**Modelling canopy conductance under contrasting seasonal conditions for a
tropical savanna ecosystem of south central Mato Grosso, Brazil**

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ABSTRACT

Temporal variations in land-atmosphere water vapor exchange are more pronounced in seasonal
environments, especially grass-dominated savannas (known as *campo sujo Cerrado*) of the
southern and eastern Amazon Basin. Recent work in *campo sujo* indicates that rates of canopy
conductance (g_c) were directly and indirectly affected by a variety of meteorological variables,
which limited our understanding of how seasonal variation in meteorology affected rates of g_c .
Thus, our overall objective here is to determine how individual meteorological variables affect

seasonal variations in g_c . Estimates of g_c were derived using the inverted Penman–Monteith equation from hourly eddy-covariance measurements of evapotranspiration made between March 2011 and December 2013. We employed the so-called Jarvis-type model to estimate g_c , which allows us to specify the functional role of each variable on g_c , to evaluate how variations in meteorology affect rates of Cerrado g_c . The model was parameterized using eddy covariance data from 2012 and tested with data collected in 2011 and 2013. Using orthogonal regression and the **Willmott** index of agreement, we found that the model estimates compared well to those derived from eddy covariance, especially in 2011. Sensitivity analyses revealed that g_c was particularly sensitive to warming and drying, particularly during the dry season when drought stress from low soil moisture availability was already limiting g_c . Warming and drying in response to climate change is expected to increase dry season duration, and dry season intensification may already be occurring in central and southern Mato Grosso. Given the high degree of surface-atmosphere coupling for this ecosystem, and the fact that g_c is an important link between canopy-scale C and water cycling, our data suggest that dry season intensification may further limit CO₂ and H₂O vapor exchange during the dry season.

Keywords: Brazilian savanna; Campo sujo; Climate Change; Cerrado; Deforestation; Evapotranspiration; Jarvis-Type Model; Land use, land cover change; Latent heat flux.

1. Introduction

The rate of water vapor (H₂O) exchange between the vegetated surface and the atmosphere is one of the most important energy exchange processes at the air–land interface (Kumagai et al., 2004). **This is especially true for tropical ecosystems, which can return 45-65%**

of the precipitation to the atmosphere as evapotranspiration (ET) annually (Hutyra et al., 2005; Vourlitis et al., 2014). However, the ET tropical ecosystems has been shown to be sensitive to climatic variation over seasonal and interannual time scales (Malhi et al., 2002; Rodrigues et al., 2013; Vourlitis et al., 2014), and climate variation is predicted to increase with human-induced climate change because of intensification of the dry season (Cramer et al. 2005; Li et al. 2008; Phillips et al., 2009; Cox et al., 2013; Gatti et al., 2014).

Temporal variations in land-atmosphere water vapor exchange are more pronounced in seasonal environments (Machado et al., 2004; da Rocha et al., 2009; Costa et al., 2010; Rodrigues et al., 2014), especially the grass-dominated savannas of the southern and eastern borders of the Amazon Basin (Giambelluca et al., 2009; Rodrigues et al., 2014; Biudes et al., 2015). Savanna covers approximately 45% of the area in South America (Scholes and Archer 1997), and Brazilian savanna (locally known as Cerrado) is the dominant vegetation in areas subjected to a prolonged dry season (Lascano, 1991; San José et al., 1998; Rodrigues et al., 2011, 2013 and 2014). The extremely seasonal environment of Cerrado is characterized by a dry season that extends between 5-6 months, with nearly all of the rainfall (ca. 90%) distributed between the months of October-March (Bucci et al., 2008; Vourlitis and da Rocha, 2011). Evaporative demand is substantially higher during the dry season (Rodrigues et al., 2013, 2014; Biudes et al., 2015), and the combination of higher evaporative demand and low soil water availability makes the Cerrado a potentially stressful environment for woody species (Bucci et al., 2008; Rodrigues et al., 2014). This is especially true for short-rooted vegetation such as grasses and shrubs, which are important components of Cerrado (Meinzer et al., 1999; Giambelluca et al., 2009; Vourlitis and da Rocha, 2011; Rodrigues et al., 2014). As a result, rates of ET may decline by 40% in tree-shrub dominated Cerrado (*sensu stricto* or *denso*) to over

50% in grass-dominated (*campo*) forms of Cerrado during the dry season (Santos et al. 2003; Oliveira et al. 2005; da Rocha et al., 2009; Giambelluca et al., 2009; Rodrigues et al. 2014).

Plant control of ET occurs by variation in stomatal conductance (g_s) (Wright et al., 1996; Harris et al., 2004; Costa et al. 2010), although variation in leaf area index (LAI) also affects rates of canopy-atmosphere water vapor exchange (Vourlitis et al., 2008; Giambelluca et al., 2009). However, “bottom-up” scaling g_s from the leaf to the canopy is difficult due to the fact that g_s varies according to species, leaf age, radiation exposure, internal CO₂ concentration, and/or nutrient content (Jarvis, 1976; Field, 1983; Leuning, 1990; Dalmagro et al. 2013). Thus, bottom-up scaling of g_s requires canopy-level estimates of leaf morphology and/or distribution, canopy structure (i.e., leaf area index), and vapor, heat, and radiative transfer (Jarvis and McNaughton, 1986; Baldocchi et al., 1991; Leuning et al., 1995; Li et al. 2008). An alternative approach is to use canopy-scale measurements to estimate canopy conductance (g_c); however, while g_c may be strongly affected by g_s it is also affected by evaporation and non-physiological terms such as the radiative and aerodynamic properties of the canopy (Jarvis and McNaughton, 1986; Baldocchi et al., 1991). In canopies that are highly coupled to the atmosphere, variations in g_c are more closely related to variations in g_s (Jarvis and McNaughton, 1986; Meinzer et al., 1993). Nevertheless, g_c represents an important link between canopy-scale carbon (C) and water cycling, and thus, is an important input to ecosystem C and water cycle models (Wang and Leuning, 1998; Harris et al. 2004; Kumagai et al., 2004).

