

Is the maximum velocity of carboxylation ($V_{c_{max}}$) well adjusted for deciduous shrubs in DGVMs? A case study for the Caatinga biome in Brazil

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Abstract $V_{c_{max}}$ is the rate of maximum velocity of carboxylation of plants and is considered one of the most critical parameters for changes in vegetation in face of global changes and it has a direct impact on gross primary productivity. Physiological processes are considered the main sources of uncertainties in dynamic global vegetation models (DGVMs). The Caatinga biome, in the semiarid region of northeastern Brazil, is extremely important due to its biodiversity and endemism. In a field work realized in an area of preserved Caatinga forest, measurements of carbon assimilation (in response to light and CO_2) were performed on 11 individuals of a native species. These results of $V_{c_{max}}$ measurements in Caatinga were compared with parameterization of models, revealing that $V_{c_{max}}$ is not well adjusted in several DGVMs. Also, the values obtained in the Caatinga field experiments were very close to empirical values obtained in the Northern hemisphere (Austria). These ecophysiological measurements can contribute in understanding of this biome.

Keywords Semiarid · Dynamic global vegetation models (DGVMs) · $V_{c_{max}}$ · Plant functional types

Introduction

The carboxylation velocity ($V_{c_{max}}$) parameter is considered one of the most critical for dynamic global vegetation models (DGVMs) in face of global changes. $V_{c_{max}}$ is the measurement of the process by which Rubisco catalyzes RuBP with CO_2 to produce the carbon compounds that eventually become triose phosphates (e.g. glyceraldehyde-3P), which are the building block for sugars and starches. $V_{c_{max}}$ has a direct impact on gross primary productivity (GPP) and is a key parameter in terrestrial biosphere models (Bonan et al. 2012; LeBauer et al. 2013; Rogers 2014; Dietze 2014; Kauwe et al. 2015). Several uncertainties have been observed in the results of DGVM simulations and they tend to underestimate maximum GPP

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(Bonan et al. 2012; Dietze 2014). There is a wide variation in $V_{c_{max}}$ values used in models with identical plant functional types (PFTs). DGVMs are used to represent the CO_2 uptake of the same biomes, which is critical due to the role of $V_{c_{max}}$ in the carbon cycle (Rogers 2014). This variation between models can be attributed to the lack of data used for proper $V_{c_{max}}$ calibration and the fact that canopy level $V_{c_{max}}$ values are used, which are lower than those observed at the leaf level (Schaefer et al. 2012; Dietze 2014). This discrepancy between leaf and canopy $V_{c_{max}}$ levels is because measurements of leaf level nitrogen content, which determines $V_{c_{max}}$, are relatively easy, however models require canopy-level nitrogen content, which is much more difficult to obtain (Schaefer et al. 2012). One methodology for $V_{c_{max}}$ estimation is to use canopy scale eddy covariance flux measurements, this approach is not effective when extrapolated to larger scales (Ziehn et al. 2011; Bonan et al. 2012). Rogers (2014) noted a wide variation in $V_{c_{max}}$ used in models that had identical PFTs and they sought to represent the CO_2 uptake of the same biomes. The source of some values of $V_{c_{max}}$ used in models is not clear (Rogers 2014). Another critical point is the use of static parameters, which implies that DGVMs cannot adjust to environmental changes (Smith and Dukes 2012). Physiological processes are considered the main sources of uncertainties in these models. However, it is expected that a plant physiology database will enable the calibration and correction of the models and thus reduce substantially these uncertainties in the next generation of DGVMs (LeBauer et al. 2013; Huntingford et al. 2013; Rogers 2014; Dietze 2014; Rezende et al. 2015).

