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Hysteresis response of daytime net ecosystem CO₂ exchange during a drought

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Abstract

Continuous measurements of net ecosystem CO₂ exchange (NEE) using the eddycovariance method were made over an agricultural ecosystem in the southeastern US. During optimum environmental conditions, photosynthetically active radiation (PAR) was the primary climatic factor controlling daytime NEE, accounting for 67 to 89% 5 of variations in NEE. However, soil water content (SWC) was the dominant factor limiting the NEE-PAR response during the peak growth stage, as NEE was significantly depressed when PAR exceeding 1300 μ mol photons m⁻² s⁻¹ coincided with a verv low soil water content (SWC<0.04 m³ m⁻³). Hysteresis was observed between daytime NEE and PAR during periods of water-stress resulting from high vapor pressure deficit 10 (VPD). This is significant since it limits the range of applicability of the Michaelis-Menten equation, and the likes, to determine daytime NEE as a function of PAR. The systematic presence of hysteresis in the response of NEE to PAR suggests that the gap-filling technique based on a non-linear regression approach should take into account the presence of water-limiting field conditions. Including this step is therefore likely to im-15 prove current evaluations of ecosystem response to climate change.

1 Introduction

Concerns over global climate change have generated an effort to understand how environmental changes, such as those seen in temperature and precipitation, influence
 net carbon exchange between ecosystem and the atmosphere. The increased temperature and lower precipitation predicted in many regions of the world, is expected to adversely affect crop growth and water availability, critically influencing the patterns of future agricultural production. In light of these likely changes in regional precipitation and resulting soil moisture amounts, an understanding of how climate variability, particularly reductions in precipitation, influences carbon exchange in the present ecosystem is a sine gua non condition to anticipate possible impacts of various climate change

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scenarios. This also provides the modeling community with a better basis to improve and validate their models.

Net ecosystem exchange of CO₂ (hereafter referred to as NEE) relies on the balance between CO₂ uptake through plant photosynthesis and CO₂ emission through
plant and soil respiration generally referred to as ecosystem respiration. The NEE can be measured directly using eddy-covariance methods (hereafter referred to as EC) (Aubinet et al., 2000; Baldocchi et al., 2001), which provide a spatially integrated carbon exchange on a continuous basis with minimal disturbance to the crop. With these continuous measurements, the derivation of annual sums of NEE or the integration over a vegetation period then becomes possible. However, due to a combination of the inherent limitations in the applicability of the measurement method and related data

robustness, data rejection and missing data are unavoidable leading to typically 65– 75% data coverage across the seasons (Baldocchi et al., 2001; Falge et al., 2001; Law et al., 2002). The large resulting gaps in the dataset must be reconstructed in order to obtain the seasonal carbon balance. Particularly, gap-filling techniques are based on

a wide range of standard procedures, including linear interpolation (Falge et al., 2001), look-up table (Falge et al., 2001), moving averages (Falge et al., 2001; Reichstein et al., 2005), non-linear regression (Goulden, 1996; Falge et al., 2001; Suyker and Verma, 2001), artificial neural networks (Papale et al., 2006; Papale and Valentini, 2003), and 20 multiple imputation method (Hui et al., 2004).

However, the traditional standard method to fill the gap in NEE data in daytime conditions has been to resort to the use of non-linear regression. This approach is based on parameterized non-linear equations (e.g. Michaelis-Menten equation) to quantify the relationship between NEE and light. While the failure using non-linear equation to de-

scribe daytime NEE only as a function of light has been previously observed in various ecosystems (Holst et al., 2008; Wang et al., 2008; Li et al., 2005; Serrano-Ortiz et al., 2007), to date a mechanistic explanation of this failure is still missing.