Recent work in grass-dominated Cerrado indicates that both ET and g_c are limited by water availability during the dry season (Rodrigues et al., 2014), which is consistent with that reported for seasonal tropical forests (Vourlitis et al., 2008), humid tropical forests (Harris et al., 2004), and Cerrado woodlands (Giambelluca et al., 2009). However, using path analysis

Rodrigues et al. (2014) found that rates of Cerrado g_c were directly and indirectly affected by a variety of meteorological variables, which limited our understanding of how seasonal variation in meteorology affected rates of g_c . Given the central role of g_c in C and water cycling, and the reliance of g_c in canopy models (Wang and Leuning, 1998; Harris et al. 2004; Kumagai et al., 2004), it is important to understand how meteorological variation affects g_c . Thus, our overall objective here is to determine how individual meteorological variables affect seasonal variations in Cerrado g_c . To fulfill our objective we employed the so-called Jarvis-type model to estimate g_c , which allows us to specify the functional role of each variable on g_c (Jarvis 1976; Harris et al., 2004). This model has been used to study meteorological controls in a variety of other Amazonian ecosystems (Dolman et al., 1991; Wright et al., 1996; Harris et al., 2004; von Randow et al., 2012), but to our knowledge this is the first time this type of model has been used for grass-dominated Cerrado. Here we evaluate how variations in meteorology affect rates of Cerrado g_c and qualitatively compare our results to those described for other Amazonian ecosystems.

2. Materials and methods

2.1 Site description

The study was conducted at the Fazenda Miranda in the Cuiaba Basin, 15 km SSE of Cuiaba, Mato Grosso, Brazil (Fig. 1). The vegetation is grass-dominated with scatter trees and shrubs, which is locally known as *campo sujo* or “dirty field” Cerrado (Rodrigues et al. 2013; 2014). Vegetation consists predominately of native and introduced grasses and the tree species *C. americana* and *Diospyros hispida* A. DC. The Koppen climate classification is Aw, tropical semi-humid, with dry winters and wet summers. The long-term (30 year) average mean monthly air temperature ranges from a minimum of 18 °C in June-July to a maximum of 29 °C in

October, and the average rainfall is 1420 mm with a dry season that extends from May-September (Vourlitis and da Rocha, 2011). The research area is on flat terrain at an elevation of 157 m above sea level. The regional soil type is locally known as a Solo Concrecionário Distrófico, which is a rocky, nutrient poor, red-yellow latosol (Radambrasil, 1982). These soils have high porosity, low water holding capacity, and drain rapidly (within 3-5 days) following rainfall (Rodrigues et al., 2013, 2014).

2.2. Micrometeorological measurements

Micrometeorological and eddy covariance measurements were conducted between March 2011 and December 2013. A 20m tall micrometeorological tower enabled the collection of data on air temperature (T_a), relative humidity (RH), wind speed (u), precipitation (P), soil temperature (T_s), heat flux (G), and moisture (θ_w), net (R_n) and solar radiation (R_s), and latent (L_e) and sensible heat flux (H). T_a and RH were measured 10 m above the ground level using thermohygrometer (HMP45AC, Vaisala Inc., Woburn, MA, USA). Wind speed was measured 10 m above the ground level using anemometer (03101 R. M. Young Company), and G was measured using heat flux plates (HFP01-L20, Hukseflux Thermal Sensors BV, Delft, The Netherlands) installed 1.0 cm below the soil surface ($n=2$), with one placed in the sandy and the other placed in a laterite soil types that are representative of the tower footprint. θ_w was measured in the two soil types described above using time-domain reflectometry (TDR) probes ($n=2$) installed 20 cm below the soil surface (CS616-L50 (Campbell Scientific, Inc., Logan, UT, USA). Values of G and θ_w obtained from each soil type were averaged to obtain an estimate for the tower footprint, which is appropriate given that each soil type is equally represented in the footprint and both soils have similar vegetative cover and water holding characteristics. R_n and R_s were measured 5 m aboveground using a net radiometer (NR-LITE-L25, Kipp & Zonen,

Delft, The Netherlands) and a pyranometer (LI200X, LI-COR Biosciences, Inc., Lincoln, NE, USA), respectively. Precipitation was measured using a tipping-bucket rainfall gauge (TR-525M; Texas Electronics, Inc., Dallas, TX, USA). The sensors were connected to a datalogger (CR1000, Campbell Scientific, Inc., Logan, UT, USA) that scanned each sensor every 30 seconds and stored average and/or total (P) quantities every 30 minutes.

Latent (L_e) and sensible heat flux (H) were quantified using eddy covariance, and measurement details have been described in detail by Rodrigues et al. (2014). Briefly, eddy covariance sensors were mounted at a height of 10 m above ground level, or 8-8.5 m above the vegetation. Wind direction was typically out of the NNW and NNE, and analysis of the upwind fetch estimated using the Schuepp et al., (1990) model indicated that about 90% of the flux originated within 1 km upwind of the tower (Arruda, 2014).

The eddy covariance system consisted of a 3-dimensional sonic anemometer-thermometer (CSAT-3, Campbell Scientific, Inc., Logan, UT, USA) to measure the mean and fluctuating quantities of wind speed and temperature and an open-path infrared gas analyzer (LI-7500, LI-COR, Inc. Lincoln, NE, USA) to measure the mean and fluctuating quantities of H_2O vapor. Both sensors sampled and output data at 10 Hz and were oriented in the direction of the mean wind. Raw (10 Hz) data and 30-min average fluxes were stored and processed using a data logger (CR1000, Campbell Scientific, Inc., Logan, UT, USA).