The Caatinga biome, in the semiarid region in Northeastern Brazil, covers 844,453 km² (MMA 2014) (Fig. 1). The Brazilian semiarid is one of the most populated areas in the world and also concentrates the poorest population of the country (Santos et al. 2014). A great portion of the population living in this region relies on agro pastoral activities and natural resources for subsistence. These activities are highly dependent on rainfall, and suffer setbacks due to adverse weather and recurrent drought cycles. Due to the scarcity of water, much of the soil presents low fertility, particularly regarding the levels of nitrogen, phosphorus and calcium. Currently, more than 10 % of the semiarid area has suffered a very high degree of environmental degradation, being susceptible to desertification (Oyama and Nobre 2004; Cunha et al. 2013; Santos et al. 2014). The Caatinga is an exclusively Brazilian biome and is extremely important due to a high biological diversity and the presence of many endemic species (MMA 2010). The Caatinga is a relatively poorly studied biome, compared to the other Brazilian biomes, despite the fact that it covers nearly 11 % of the Brazilian territory. In 2012 and 2013 this region experienced one of the most severe drought events in the last 50 years (Santos et al. 2014).

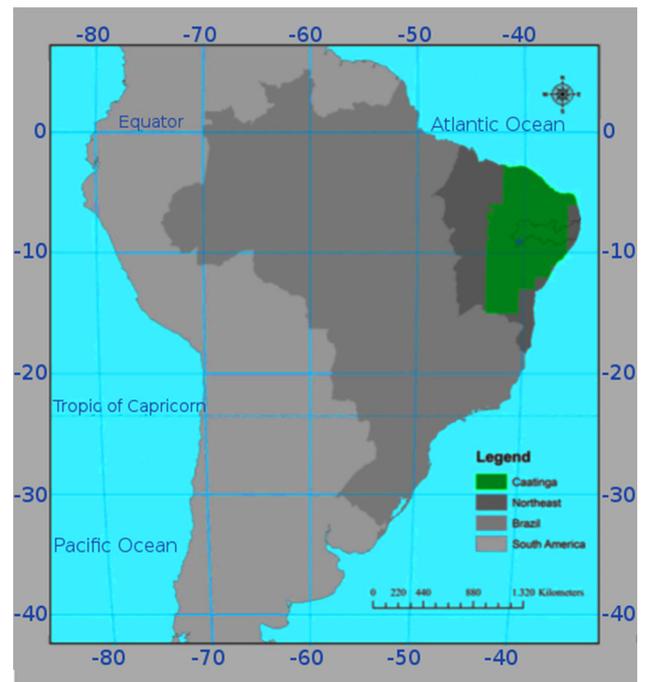


Fig. 1 Map of the Caatinga region in the northeastern Brazil. (*) Spatial localization of the Petrolina PE site is shown (adapted from Santos et al. 2014)

Materials and methods

Field measurements

The field work was conducted in a 600 ha area of preserved Caatinga forest, located in the headquarters of Embrapa Tropical Semiarid in Petrolina, Pernambuco, during the rainy seasons of February 2013 and 2014, with the purpose of performing CO_2 measurements. The Caatinga vegetation in this region is classified as Savannah Steppe trees and shrubs. This type of Caatinga vegetation represents 75.72 % of the total area of the Caatinga biome (PROBIO 2007). The soil of the experimental area is classified as Argisol, which is characterized by low water retention and poor fertility. Caatinga is characterized by low annual precipitation and prolonged drought periods (6–8 months each year). The rainy season in Petrolina is from December to April and the dry season is from May to October. In a data series from CPTEC-INPE covering 14 years (1997–2011), the monthly mean maximum temperatures reach their highest in November (~ 34 °C) and the average monthly minimum temperatures reach their lowest values in July (~ 20 °C). The average monthly rainfall for this period shows that February is the month of highest rainfall (~ 88 mm); and August is the month of lowest rainfall (~ 1 mm). The species selected was *Poincianella microphylla* (Mart. ex G. Don) L. P. Queiroz because it has a high occurrence in the Caatinga and it belongs to the