Peanut (Arachis hypogaea L.) is a major crop grown under both rainfed and irrigated conditions in the southeastern US. Typically, peanut plants have to cope with 6, 10707-10735, 2009

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unfavorable environmental factors such as high temperature, low soil moisture, and high vapor pressure deficit (hereafter referred to as VPD), often resulting in drought stress. Drought affects nearly all aspects of plant growth and most physiological processes; however, the stress response depends on the intensity, rate, and duration of exposure and the stage of crop growth. Inconsistent effects of these environmental stresses on physiological depression have been reported in previous studies (e.g. Bhagsari et al., 1976; Nautiyal et al., 1995; Lauriano et al., 2004; review by Reddy et al., 2003). Drought stress also alters the development of leaf area and changes the plant physiology. As the cumulative deficit in soil water grows, plants close their

- ¹⁰ stomates, decreasing their stomatal conductance to diminish water loss through transpiration (Reddy et al., 2003). As a consequence, the CO_2 assimilation is also reduced. The decrease in conductance of the mesophyll cells due to water deficit has generally been attributed to the limitation of CO_2 assimilation in addition to the reduction in photosynthesis (Bhagsari et al., 1976). The long-term effect of soil water deficit on canopy assimilation is a reduction in leaf area. Drought reduces leaf area by folding, wilting,
- assimilation is a reduction in leaf area. Drought reduces leaf area by folding, withing, slowing leaf expansion, and shutting off the supply of carbohydrates (Reddy et al., 2003; Clifford et al., 1993; Collino et al., 2001). The consequent reduction in leaf area determines a decrease in the crop's ability to capture light resources (Chapman et al., 1993b; Collino et al., 2001), resulting in a negative influence on both crop productivity and dry matter production.

Measurements made in most the above studies were conducted at the leaf scale (Nautiyal et al., 1995; Bhagsari et al., 1976; Lauriano et al., 2004). There is still a lack of information on a continuous basis of the effects of drought stress on carbon exchange at the canopy scale. To this end, the EC flux measurements were carried out in a rainfed peanut field. The objectives of the present study are to 1. examine the in-

In a rainfed peanut field. The objectives of the present study are to 1. examine the influence of drought stress on daytime NEE and 2. to explain the inadequacies of using the Michaelis-Menten equation to describe the NEE-PAR relationship.

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2 Materials and methods

2.1 Site description

The experiment was conducted in a non-irrigated peanut field located in Unadilla, Georgia, USA (32° 10′ 39.72″ N, 83° 38′ 24.48″ W) in 2007. The top 10 cm of soil is classified as sandy loam, composed of 74% of sand, 16% of silt, and 10% of clay with a bulk density of 1.19 gcm⁻³. The field capacity was 0.118 m³m⁻³ and the permanent wilting point was 0.042 m³m⁻³. Total carbon and nitrogen content of soil were 0.43% and 0.03%, respectively. Fertilizer (N:P:K) with 336 kgha⁻¹ was applied on day of year (hereafter referred to as DOY) 93. Peanut was planted with 6.6 kgha⁻¹ of phorate on DOY 125. Herbicides included of Gramoxone (1.75 Lha⁻¹), Storm (1.17 Lha⁻¹), and 2, 4-DB (0.44 Lha⁻¹) were applied on DOY 157. Leaf spot and white mold were controlled using Bravo Ultrex (on DOY 197, DOY 232, and DOY 253) and Headline 2.09EC (on DOY 176 and DOY 211). Peanut was harvested on DOY 283 with the yield of 4783 kgha⁻¹.

15 2.2 Experimental measurements and data processing

Fluxes of carbon dioxide, water vapor, heat and momentum were continuously measured using the EC method from DOY 172 to DOY 271. The flux system was mounted at 1.5 m above the ground and consisted of a fast response omnidirectional sonic anemometer (CSAT3, Campbell Scientific, Logan, UT) and a fast response open-path
CO₂/H₂O infrared gas analyzer (Li 7500, Li-Cor Inc., Lincoln, NE). The three wind components, sonic virtual temperature, water vapor, and CO₂ density were sampled at rate of 10 Hz. Half-hourly fluxes were calculated on-line and collected by CR1000 dataloggers (Campbell Scientific, Logan, UT). All raw 10 Hz data were saved to a compact flash card (Sandisk, Sunnyvale, CA) for later reprocessing. The eddy-covariance flux system was powered by two 12 VDC deep cycle batteries that were charged using 120 W solar panels. The EC tower was located approximately in the centre of the field,

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with a minimum fetch of 210 m in all directions.