Average fluxes of L_e and H were obtained by calculating the covariance between the fluctuations in vertical wind speed and H_2O vapor density and temperature, respectively over a 30-min interval following a coordinate rotation of the wind vectors (McMillen, 1988). Water vapor flux was corrected for the simultaneous fluctuations in heat following Webb et al. (1980).

System performance was assessed by linear regression of the energy balance closure with $H+L_e$ measured from eddy covariance as the dependent variable and R_n-G measured from the meteorological sensors as the independent variable (McMillen, 1988). Instantaneous (30min average) measurements $H+L_e$ accounted for only about 75% of R_n-G , and there was a significant y-intercept (Rodrigues et al. 2014). Furthermore, there was no improvement in energy balance closure using daily totals of L_e+H and R_n-G (Rodrigues et al., 2014), indicating that errors associated with energy storage were negligible. Thus, the eddy covariance data tended to underestimate the net energy loss at night and the net energy gain during the day, but the degree of closure is comparable to that reported for other temperate and tropical forest eddy covariance systems (Aubinet et al., 2000; Araújo et al., 2002; Malhi et al., 2002; Vourlitis et al., 2008; Giambelluca et al., 2009).

2.3. Canopy conductance calculation

Canopy conductance (g_c) was calculated during daytime periods (0800-1600 h local time) from micrometeorological and eddy covariance data using the inverted Penman–Monteith equation (Monteith, 1981; Dolman et al., 1991; Harris et al., 2004; Rodrigues et al., 2014),

$$g_c^{obs} = g_a \left[\frac{(\Delta Q + \rho C_p D g_a)}{\gamma L_e} - \frac{\Delta}{\gamma} - 1 \right]^{-1} \quad (\text{equ. 1})$$

where g_a is the aerodynamic conductance (ms^{-1} ; described below), Δ is the slope of the saturation vapor pressure vs. temperature curve (kPa/K), ρ is the density of dry air (g m^{-3}), C_p is the specific heat capacity ($\text{J g}^{-1} \text{K}^{-1}$), D is the atmospheric vapor pressure deficit (kPa), γ is the psychrometric constant (kPa.K^{-1}), and Q is the available energy calculated as R_n-G ($\text{J m}^{-2} \text{s}^{-1}$).

Following Gash et al. (1999) and Rodrigues et al. (2014), when momentum flux, or friction velocity (u^*), is measured directly from the fluctuations in vertical and horizontal wind speed, the momentum aerodynamic conductance, g_a (m s^{-1}), can be calculated directly as

$$g_a = \frac{u_*^2}{u} \quad (\text{equ. 2})$$

where u = wind speed measured from the tri-axial sonic anemometer, u^* = frictional velocity calculated from eddy covariance measurements of momentum flux (Baldocchi et al., 1991). No attempt was made to adjust g_a to variations in atmospheric stability because u^* was measured directly, as opposed to estimated using flux-gradient methods, and adjustments often lead to errors in the estimation of g_a , or are highly uncertain, in areas like the *campo sujo* studied here where tree coverage is sparse (see Lankreijer et al., 1993; Gash et al., 1999 for a thorough discussion).

2.4. Canopy conductance model

Canopy conductance estimates from eddy covariance were used to parameterize and test a “Jarvis-type” model of g_c (Jarvis, 1976; Harris et al., 2004). This model was initially designed to describe stomatal conductance (g_s) as a function of the maximum rate of g_s ($g_s^{\max}$) and environmental limitations to $g_s^{\max}$ including ambient CO_2 concentration, radiation, humidity, temperature, and soil moisture (Jarvis, 1976); however, this model has been extended to canopy scales by assuming that g_c is analogous to g_s (Baldocchi et al., 1991; Lloyd et al., 1995; Harris et al., 2004). As mentioned above, this assumption is debatable because non-physiological processes such as the net radiation balance, aerodynamic conductance inside the canopy, and surface evaporation will affect g_c (Baldocchi et al., 1991). However, the Cerrado stand evaluated here was found to be highly coupled to the overlying atmosphere (Rodrigues et al., 2014), suggesting that g_c for this surface may be controlled relatively less by non-physiological processes and more so by stomatal conductance (Jarvis and McNaughton, 1986).

205 The instantaneous (30 minute average) rate of g_c was estimated using the multiplicative
 206 algorithm defined by Stewart (1988) and last modified by Wright et al. (1996) following Jarvis
 207 (1976):

$$208 \quad g_c^{\text{mod}} = g_c^{\text{max}} f(R) f(T) f(D) f(W) \quad (\text{equ. 3})$$

209 where g_c^{mod} is the estimated canopy conductance using the Jarvis approach (ms^{-1}), and g_c^{max} is
 210 the maximum canopy conductance (ms^{-1}) found using eddy covariance (equ. 1). The functional
 211 scalars ($f(X)$) described how rates of g_c^{max} are altered by temporal variations in shortwave
 212 radiation ($f(R)$), air temperature ($f(T)$), vapor pressure deficit of the atmosphere ($f(D)$), and soil
 213 moisture status as soil water deficit relative to field capacity ($f(W)$). Each scalar varies between
 214 0 (full stomatal closure) to 1 (maximum stomatal opening). Following Jarvis (1976) and Harris
 215 et al. (2004), the scalar terms are given by:

$$216 \quad f(R) = (R_s/1100) * ((1100 + a_1)/(R_s + a_1)) \quad (\text{equ. 4})$$

$$217 \quad f(T) = ((T - T_0) * (T_m - T))^{\tau} / ((a_2 - T_0) * (T_m - a_2))^{\tau} \quad (\text{equ. 5})$$

$$218 \quad \text{and } \tau = ((T_m - a_2)/(a_2 - T_0))$$

$$219 \quad f(D) = \exp(-a_3 * \text{VPD}) \quad (\text{equ. 6})$$

$$220 \quad f(W) = ((\theta_w - a_4)/(a_5 - a_4)), \text{ if } a_4 < \theta_w < a_5 \quad (\text{equ. 7})$$

$$221 \quad = 0 \text{ if } \theta_w \leq a_4$$

$$222 \quad = 1 \text{ if } \theta_w \geq a_5$$

223 where coefficients (a_1 - a_5) were estimated using multivariate non-linear regression (Table 1).