Fabaceae family, which represents 50.63 % of the species in the area (Drummond et al. 2002). Eleven individuals of this species were selected and geo-referenced using a global positioning system (GPS). Physiological measurements were made using a LI-6400 photosynthesis and fluorescence analyzer (Li-Cor, Nebraska, USA) and were performed on fully expanded and sun-exposed leaves (one leaf per plant), directly on the standing plants. Leaf temperature and chamber relative humidity were not controlled and they varied according to environmental conditions. The time of measurements was between 7:00 AM and 3:00 PM local time. The values for light response curves ($A \times \text{Photosynthetic Active Radiation} - \text{PAR}$) were between 0 and $800 \mu\text{mol m}^{-2} \text{s}^{-1}$, performed under Light Emitting Diode (LED) source light with blue = 10 % and CO_2 concentration fixed at $400 \mu\text{mol mol}^{-1}$. Some tests were performed for $A \times \text{PAR}$ curves and we concluded that plants saturate net photosynthesis in values close to $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ (instead of $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ which is the most common saturating light intensity for C_3 species) (Rezende et al. 2016). We understand that even with a high amount of available light, water limitation makes this species adopt a more conservative strategy and not cope well with high radiation, especially in periods when soil moisture is not abundant. The equations used to calculate CO_2 assimilation (A), stomatal conductance (g_s) and intercellular concentration (C_i) followed von Caemmerer and Farquhar (1981). Applying the non-rectangular hyperbola model (Long and Hällgren 1993) $A \times \text{PAR}$ curves were produced in order to identify the plants' photosynthetic saturation point.

The curves of photosynthetic response to CO_2 intercellular concentration ($A \times C_i$) were performed under LED source light (red–blue, 10 % blue) set to a PAR of $800 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. CO_2 curves were initiated with a CO_2 air concentration from 50 until $1200 \mu\text{mol mol}^{-1}$. Carbon assimilation was estimated according to the models of Farquhar et al. (1980), von Caemmerer and Farquhar (1981), Farquhar and von Caemmerer (1982) and von Caemmerer (2000) and is expressed as a minimum of the principal limitations in the plant capacity to fix carbon: light-limited and Rubisco-limited photosynthesis rates. The triose phosphate limitation was not considered.

Comparison of $V_{c_{\max}}$ values

We compared empirical measurements of $V_{c_{\max}}$ for deciduous shrubs with values parameterized in deciduous shrub PFTs used in DGVMs. These sources were: (1) data observed for shrubs located in Austria and New Zealand (Bonan et al. 2012; Kattge et al. 2009; Kattge and Knorr 2007); (2) data for shrubs obtained in campaigns in the

Brazilian semiarid biome, published here in this article and partially by Rezende et al. (2016); (3) values of $V_{c_{\max}}$ defined in the models. All $V_{c_{\max}}$ values (from models and observed) were normalized to 25°C (Bernacchi et al. 2001). The values used in the models were compiled by Rogers (2014). The models used for comparison were BETHY (Knorr 2000; Ziehn et al. 2011), BIOME-BGC (Running et al. 2010), CLM (Oleson et al. 2013), HYBRID (Friend 2010), INLAND (Tourigny 2014) and JULES (Mercado et al. 2007; Best et al. 2011; Clark et al. 2011).