The raw 10 Hz data from sonic anemometer and infrared gas analyzer were checked for spiking before calculating eddy-covariance fluxes, in a manner analogous to the method described in Vickers and Mahrt (1997). Each individual data point of the three ⁵ velocity components from the sonic anemometer were also rotated according to a planar fit rotation to align the sonic anemometer axis along the long-term streamlines (Wilczak et al., 2001). Before half-hourly fluxes of CO₂ (NEE), latent heat (λE : where λ is the latent heat of evaporation and *E* is the evapotranspiration), and sensible heat (*H*) were calculated, the time series were linearly detrended. Finally, the flux data were then corrected for variations in air density due to fluctuations in water vapor and heat fluxes in accordance with Webb et al. (1980). The records collected during wet half

- hours and up to 1 h after rain events were rejected because of the poor performance of the open path gas analyzer in wet weather. The analyses were conducted using a C++ program written in-house.
- ¹⁵ It is recognized by the flux monitoring community that the EC technique is likely to underestimate eddy fluxes under calm conditions at night, but there is no consensus as to how best to correct the problem. Most of the researchers screen nighttime data on the basis of a friction velocity (u_*) threshold (Goulden et al., 1997; Aubinet et al., 2000; Reichstein et al., 2005; Papale et al., 2006). The determination of the u_* threshold was applied using the online calculation in http://gaia.agraria.unitus.it/database/eddyproc. The estimation of u_* threshold values followed the method used by Reichstein et al. (2005). Gaps in solar radiation, temperature, and precipitation data were filled with
- data from a nearby meteorological station located approximately 8 km from the study site. DDuring calm nights 78.68% of the carbon flux data was rejected so nighttime flux data are not presented in this study.

Along with the EC tower, standard meteorological and soil parameters were measured continuously with an array of sensors. Net radiation was measured using a net radiometer (Model NR-LITE, Kipp and Zonen USA Inc., Bohemia, NY) mounted on the EC tower, 1.8 m above the ground surface. Canopy temperature was measured

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at canopy height using a precision infrared thermocouple sensor at an accuracy of ±0.4°C (IRTS-P5, Apogee Instrument Inc., Logan, UT). Belowground measurements was made at the base of tower, include soil temperature, and volumetric soil water content profiles. Soil temperature at depths of 0.02, 0.05, 0.08, and 0.30 m was measured using a custom-built chromel-constantan thermocouple. Soil volumetric water content 5 was measured using time domain reflectometry sensor (CS615, Campbell. Scientific, Logan, UT) at depths of 0.02 and 0.02 to 0.05 m. All channels from meteorological and belowground measurements data were averaged over 30-min periods and stored to dataloggers (CR10X, Campbell. Scientific, Logan, UT). The automatic weather station (ET106, Campbell Scientific, Logan, UT) with 30-min average data output was installed 10 at 2 m above the ground surface at the study site to measure air temperature, relative humidity, wind speed and wind direction, solar radiation, and precipitation. The station was powered by a 7 Ah sealed-rechargeable battery that was charged with a 1000 W solar panel. In addition, the leaf area index (hereafter referred to as LAI) was determined at intervals of 7 to 10 d with an electronic leaf area meter (LAI-2000, Li-COR Inc., 15 Lincoln, NE) throughout the season. The canopy temperature sensor was replaced on

DOY 180. Incident photosynthetically active radiation (hereafter referred to as PAR) was estimated from solar radiation: PAR (μ molphotonsm⁻²s⁻¹)=2.16×solar radiation (Wm⁻²) (Weiss and Norman, 1985).