224 Following Harris *et al.* (2004), T_0 and T_m are the minimum (0°C) and maximum (40°C) ambient
 225 temperatures, respectively where $g_c = 0 \text{ m/s}$.

226 The model was optimized using eddy covariance data collected between January 1, 2012
 227 and December 31, 2012. This period was selected because it encompassed the seasonal

variations in soil water availability and meteorology, eddy covariance and meteorological data were complete for both wet and dry seasons, and system performance was optimal. The models were optimized using Solver function in Excel version 2010 by minimizing the sum of square errors between modelled (g_c^{mod}) and observed (g_c^{obs}) derived from eddy covariance. The optimized model was then used to estimate g_c^{mod} for 2011 and 2013.

Although stomata may not always be closed during the night (García-Santos 2007), g_c^{mod} was estimated only for daytime hours (0800-1600h local time), both to simplify the model application and because the low rates of nocturnal transpiration did not follow a fixed pattern. In addition, only dry-canopy conditions were considered (Sommer et al. 2002; Harris et al. 2004; Vourlitis et al. 2008; Rodrigues et al. 2014) and all hours with measured rainfall or fog, including a 2 h post-precipitation period to allow the canopy to fully dry out, were excluded.

2.5. Data Analysis

Daily averages and/or totals were summarized as mean ($\pm$ sd) values calculated over 15 d intervals unless specified. Diurnal (0800-1600h local time) averages of energy flux density, micrometeorology and conductance were calculated by averaging each 30-min datum for a particular time (e.g., 0800–0830 h). Sensor and/or infrastructure failures caused gaps in data collection, and short-term events such as intense rainfall and/or fog, led to the rejection of data. Gaps were filled using linear regression where the missing data series (i.e., R_n , L_e and H) was estimated from a similar variable (i.e., R_s). These gaps accounted for < 5% of the total possible measurements during the study period.

Orthogonal regression was used to assess the relationship between g_c^{mod} and g_c^{obs} because of the potential for errors in both time series (Leng et al., 2007). Willmott's index of agreement (d) was used to quantify the degree of correspondence between g_c^{mod} and g_c^{obs} , where $d = 1$

indicates complete correspondence and $d=0$ indicates no correspondence between measured and modeled values (Willmott, 1982). The systematic root mean square error (RMSEs) and unsystematic RMSE (RMSEu) were used to quantify the amount of error due to systematic and random variations, respectively between the measured and modeled values (Willmott, 1982). The sum of MSEs and MSEu is the total MSE, and a “good” model (i.e., one without significant structural flaws) should have a $RMSE_s < RMSE_u$ (Willmott, 1982).

Seasonal mean ($\pm 95\%$ CI) meteorological variables, soil water content, and g_c^{mod} and g_c^{obs} were calculated by bootstrap resampling techniques (Efron and Tibshirani 1993) over 1000 iterations. The dry season was defined as the period when precipitation was less than 100 mm/month (Hutyra et al., 2005). Lack of overlap of a given mean ($\pm 95\%$ CI) value between seasons indicated that there was a significant difference for that variable between the wet and dry season.

Average diel (0800-1600 h local time) time series of air temperature, VPD, and θ_w calculated over 15 day intervals were used to simulate the sensitivity of g_c^{mod} to $\pm 10\%$ variations in meteorology and soil water availability. For example, to simulate the effects of warming on g_c^{mod} we (1) created a new time series consisting air temperature $\times 0.10$ (10% temperature time series), (2) calculated the standard deviation of the 10% temperature time series, and (3) added each 10% (± 1 sd) temperature value to the corresponding temperature measurement from which it was calculated. To estimate random variability in the recalculated temperature time series we randomly added or subtracted the standard deviation calculated for the 10% temperature time series to each individual 10% temperature datum. This procedure resulted in a re-calculated temperature time series that was on average (± 1 sd) 10% higher than the original time series. To simulate the effects of cooler temperatures we simply subtracted 10% (± 1 sd) from the

temperature time series. The model was then re-run given the new temperature time series, and average daily g_c^{mod} was re-calculated given the new temperature conditions. This procedure was repeated 100 times to assess random variability in the recalculated time series. Differences between the average simulated and control g_c^{mod} were calculated as $[(\text{control-simulated})/\text{control}] \times 100$. Only variations in air temperature, VPD, and θ_w were simulated because variations in R_s were found to affect g_c^{mod} minimally (Fig. 2a). Data for 2011 data were used because of the superior model performance during this year.