Results

$V_{c_{\max}}$ measurements

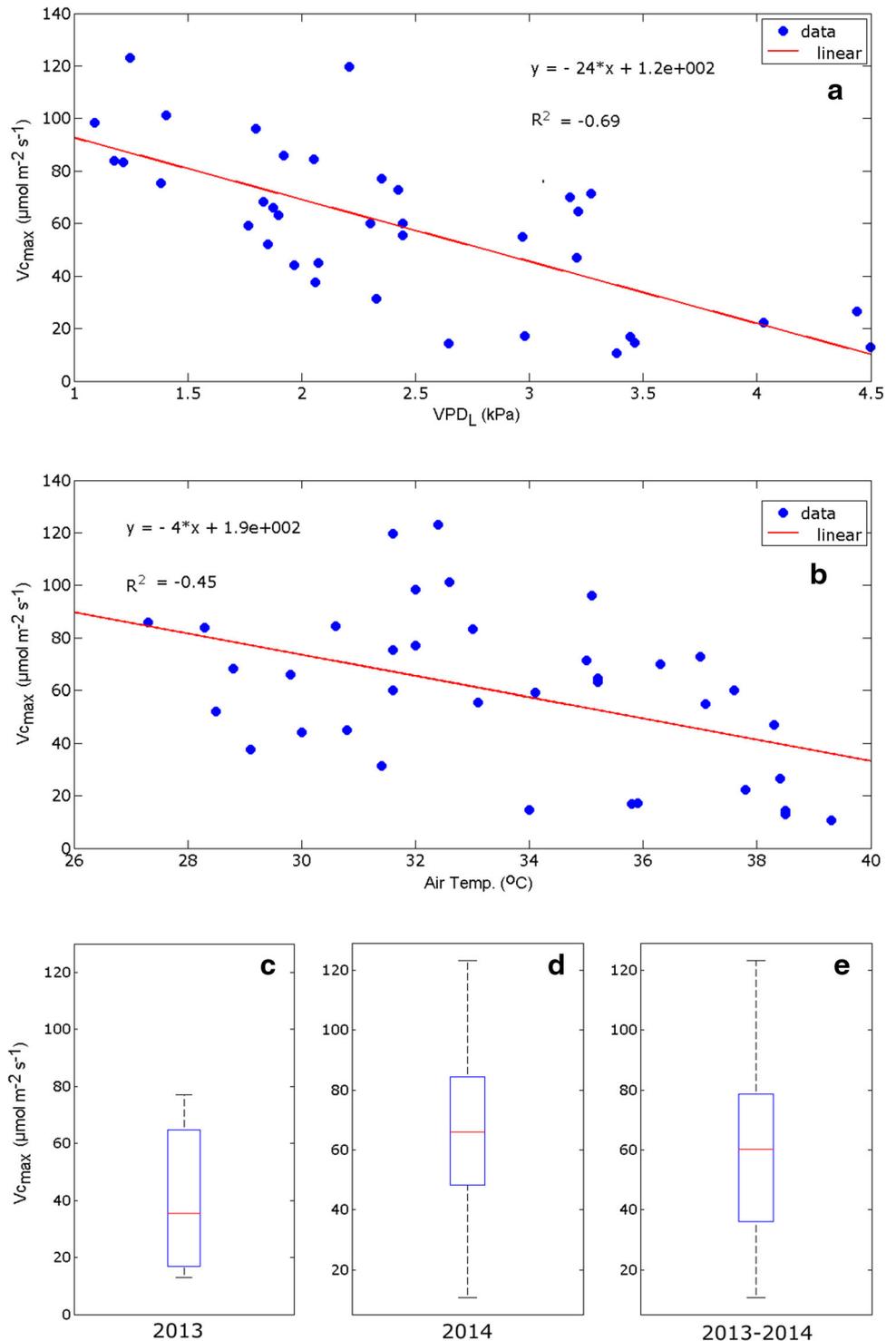
The measurements of vapor pressure deficit at leaf level (VPD_L), air temperature (Air Temp) and maximum velocity of carboxylation ($V_{c_{\max}}$) estimation obtained in the field campaigns of 2013 and 2014 are shown in Fig. 2a, b. It is observed that for a VPD_L above 2 kPa, $V_{c_{\max}}$ values are lower (Fig. 2a). The $V_{c_{\max}}$ values above $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ occurred with VPD_L below 2.5 kPa. On the other hand, highest values were reached in a range of temperature between 31 and 35°C (Fig. 2b). In the box plots shown in Fig. 2c–e, it was observed that $V_{c_{\max}}$ values were higher in the 2014 campaign than in the 2013 one. The $V_{c_{\max}}$ median in the 2013 campaign was $\sim 38 \mu\text{mol m}^{-2} \text{s}^{-1}$, for the 2014 campaign it was $\sim 67 \mu\text{mol m}^{-2} \text{s}^{-1}$ and the median of both campaigns was $\sim 60 \mu\text{mol m}^{-2} \text{s}^{-1}$. This difference between the two campaigns is attributed to differences in soil moisture, impacting photosynthetic activity. During the days of the 2014 campaign rainfall events occurred in the measurement site (~ 43 mm), while during the 2013 campaign there were rainfall events only 30 days (102 mm) prior the realization of field measurements. Environmental variables (soil moisture, DPVL, air temperature) do not directly influence $V_{c_{\max}}$, but they influence photosynthetic production. Still, photosynthesis and $V_{c_{\max}}$ have positive correlation. The sensitivity of $V_{c_{\max}}$ to environmental variables can be observed in Fig. 2a–e.