20 2.3 Data analysis

In daytime, defined in this paper as the daily period with solar radiation >20 Wm⁻², half-hourly data were fitted using a Michaelis-Menten equation (Michaelis and Menten, 1913) to test the ability of the following model to describe the dependence of NEE (μ molCO₂m⁻²s⁻¹) on solar PAR (μ molphotonsm⁻²s⁻¹):

²⁵ NEE =
$$\frac{\alpha.PAR.NEE_{sat}}{\alpha.PAR + NEE_{sat}} + R_{e}$$
, (1)

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where α is the apparent quantum yield or the initial slope of the light response curve (μ molCO₂ μ mol⁻¹photons), NEE_{sat} is the saturation value of NEE at an infinite light level, and R_e is the ecosystem respiration in daytime conditions.

The stomatal conductance or canopy conductance was used to assess stomatal control on CO_2 gas exchange and evapotranspiration. With no independent measurements of transpiration or soil evaporation available in this study, a clean separation of the two components is not possible with the eddy-covariance measurements. Therefore, half-hourly surface conductance (hereafter referred to as g_s) was calculated by rearranging the Penman-Monteith equation (Monteith and Unsworth, 1990):

10
$$\frac{1}{g_s} = \left[\left(\frac{\Delta}{\gamma} \right) \beta - 1 \right] \left(\frac{1}{g_a} \right) + \frac{\rho C_{\rho} \text{VPD}}{\gamma \lambda E},$$

where Δ is the rate of change of saturation vapor pressure with temperature, γ the psychometric constant, β the Bowen ratio which is $H/\lambda E$, ρ and C_{ρ} the density and specific heat of air, respectively, VPD the vapor pressure deficit which is calculated from air temperature and relative humidity data, and g_a the air conductance was obtained from sonic anemometer output as (Monteith and Unsworth, 1990):

$$\frac{1}{g_a} = \frac{u}{u_*^2} + 6.2u_*^{-0.67}$$

where u is the mean wind speed.

3 Results and discussion

3.1 Seasonal variation in environmental conditions and leaf area index

²⁰ Over the study period, the seasonal trends of soil and canopy temperature followed a pattern similar to that of air temperature (hereafter referred to as T_a). Daily average of soil, canopy and, air temperature varied from 21.7 to 31.7°C, 20.6 to 33.7°C, and

(2)

(3)

19.4 to 31.2°C, respectively. Canopy temperature was slightly higher than soil temperature and air temperature, however, maximum values were observed on DOY 222 (Fig. 1a). Total rainfall at the study site was 328 mm (Fig. 1b). Soil water content (hereafter referred to as SWC) followed patterns of precipitation. Maximum daily average SWC $(0.135 \text{ m}^3 \text{m}^{-3})$ across the upper soil layer (0.02-0.05 m) occurred on DOY 184. In particular, there was a gradual decrease in soil water content below wilting point (0.042 m³m⁻³) on DOY 217–228 and DOY 250–255, suggesting that peanut plants may have experienced water-stress during those periods (Fig. 1b). LAI rapidly increased during crop development reaching the maximum value of 7.81 $m^2 m^{-2}$ around DOY 210. While the minimum LAI of $2.92 \text{ m}^2 \text{m}^{-2}$ was found during the water-stress period (DOY 217-228), the corresponding LAI reduction is due to either by droughtinduced limitation of leaf area expansion or by temporary leaf wilting or rolling during periods of severe stress (Chapman et al., 1993a; Clifford et al., 1993). With 52 mm of total precipitation on DOY 235, LAI subsequently recovers reaching the values of $5.06 \,\mathrm{m^2 m^{-2}}$ to then steadily decline throughout the end of study period as the plant senesces (Fig. 2).

3.2 Responses of daytime NEE to PAR

PAR is the main climatic factor that drives photosynthesis processes. To examine how NEE responds to change in PAR, we use a rectangular hyperbolic Michaelis-Menten
²⁰ function (Eq. 1) to describe the responses of NEE averaged over 30-min period (Fig. 3). In general, the peanut is a fast-growing crop and therefore the functional response of NEE to PAR was considered with respect to the growing stage (Table 1). During the study, the rectangular hyperbolic function was used successfully to describe the relationship between NEE and PAR. Other than during DOY 219–226 and DOY 227–234, days during which both temperature (32±4.1 and 31.5±4.1°C, respectively) and VPD