3. Results and discussion

3.1. Scalar functions

Optimized values of g_{cmax} for *camp sujo* Cerrado were approximately 1.4-6 times lower than values estimated for other topical ecosystems; however, there did not seem to be a pattern in g_{cmax} as a function of vegetation type and/or annual rainfall (Table 1). For example, g_{cmax} varied by a factor of 4 (20.8-80.1 mm/s) for Amazonia forests and by over 2 (21.0-44.0 mm/s) for Amazonian pastures, indicating that g_{cmax} can vary substantially within and between vegetation types. The reason for the lower value estimated for our Cerrado stand is undoubtedly due to the lower soil water holding capacity and lower leaf area index (LAI) associated with our site. For example, the grass-dominated pasture sites described by Wright et al. (1996) had a LAI of 1.5 and 3.9 m^2/m^2 , with a corresponding g_{cmax} of 27.1 and 44.0 mm/s, respectively (Table 1); while the LAI for our Cerrado stand was approximately 1.3 m^2/m^2 . However, variations in LAI may not completely explain variations in g_{cmax} because the Amazonian pasture site described by von Randow et al. (2012) had a LAI of only 0.77 m^2/m^2 and a g_{cmax} of 21.0 (Table 1). Rather, all of the pasture stands described by Wright et al. (1996) and von Randow et al. (2012) had clay-rich

soils, with a field capacity of $0.23\text{--}0.49\text{ m}^3/\text{m}^3$, which is substantially higher than that observed for our Cerrado stand (Table 1).

The behavior of the optimized scalar functions was quantitatively similar to those estimated for other tropical ecosystems (Fig. 2); however, differences in $f(R)$ (Fig. 2a) and $f(D)$ (Fig. 2c) were notable. The optimized $f(R)$ for the Cerrado stand saturated at R_s values $\geq 50\text{ J m}^{-2}\text{ s}^{-1}$, indicating virtually no sensitivity of g_c to daytime (0800-1600 h local time) variations in radiation, while the $f(R)$ scalars for tropical forests exhibited saturation only at R_s values $>900\text{ J m}^{-2}\text{ s}^{-1}$ (Fig. 2a). The lack of sensitivity to radiation for Cerrado g_c is not too surprising given the importance of other variables, such as $f(D)$ and $f(W)$, in controlling diel and seasonal patterns of g_c . If anything, diel variations in measured and modeled g_c appeared to be negatively correlated with diel patterns of R_s (Fig. 4), again pointing to the importance of other variables in controlling diel patterns of g_c .

The temperature scalar exhibited a peak at 20°C and a decline at sub- and super-optimal temperatures, which is similar to that estimated for other tropical forests except for the forests studied by Wright et al. (1996) (Fig. 2b). However, $f(D)$ declined much more gradually as VPD increased for the Cerrado stand compared to the forests and Amazonia pastures (Fig. 2c), suggesting that the Cerrado vegetation is less sensitive to high VPD. The optimized soil moisture function $f(W)$ increased linearly from 0 at threshold θ_w of $0.01\text{ m}^3\text{ m}^{-3}$ to a maximum value of 1 at a θ_w of $0.055\text{ m}^3\text{ m}^{-3}$ (Fig. 2d). These threshold values are substantially lower than those reported for other tropical ecosystems (Table 1), reflecting the low water holding capacity of the sandy and rocky soils that are typical of our study site (Vourlitis et al. 2013; Rodriguez et al., 2014).

3.2. Model performance

The performance of the g_c model was tested using data obtained for 2001 and 2013, and there were clear differences in model performance between these years (Table 2; Fig. 3). For 2011, the slope of the orthagonal regression between g_c^{mod} and g_c^{obs} was only slightly below unity for the diurnal (0800-1600 h local time) average data but was not significantly different from unity for the 15 day average data, while the intercept of the regression was not significantly different from zero for both the diurnal and 15 day average values (Table 2; Fig. 3). In contrast, for 2013 the slope of the orthagonal regression between g_c^{mod} and g_c^{obs} was significantly below unity and the intercept was significantly above zero for both diurnal and 15 day average values (Table 2; Fig. 3).

Analysis of the **Willmott** statistic (d) indicates excellent correspondence between measured and observed values for 2011 ($d = 0.94$ and 0.96 for average diurnal and 15 day values, respectively), and relatively more of the difference between g_c^{mod} and g_c^{obs} was due to random (unsystematic) errors (Table 2). Thus, discrepancies between the modeled and observed values were likely due to random variations in both time series (**Willmott**, 1982). Estimates of **Willmott**'s d were lower for 2013 ($d = 0.85$ and 0.92 for average diurnal and 15 day values, respectively), but even so, these values indicate good correspondence between g_c^{mod} and g_c^{obs} (**Willmott**, 1982). However, a larger proportion of the error was due to systematic differences between the modeled and observed values (Table 2).

3.3. Seasonal patterns in g_c

Canopy conductance derived from eddy covariance was generally highest in the morning (0800 h local time) and lowest during the midday (1200-1400 h local time), and this pattern was consistent for each year and season observed (Fig. 4). During some months, typically those

during the wet season, there was a late-afternoon recovery in g_c ; however, the recovery was never as high as the morning value (Fig. 4). Diurnal values were also higher during the wet season than the dry season, indicating that the onset of drought caused a rapid decline in diurnal g_c (Harris et al., 2004; Vourlitis et al., 2008; Rodrigues et al., 2014). The decline in g_c over the course of the day is consistent with other Cerrado (Giambelluca et al., 2009) and tropical semi-deciduous forests (Vourlitis et al., 2008) but is opposite to that observed for humid tropical forests (Malhi et al., 2002; Harris et al., 2004; da Rocha et al., 2004), and presumably, these differences reflect differences in the relative importance of radiation and VPD in controlling g_s and g_c between radiation-limited forests and water-limited savannas.