Comparison of $V_{c_{\max}}$ values (empirical data and models)

Figure 3 shows that data observed for deciduous shrubs by Bonan et al. (2011) were similar the values obtained in this study (a mean value of $58 \mu\text{mol m}^{-2} \text{s}^{-1}$ for shrubs in Austria and a mean value of $59 \mu\text{mol m}^{-2} \text{s}^{-1}$ in Caatinga, respectively).

Moreover, the values used in BETHY and INLAND models are relatively close (65 and $69 \mu\text{mol m}^{-2} \text{s}^{-1}$,

Fig. 2 Data of *P. microphylla* obtained in the 2013 and 2014 campaigns in Petrolina-PE— **a** vapor pressure deficit at leaf level (VPD_L) and maximum velocity of carboxylation ($V_{c_{max}}$); **b** air temperature (Air Temp) and maximum velocity of carboxylation ($V_{c_{max}}$); **c** box plot of $V_{c_{max}}$ measurements in 2013; **d** box plot of $V_{c_{max}}$ measurements in 2014; **e** box plot of $V_{c_{max}}$ measurements in 2013 and 2014. $V_{c_{max}}$ measurements were normalized to 25 °C (Bernacchi et al. 2001)



respectively). The values used in JULES and HYBRID are also very close to each other (48 and 51 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively). The values of $V_{c_{max}}$ defined for BIOME-BCG and CLM (34 and 31 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively) are lower than half of the largest $V_{c_{max}}$ values used in other models (e.g. INLAND at 69 $\mu\text{mol m}^{-2} \text{s}^{-1}$).

Conclusions

In light of this study, a discrepancy in the values of $V_{c_{max}}$ used in the models was observed, confirming available literature. This discrepancy was also observed for deciduous shrubs PFT. In some models (INLAND and BETHY) values

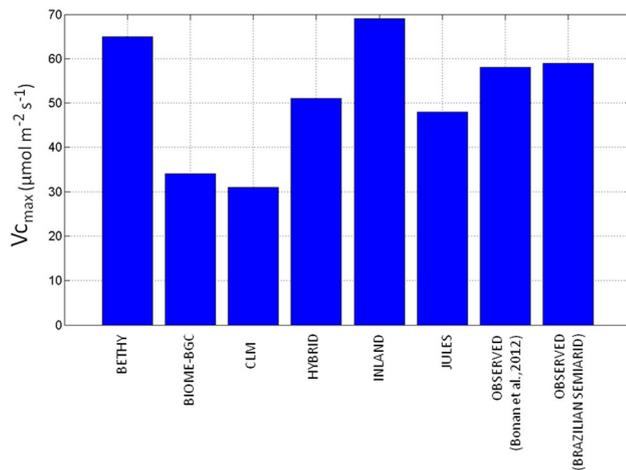


Fig. 3 Comparison of $V_{c_{max}}$ values of the deciduous shrubs PFT used in various models and data observed in Austria (Bonan et al. 2011) and in the Caatinga biome (all values obtained in the campaigns in Petrolina-PE of the present study)

of $V_{c_{max}}$ are overestimated and are higher than values observed in Austria and Caatinga. The closeness of average values for Austria and for the Caatinga may be only coincidence. This needs to be confirmed with data from other campaigns. Only two models (BIOME-BGC and CLM) use $V_{c_{max}}$ that are underestimated in comparison to observed data. This finding accentuates the need to have more empirical data for more accurate model calibration. The Caatinga biome is poorly studied and these ecophysiological measurements obtained in the field are novel and can contribute to a better understanding of this biome.

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