 $(20.0\pm11.8 \text{ and } 20.6\pm11.9 \text{ hPa}, \text{ respectively})$ were high and SWC $(0.037\pm0.002 \text{ and } 0.048\pm0.020 \text{ m}^3 \text{m}^{-3}$, respectively) was very low (Table 1), the Michaelis-Menten func-



tion failed to describe NEE-PAR relationship. It is worth noting the large scatter of the data points during these periods (Fig. 3c), highlighting the dependence of NEE-PAR relationship on other environmental factors, as discussed later. Based on the statistical analysis using Eq. (1), the regression coefficients indicated that change in PAR accounted for 67 to 89% of the variations in NEE. The α values varied from -0.0183 to $-0.0438 \,\mu$ molCO₂ μ mol⁻¹ photons. This value was well within the range of α reported for crops and grasslands (-0.008 to $-0.465 \,\mu$ molCO₂ μ mol⁻¹ photons; Ruimy et al., 1995; Suyker et al., 2004; Suyker and Verma, 2001; Valentini et al., 1995). The low α at the end of the study period was most likely due to the crop being in the senescent phase.

In order to further examine the dependence of the NEE-PAR response on T_a , VPD, and SWC, daytime NEE obtained during the peak growing stage (DOY 201–240) were separate into three T_a classes ($T_a < 28^{\circ}$ C, $28 < T_a < 32^{\circ}$ C, and $T_a > 32^{\circ}$ C), three VPD classes (VPD<10 hPa, 10 < VPD < 20 hPa, and VPD>20 hPa), and three SWC classes (SWC<0.04 m³m⁻³, 0.04 < SWC < 0.07 m³m⁻³, and SWC> $0.07 \text{ m}^3 \text{m}^{-3}$) (Fig. 4a–c). Within each group, the NEE data were further subdivided by PAR into $200 \,\mu \text{molCO}_2 \,\mu \text{mol}^{-1}$ photons increments ranging from 0 to $2200 \,\mu \text{molCO}_2 \,\mu \text{mol}^{-1}$ photons and then were bin averaged for each PAR subgroup. Regardless of T_a , NEE increases as PAR increased for all temperature conditions 20 (Fig. 4a). These results are in general agreement with previous findings demonstrating

²⁰ (fig. 4a). These results are in general agreement with previous infullings demonstrating that peanuts perform well in the temperature range between 24 to 33°C (Saxena et al., 1983). However, at high temperature range (T_a >32°C), NEE was lower than the other two temperature ranges. Similar to T_a , NEE increased with PAR increased at all VPD ranges (Fig. 4b). NEE-PAR response curves at VPD<10 hPa and 10<VPD<20 hPa mostly overlapped each other, indicating that there were no significant effects on NEE-PAR relationships between these two VPD ranges. When peanut was subjected to high VPD (>20 hPa), NEE was lower than the other two VPD conditions. Unlike T_a and VPD, there were pronounced differences in the light-response curves among different soil water regimes (Fig. 4c). When SWC was not limiting (SWC>0.04 m³ m⁻³),

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NEE increased with PAR and there was no indication of canopy light saturation. For very low SWC (<0.04 m³ m⁻³), NEE increased with PAR at first and then decreased considerably (NEE gets more positive resulted from ecosystem loss carbon to the atmosphere) when PAR exceeded 1300 μmolphotonsm⁻²s⁻¹. A reduction in NEE in dry
⁵ conditions has been observed in different ecosystems (Fu et al., 2006; Hastings et al., 2005; Holst et al., 2008; Wang et al., 2008; Li et al., 2005; Aires et al., 2008; Sims and Bradford, 2001) and caused by midday stomata closure when irradiance, temperature, and VPD are all high and when SWC is low (Aires et al., 2008; Sims and Bradford, 2001; Li et al., 2005) and by enhanced ecosystem respiration at high temperature (Fu et al., 2006; Holst et al., 2008).