The diurnal trends observed for g_c^{mod} were similar to that observed for g_c^{obs} , with the highest rates in the early morning and the lowest rates observed in the mid-afternoon (Fig. 4). Again, g_c^{mod} displayed some recovery in the late-afternoon during the wet season and a consistent decline in g_c from the wet to the dry season (Fig. 4). The largest differences between g_c^{mod} and g_c^{obs} tended to occur during the transition periods between the wet and dry seasons, which typically occur during the months of April-May and September-October, respectively (Vourlitis and da Rocha, 2011). During the wet-dry season transition rainfall can become more sporadic, and given the rapid drainage characteristics of the regional soil type, surface water availability may be transient (Rodrigues et al. 2013; 2014; Biudes et al., 2015). Thus, during the wet-dry season transition (April-May) g_c^{mod} may underestimate g_c^{obs} because the model is responding to transient variations in surface water availability while cerrado trees and grasses may be responding to deeper, more consistent soil water reserves that accumulated during the wet season (Rodrigues et al. 2013; 2014; Dalmagro et al., 2014). Unfortunately, soil water content depths > 20 cm is unknown, but the soils associated with the research site are shallow

and bedrock is often encountered within the upper 30-50 cm soil layer (Radambrasil 1982). Even so, nearly 60% of the total root biomass and 75% of the fine root biomass of tropical savanna plants is reportedly in the upper 30- to 50-cm soil layer (Jackson et al. 1996; Lilienfein et al. 2001), so even small increases in soil water content at depth would likely buffer the vegetation response to fluctuations in surface soil moisture during the wet-dry season transition.

In contrast, during the dry-wet season transition (September-October), transient increases in surface soil water content may cause g_c^{mod} to overestimate g_c^{obs} because transpiration by cerrado trees and shrubs may still be limited by the soil water deficit that developed during the 5 month dry season (Rodrigues et al. 2013; 2014; Dalmagro et al., 2014).

Seasonal variations in mean ($\pm 1\text{sd}$) surface θ_w were highly positively correlated with rainfall ($r = 0.77$; $p < 0.05$), resulting in generally higher, but variable, θ_w during the wet season and lower, but more consistent, θ_w during the dry season (Fig. 5a; Table 3). In turn, the vapor pressure deficit (VPD) increased from the wet to the dry season and was 2-3-fold higher during the peak of the dry season than during the wet season, resulting in significantly higher dry season VPD in two of the three years studied (Table 3). Air temperature generally declined during the dry season (Fig. 5b) because of periodic cold fronts that arise from southern South America during this period (Machado et al., 2004); however, significant differences between wet and dry season air temperature were only observed in 2013 (Table 3). Seasonal variations in R_s and R_n were positively correlated ($r = 0.51$; $p < 0.05$), and while highly variable, both generally increased from the dry into the wet season and peaked during the austral summer solstice (Fig. 5c). However, seasonal variations in R_s were not statistically significant while seasonal variations in R_n were statistically significant in two of the three years studied (Table 3). For R_n , some of this seasonal variation is due to the variations in R_s and the seasonal dynamics in leaf

area index, which declines substantially during the dry season (Ratana et al. 2005; Rodrigues et al., 2014; Dalmolin et al., 2015).

The correspondence between g_c and the seasonal and annual variations in meteorology were much more apparent in the 15-day average time series (Fig. 5). Variations in both g_c^{obs} and g_c^{mod} followed the seasonal patterns in θ_w and VPD closely, with peaks during the wet season months of December-February that were 6-8 times higher than the minimum values observed during the dry season months of August-September (Fig. 5d). These trends are similar to those observed for other Cerrado (Giambelluca et al., 2009), pasture (von Randow et al., 2012), and semi-deciduous tropical forest (Vourlitis et al., 2008) and highlight the dynamic nature of g_c for these seasonal tropical ecosystems. Furthermore, estimates of g_c^{mod} and g_c^{obs} were not statistically different, further indicating that g_c^{mod} captured the seasonal variation estimated from eddy covariance (Table 3). **Seasonal variations in aerodynamic conductance (g_a) were also observed, but only during the last year of the study when wet seasonal values were higher than dry season values (Table 3), which may have been due to increases in wind speed that accompany synoptic storms (da Rocha et al., 2004).**

3.4. Sensitivity of g_c to variations in meteorology and soil water content

Rodrigues et al. (2014) used path analysis to demonstrate that the seasonal variation in g_c was both directly and indirectly affected by variation in meteorology. However, because many of the variables used in the analysis were correlated it was unclear how individual variations in meteorology affected g_c . With a Jarvis-type model, individual variables can be altered to test how sensitive g_c is to a change in a given variable (Jarvis 1976; Harris et al., 2004). Thus, we used 2011 data to assess the sensitivity of g_c^{mod} to meteorological variation and soil water availability. Variations in the air temperature, VPD, and θ_w time series were either increased or

decreased by 10%, and the average percent change in g_c^{mod} to the control condition over 100 random simulations was calculated as $[(\text{change}-\text{control})/\text{control}] \times 100$.

Our results indicate that g_c^{mod} is sensitive to variations in temperature, VPD, and θ_w , but the magnitude of this sensitivity varies substantially over seasonal time scales (Fig. 6). For example, a 10% decline in temperature increased g_c^{mod} by only about 2-5% over the simulated 2011 year (Fig. 6), presumably because average temperatures are slightly above the 20°C temperature optimum for $f(T)$. However, a simulated 10% increase in temperature caused a 10-30% decline in g_c^{mod} during the wet season and an nearly a 40% decline in g_c^{mod} at the end of the dry season (late-August) when air temperature reached a seasonal peak (Fig. 5b). The temperature-induced decline in g_c^{mod} was proportional to how far the air temperature was above the temperature optimum for g_c^{mod} . While not explicitly estimated with our sensitivity analysis, these super-optimum temperatures at the end of the dry season will likely interact with water stress to further limit g_c . Given that anthropogenic warming and drying are estimated to increase the intensity of the dry season (Costa and Pires, 2010), the high temperature sensitivity in g_c has implications for future H₂O and C cycling in grass-dominated Cerrado.

