatal conductance models under varying soil moisture conditions, (2) test the hypothesis that stomatal conductance relies on the interaction between meteorological factors and soil moisture conditions, and (3) explore ways to determine the suitable range of soil moisture for four stomatal conductance models. Our findings may provide a new basis for crop drought monitoring and warning.

2. Materials and methods

2.1. Experiment design and environmental conditions

The experiment was carried out from June to October in 2014 at the Gucheng Ecological Environment and Agrometeorological Experiment Station of China Meteorological Administration in Baoding City, Hebei Province, North China Plain (39°08′N, 115°40′E, elevation 15.2 m above sea level). The study area has a warm temperate continental monsoon climate, with an annual average temperature of 12.2 °C, mean annual precipitation of 528 mm, and average annual sunshine hours of 2264 h. The soil type in the plot is sandy loam, with total nitrogen 0.98 g/kg, total phosphorus 1.02 g/kg, total potassium 17.26 g/kg, and a pH value of 8.1 (Fang et al., 2013). The area of each plot was 8 m^2 ($2\ m * 4\ m$), with a 3 m deep concrete separation wall between the plots.

The maize variety Zhengdan 958 was planted in the plots. One month before sowing (early June), the soil moisture of each plot was measured and then irrigated to make the soil moisture in each plot identical. The maize seeds were sown on June 24 and well-watered to ensure the emergence of seedlings. With the emergence of the third leaf, the maize was irrigated just once with six different irrigation amounts (10, 30, 60, 90, 120 and 150 mm) on July 2, which were set as 7%, 20%, 40%, 60%, 80% and 100% of the average precipitation in July (150 mm) over the past 30 years to form six soil moisture treatments, i.e., W1, W2, W3, W4, W5 and W6. Each treatment was randomly arranged with three replicates for a total of 18 plots in all. The plots in the treatments received no more water after the irrigation and a large mobile rain shelter was devised to reduce the risk of rain intrusion. Measurements were made on July 10, July 18 and July 31, i.e. 8 days, 16 days, and 29 days after the plants were subjected to different irrigation amounts. During this period, the maize was in the vegetative stage.

2.2. Soil water content measurement

The soil water content (θ) was measured using the gravimetric method from 0 to 40 cm soil, per 10 cm soil as a layer. Three replicates were used for each θ determination. The θ (%) is expressed as follows:

$$\theta = \frac{W_C - W_D}{W_D - W_P} \times 100 \tag{1}$$

where W_C is the weight for empty soil pot and wet soil (g), W_P is the empty soil pot weight (g), W_D is the weight for empty soil pot and dry soil (g).

The soil relative water content (SRWC, the ratio between the current soil moisture and the field capacity, %) was then calculated as

$$SRWC = \frac{\theta}{\theta_f} \times 100 \tag{2}$$

where θ_f is the soil field capacity (%).

2.3. Leaf gas exchange measurements

Three plants for each treatment were selected (one plant from each plot), and the gas exchange parameters were measured on the youngest