3.3 Response of daytime NEE to water-stress

As discussed above, carbon uptake in this ecosystem is the result of several factors, including PAR, LAI, Ta, VPD, and SWC. Among these factors, SWC was the dominant factor limiting the NEE-PAR response of peanut during the peak growing stages (Fig. 4c). To illustrate the underlying physiological mechanisms of depres-15 sion of NEE, we investigated the diurnal course of NEE and g_s on clear days in two contrasting conditions. During non-stress days, corresponding to an average of SWC of $0.075\pm0.026 \text{ m}^3 \text{m}^{-3}$, similar trends were observed for T_a and VPD. T_a and VPD increased during the daytime reaching the maximum at 31.7±1.4°C and 20.5±3.9 hPa, respectively, in the late afternoon (Fig. 5a). NEE increased to a max-20 imum of 26.71±5.72 μ mol CO₂ m⁻² s⁻¹ at about midday and then decreased as the afternoon progressed (Fig. 5b). The maximum g_s appeared around noon, which indicates sufficient water available for the ecosystem (Fig. 5b). In the water-stress days, with the average of SWC of $0.037 \pm 0.002 \text{ m}^3 \text{ m}^{-3}$, the diurnal course of T_a and VPD were similar to those on the non-stress days, but the maximum values (36.9±1.6 °C for T_a , 39.3±8.3 hPa for VPD) were much higher than during the non-stress days (Fig. 5c). The diurnal trends of NEE followed a pattern similar to g_{s_1} which increased to a maxi-

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mum (15.98±3.16 μ molCO₂m⁻²s⁻¹ for NEE, 0.0107±0.0074 ms⁻¹ for g_s) around midmorning and then rapidly declined throughout the remainder of the day as VPD increased (Fig. 5d). The reduction of photosynthesis under dry conditions is usually caused by either stomatal or non-stomatal limitations. The former could be partially attributed to stomatal closure, while the latter could be the decrease of leaf photosynthetic activity which can lead to irreversible reduction of plant photosynthesis (Fu et al., 2006; Reddy et al., 2003; Bhagsari et al., 1976). It is evident that the reduction of photosynthesis was related to the variation of g_s with water-stress (Aires et al., 2008; Anthoni et al., 2002). Aires et al. (2008) and Oguntunde (2005) indicated that VPD plays a strong role in controlling g_s when the soil moisture is not adequate. Fig. 6 illustrates the dependence of g_s on VPD under water-stress days. Without the limitation of PAR (>1000 μ molphotonsm⁻²s⁻¹), decreasing in g_s was explained by the changes in VPD, indicating that g_s values are sensitive to VPD in the present study.

- The limitation of using the Michaelis-Menten equation to describe the NEE-PAR relationship has been well documented in water-limited ecosystems (Li et al., 2005; Wang et al., 2008; Holst et al., 2008; Serrano-Ortiz et al., 2007). However, the mechanistic explanation of the processes inducing this limitation is still missing. The distinct hysteresis loop was evident in the relationship between NEE and PAR for both non-stress and water-stress days (Fig. 7a,b). However, the hysteresis loop was much reduced
- in area on the non-stress days as compared to the water-stress days. On non-stress days, as PAR increased in the morning, NEE increased (gets more negative) and as PAR decreased in the afternoon, NEE declined (Fig. 7a). The result suggests that T_a , VPD, and SWC are not the limiting factors in the NEE-PAR response. During water-
- ²⁵ stress conditions, as PAR increased in the morning, NEE increased, reaching the peak value at PAR of 1100 μ molphotonsm⁻²s⁻¹ and then rapidly decreased, reaching almost zero at the end of morning. As PAR decreased, NEE remained constant nearly zero throughout the afternoon (Fig. 7b). Hysteresis has been found in the responses of NEE to PAR in a tropical transitional forest in Brazilian Amazon (Vourlitis et al., 2005).

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Counter-intuitively, the magnitude of the hysteresis is lower during the wet season than during the dry season (Vourlitis et al., 2005). The causes of hysteresis in the response of NEE to PAR remain poorly understood.