Decreases in the VPD caused g_c^{mod} to vary by $\pm 5\%$ compared to the control condition, while increases in the VPD cause g_c^{mod} to consistently decline by 5-10% during the wet season to nearly 20% during the dry season (Fig. 6). While a 20% decline in g_c^{mod} during the peak of the dry season is substantial, it is surprising that the decline in g_c^{mod} was not larger given the importance of VPD in controlling diel and seasonal rates of g_c^{mod} (Vourlitis et al., 2008; Giambelluca et al., 2009; Rodrigues et al., 2014). However, the optimized $f(D)$ curve for our Cerrado stand declined more gradually than those estimated for other tropical ecosystems (Fig. 2c; Table 1), suggesting less sensitivity of *campo sujo* g_c to variations in VPD.

Variations in θ_w caused the largest variations in g_c^{mod} compared to temperature and VPD (Fig. 6). Increases in θ_w at the beginning of the wet season caused slight reduction (ca. 5%) in g_c^{mod} ; however, a 10% increase in θ_w during the dry season led to a 10-20% increase in g_c^{mod} . The dry-season increase in g_c^{mod} diminished over time, but even into the early part of the wet season g_c^{mod} was still 10% higher compared to the control value (Fig. 6). Decreasing θ_w by 10% had an opposite, and quantitatively larger, effect on g_c^{mod} . Again, at the end of the wet season a decline in θ_w caused little change in g_c^{mod} ; however, at the onset of the dry season, g_c^{mod} rapidly declined under drier conditions. Estimated rates of dry season g_c^{mod} were 20-30% lower under simulated drying, and full recovery was never observed even into the peak of the wet season in December (Fig. 6). These results indicate that g_c is especially sensitive to soil drying in these course soils that have inherently low water holding capacity.

4. Conclusions

The Jarvis-type model indicated that the g_c of a grass-dominated (“campo sujo”) Cerrado stand in the Cuiaba Basin of southern Mato Grosso was sensitive to variations in temperature, θ_w , and to a lesser extent VPD, but not radiation. These results are not particularly surprising given the large seasonality in rainfall for this region and the previously reported high seasonal variability in mass and energy exchange. However, the ability to assess the sensitivity of g_c in response to individual variations in meteorology and water availability, which was possible using the Jarvis-type model described here (Jarvis 1976; Harris et al., 2004), represents a key advantage over previous analyses and provides greater insight regarding how g_c may be altered by climate variability.

Our results indicated that increases in temperature alone may be important in limiting canopy conductance for this Cerrado ecosystem. Furthermore, the decline in g_c as temperature

increased was especially **severe** during the dry season when drought stress from low θ_w was already limiting g_c . Warming and drying in response to anthropogenic climate change is expected to increase dry season duration and/or intensity throughout the Amazon Basin and Cerrado region (Cramer et al. 2005; Li et al. 2008; Phillips et al., 2009; Cox et al., 2013; Gatti et al., 2014), and indeed, dry season intensification may already be occurring in the Amazon Basin (Li et al. 2008), and specifically central and southern Mato Grosso (Vourlitis et al., 2014). Given the high degree of surface-atmosphere coupling for this ecosystem (Rodrigues et al. 2014), and the fact that g_c is an important link between canopy-scale C and water cycling (Wang and Leuning, 1998; Harris et al. 2004; Kumagai et al., 2004), our data suggest that dry season intensification may further limit CO_2 and H_2O vapor exchange during the dry season.

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Figure captions

Fig. 1. Map of the Brazil with the location of the study area Fazenda Miranda (FM) located approximately 15 km SSE of Cuiaba, Mato Grosso, Brazil (inverted-black-diamond). Also shown are the Amazonia forest (black-circles) and pasture (white-circles) sites for which Jarvis-type models have been developed. Forest sites include Reserva Ducke (RD) and Cuieiras (CUE) near Manaus, Amazonas, Ji-Parana (JP), Rondonia, and Sinop (SIN), Mato Grosso, and pasture sites include Fazenda Nossa Senhora (FNS) near Ji-Parana, Rondonia, Fazenda Dimona (FD) near Manaus, Amazonas, and Fazenda Colosso (FC) near Manaus, Amazonas.

Fig. 2. Scalar functions for radiation (a), air temperature (b), vapor pressure deficit (c), and soil water content (d) that were optimized for this study and for other tropical ecosystems reported in the literature. Scalar functions were optimized from the eddy covariance estimates of canopy conductance using the Solver function of Microsoft Excel. See Table 1 for the optimized coefficient values.

Fig. 3. Scatterplots of the eddy covariance and modeled canopy conductance for 2011 (top-panels), 2012 (middle-panels), and 2013 (bottom panels) for data summarized as diel (0800-1600 h local time) averages (left-panels) or 15-day averages (right-panels). The modeled data were parameterized using data from 2012 and were tested using data from 2011 and 2013. The diagonal line in each panel corresponds to the 1:1 line. See Table 2 for the performance statistics.

Fig. 4. Average ($\pm$ sd) diel (0800-1600 h local time) time series of eddy covariance (closed-symbols, solid-lines) and modeled (open-symbols, solid-line) canopy conductance for 2011

(top-panel), 2012 (middle-panel), and 2013 (bottom-panel). The shaded area in each graph depicts the dry season, or the consecutive months when precipitation < 100 mm.

Fig. 5. (a) Time series of precipitation (closed-bars) and surface (20 cm) soil water content (open-circles), (b) air temperature (closed-circles) and vapor pressure deficit (open-circles), (c) net (closed-circles) and solar (open-circles) radiation, and (d) eddy covariance (closed-circles) and modeled (open-circles) canopy conductance for the 2011-13 study period. Data for precipitation are 15-day totals while data for all other variables are 15-day mean ($\pm$ sd) values. The shaded area in each graph depicts the dry season, or the consecutive months when precipitation < 100 mm.

Fig. 6. Simulated sensitivity of modeled canopy conductance to a maximum 10% increase (black-circles, solid-lines) or decrease (open-circles, dashed-line) in air temperature (top-panel), vapor pressure deficit (middle-panel), and soil water content (bottom panel) over 15-day intervals for 2011. The shaded area in each graph depicts the dry season, or the consecutive months when precipitation < 100 mm.