- Hysteresis occurs when an increase in an independent variable, *x* does not cause the same response in a dependent variable, *y*, when the variable *x* decreases (Zeppel et al., 2004). In the morning, as PAR increased, carbon uptake increased, but in the afternoon, carbon uptake at any given PAR was lower than the rate in the morning at the same PAR. The magnitude of hysteresis observed during water-stress days is larger than that for the non-stress days, and is related to the variation of g_s with VPD. The observed decrease in g_s with increasing VPD corresponds to a decrease in carbon
- uptake during water-stress days, indicating strong stomatal control. Stomatal sensitivity to VPD increased in the afternoon and therefore the degree of closure increased, causing a reduced carbon uptake. These results inferred that during times when plants were subject to water-stress, stomatal limitation caused by high VPD was responsible for a large hysteresis loop. The consistent presence of hysteresis limited the ability of
- a non-linear equation (Michaelis-Menten function) to adequately predict daytime NEE as a function of light.

To consider the consistent presence of a hysteresis loop in the response of the NEE to PAR during water-stress conditions (DOY 219–234), half-hourly daytime NEE during ²⁰ this period were distinguished into three different subsets. A first subset of data corresponded to measurements taken in the morning with SWC less than $0.042 \text{ m}^3 \text{m}^{-3}$ (Fig. 8b). A second group comprised data obtained in the afternoon when SWC less than $0.042 \text{ m}^3 \text{m}^{-3}$ (in Fig. 8c). A third subset (Fig. 8d) comprised data with following rainfall event i.e. SWC greater than $0.042 \text{ m}^3 \text{m}^{-3}$. The results show that the model accounted for the consistent presence of hysteresis loop (Fig. 8b–d) in the response of NEE to PAR simulated daytime NEE better than the Michaelis-Menten equation (Fig. 8a) alone (R^2 =0.70, P<0.01 vs. R^2 =0, Fig. 9a,b). The fit of our model indicates that the gap-filling technique based on a non-linear regression needs to take into account the systematic presence of hysteresis in the NEE response to PAR during

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water-stress conditions.

4 Conclusions

We quantified NEE and its response to drought stress over a rainfed peanut field during a growing season using the eddy-covariance (EC) method. As observed, PAR
was the primary climatic factor controlling daytime NEE, accounting for 67 to 89% variations of NEE during peanut growing season. However, the model Michaelis-Menten describing NEE during daytime as a function of PAR could not be used during a peak growing stage, indicating that other environmental variables became proportionally more important in controlling NEE. We found that for very low soil water content (SWC<0.04 m³m⁻³), NEE significantly decreased when PAR exceeded 1300 μmolphotonsm⁻²s⁻¹. Results suggest that SWC was the dominant factor limiting the NEE-PAR response of peanut during the peak growing stage.

A pronounced hysteresis in NEE was observed in both non-stress and water-stress conditions as a function of PAR. However, the magnitude of hysteresis was larger during water-stress days than non-stress days. We found that 95% of variation in *g*_s is explained by changes in VPD on water-stress days. This result indicates that the strong stomata control of CO₂ exchange is responsible for a large part of the hysteresis loop, in turn leading to the failure of the Michaelis-Menten function to describe the NEE-PAR relationship. Further studies of water-limited ecosystems are needed to develop improved models during these extreme environmental conditions to more reliably predict the long-term NEE of these ecosystems and improve our current estimation of

their contribution to the global carbon balance.

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Table 1. Values of the parameters describing features of the Michaelis-Menten function responses of daytime net ecosystem CO_2 exchange (NEE) to incident photosynthetically active radiation (PAR) (Eq. 1).

Treatment	LAI	SWC	T _a	VPD	α	NEE _{sat}	R _e	n	R^2
	(m ² m ⁻²)	(m ³ m ⁻³)	(°C)	(hPa)	$(\mu mol \mu mol^{-1})$	$(\mu molCO_2 m^{-2} s^{-1})$	$(\mu molCO_2 m^{-2} s^{-1})$		
DOY 181-190	4.72	0.073±0.026	27.1±3.3	12.2±7.1	-0.0358±0.0061	-35.69 ± 2.08	5.35±1.06	235	0.78
DOY 191-200	4.55	0.061±0.018	27.9±3.1	12.0±7.0	-0.0350 ± 0.0041	-56.22±3.76	5.27±0.96	234	0.88
DOY 201-210	6.00	0.074±0.035	27.3±3.4	12.3±6.9	-0.0328 ± 0.0044	-62.58±6.26	4.65±1.06	244	0.84
DOY 211-218	7.81	0.065±0.029	28.8±3.3	12.8±7.3	-0.0359 ± 0.0069	-51.35±4.87	6.14±1.54	192	0.76
DOY 219-226		0.037±0.002	32.1±4.1	20.0±11.8	$-0.4306 \pm 0.9883^{*}$	-24.02±21.67*	16.68±22.17*	188	0.10
DOY 227-234	2.92	0.048±0.020	31.5±4.1	20.6±11.9	-0.0921±0.1226*	-18.71±6.92	8.60±7.96*	183	0.16
DOY 235-244	5.06	0.088±0.025	26.8±3.0	7.0±5.2	-0.0321±0.0036	-50.23±3.70	5.22±0.78	194	0.89
DOY 245-254	4.74	0.050 ± 0.023	27.6±2.9	13.1±7.0	-0.0438±0.0091	-28.72±1.18	5.63±1.26	233	0.75
DOY 255-264		0.064±0.024	24.4±3.1	8.0±5.0	-0.0305±0.0077	-20.56±1.17	3.87±1.04	203	0.67
DOY 265-271	4.06	0.075±0.016	26.3±3.3	8.9±6.4	-0.0183±0.0057	-19.06 ± 2.19	4.03±1.00	129	0.69

LAI, leaf area index; SWC, soil water content at 2–5 cm depth; T_a , air temperature at 2 m above the ground; VPD, atmospheric water vapor deficit at T_a ; α , the apparent quantum yield; NEE_{sat}, the saturation value of NEE at an infinite light level not significant; R_e , the ecosystem respiration during the daytime; *n*, observation; and R^2 , the coefficient of determination

* not significant at $P \le 0.05$

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Fig. 2. Seasonal variation in leaf area index (LAI)±standard error over the course of the study.

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Fig. 4. Relationship between net ecosystem CO_2 exchange (NEE) and photosynthetically active radiation (PAR) under **(a)** different air temperature (T_a), **(b)** different vapor pressure deficit (VPD), and **(c)** under different soil water content (SWC) during the peak growing stages (DOY 201–240). NEE data were averaged with PAR bins. Bin width is 200 μ molphotonsm⁻²s⁻¹. Bars indicate standard deviation.



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Fig. 5. Diurnal variations of negative net ecosystem CO_2 exchange (-NEE), surface conductance (g_s) and correspondingly environmental factors of air temperature (T_a) and vapor pressure deficit (VPD) on clear days under non-stress condition (**a** and **b**, measured on DOY 210, 212, 213, 214, and 216) and water-stress condition (**c** and **d**, measured on DOY 220, 222, 225, 226, and 227). Bars indicate standard deviations.





Fig. 6. Response of half-hour surface conductance (g_s) to vapor pressure deficit (VPD) during water-stress condition (measured on DOY 220, 222, 225, 226, and 227) when PAR>1000 μ molphotonsm⁻²s⁻¹.

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Fig. 7. The relationship between photosynthetically active radiation (PAR) and net ecosystem CO_2 exchange (NEE) on clear days under **(a)** non-stress conditions (measured on DOY 210, 212, 213, 214, and 216) and **(b)** water-stress conditions (measured on DOY 220, 222, 225, 226, and 227). The arrows indicate the direction of the hysteresis effect.



Fig. 8. Relationship between net ecosystem CO_2 exchange (NEE) and photosynthetically active radiation (PAR) during water-stress conditions (DOY 219 to 234) (a) whole data set, (b) morning data set, (c) afternoon data set, and (d) following rainfall data set. The Quadratic equation was used to fit the morning and afternoon data set (solid line in (b) and (c)). The Michaelis-Menten equation as described in Eq. (1) was used to fit whole and following rainfall data set (solid line in (a) and (d). Correlation coefficients (R^2) for each model are also shown.