Table 1. Optimized coefficients used to parameterize the Jarvis-type model of canopy conductance (equations 3-6). Model coefficients for this study were optimized using the Solver function of MicroSoft Excel. Also shown are coefficients used to parameterize Jarvis-type models of canopy conductance from selected studies of Brazilian tropical ecosystems. Location IDs are from Fig. 1.

			mm/s	$\text{J m}^{-2} \text{s}^{-1}$	$^{\circ}\text{C}$	kPa	(m^3/m^3)	(m^3/m^3)
Data source	Location ID	Ecosystem type	g_c^{max}	a_1	a_2	a_3	a_4	a_5
This study	FM	Cerrado <i>campo sujo</i>	12.6	0.003	25.0	0.20	0.01	0.06
Harris et al. (2004)	CUE	Amazonian forest	52.6	1785	23.9	0.54	0.56	0.62
Dolman et al. (1991)	RD	Amazonian forest	20.8	250	30.2	0.64	—	—
Wright et al (1996)	JP	Amazonian forest	80.1	3916	43.1	1.25	—	—
Wright et al (1996)	FD	Pasture (LAI = 1.5)	27.1	2922	28.5	0.67	0.33	0.39
Wright et al (1996)	FNS	Pasture (LAI = 3.9)	44.0	38528	41.1	0.87	0.15	0.23
von Randow et al. (2012)	FC	Pasture (LAI = 0.8)	21.0	616	—	0.90	0.33	0.49
Vourlitis (unpublished)	SIN	Semi-deciduous forest	32.0	1586	22.2	0.43	0.05	0.42

Table 2. Performance statistics for the Jarvis-type model of canopy conductance for the two test years (2011 and 2013) using diel average and 15-day average data. Shown is the mean ($\pm 95\%$ confidence interval) slope, intercept, and coefficient of determination (R^2) value from an orthogonal regression, and Willmott's index of agreement (d), and the total, systematic (RMSEs), and unsystematic (RMSEu) root mean square error (RMSE) between the observed and modeled canopy conductance.

Variable	2011		2013	
	Diel average	15 day average	Diel average	15 day average
Slope	0.89 $\pm$ 0.06	0.88 $\pm$ 0.14	0.57 $\pm$ 0.05	0.66 $\pm$ 0.11
Intercept	1.08 $\pm$ 0.21	1.05 $\pm$ 0.50	2.58 $\pm$ 0.30	1.96 $\pm$ 0.59
R^2	0.81 $\pm$ 0.03	0.91 $\pm$ 0.04	0.66 $\pm$ 0.06	0.85 $\pm$ 0.08
Willmott's d	0.94	0.96	0.85	0.92
RMSEu	1.12	0.69	1.44	0.92
RMSEs	0.70	0.70	1.94	1.33
RMSE	1.32	0.99	2.42	1.61

Table 3. Mean ($\pm 95\%$ confidence interval (CI)) wet and dry season solar (R_s) and net (R_{net}) radiation, air temperature (T_a), vapor pressure deficit (VPD), precipitation (P), soil water content (W), **aerodynamic conductance (g_a)**, and eddy covariance (g_c^{obs}) and Jarvis-type model (g_c^{mod}) canopy conductance for the Cerrado ecosystem. Bold values are significantly different between seasons. For g_c^{obs} and g_c^{mod} , values with the same lower cased letter are not significantly different within a given season based on the lack of overlap of the $\pm 95\%$ CIs.

Variable	Units	2011		2012		2013	
		Wet	Dry	Wet	Dry	Wet	Dry
R_s	W/m ²	209 $\pm$ 23	201 $\pm$ 7	199 $\pm$ 13	192 $\pm$ 10.9	195 $\pm$ 18	193 $\pm$ 11
R_{net}	W/m ²	132$\pm$14	107$\pm$9	135$\pm$12	98$\pm$15	135 $\pm$ 16	112 $\pm$ 7
T_a	°C	27.0 $\pm$ 0.7	25.7 $\pm$ 1.1	26.2 $\pm$ 0.7	26.3 $\pm$ 1.5	27.4$\pm$0.6	25.6$\pm$1.0
VPD	kPa	1.1 $\pm$ 0.3	1.6 $\pm$ 0.3	0.9$\pm$0.5	1.8$\pm$0.1	0.8$\pm$0.1	1.3$\pm$0.2
P	mm/d	5.4$\pm$2.9	0.8$\pm$0.6	3.8$\pm$1.3	0.7$\pm$0.5	6.1$\pm$3.1	0.8$\pm$0.4
W	%/vol.	5.7$\pm$1.3	3.7$\pm$0.6	5.3$\pm$0.5	3.3$\pm$0.3	6.5$\pm$0.8	4.1$\pm$0.4
g_a^{obs}	mm/s	70.5 $\pm$ 12.4	57.7 $\pm$ 8.0	55.7 $\pm$ 4.2	47.6 $\pm$ 6.9	61.2$\pm$3.7	55.2$\pm$1.9
g_c^{obs}	mm/s	7.4 $\pm$ 1.2 ^a	2.8 $\pm$ 0.8 ^a	7.7 $\pm$ 0.9 ^a	2.5 $\pm$ 0.7 ^a	9.6 $\pm$ 0.9 ^a	5.1 $\pm$ 1.4 ^a
g_c^{mod}	mm/s	6.9 $\pm$ 1.8 ^a	3.7 $\pm$ 0.8 ^a	7.3 $\pm$ 0.7 ^a	3.4 $\pm$ 0.9 ^a	8.8 $\pm$ 0.7 ^a	5.1 $\pm$ 0.8 ^a

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6