

Hysteresis response of daytime net ecosystem exchange during drought

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Abstract. Continuous measurements of net ecosystem CO₂ exchange (NEE) using the eddy-covariance method were made over an agricultural ecosystem in the southeastern US. During optimum environmental conditions, photosynthetically active radiation (PAR) was the primary driver controlling daytime NEE, accounting for as much as 67 to 89% of the variation in NEE. However, soil water content became the dominant factor limiting the NEE-PAR response during the peak growth stage. NEE was significantly depressed when high PAR values coincided with very low soil water content. The presence of a counter-clockwise hysteresis of daytime NEE with PAR was observed during periods of water stress. This is a result of the stomatal closure control of photosynthesis at high vapor pressure deficit and enhanced respiration at high temperature. This result is significant since this hysteresis effect limits the range of applicability of the Michaelis-Menten equation and other related expressions in the determination of 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-limited field conditions. Including this step is therefore likely to improve current evaluation of ecosystem response to increased precipitation variability arising from climatic changes.

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 terrestrial ecosystems and the atmosphere. In addition to changes in average temperature and precipitation, the Intergovernmental Panel on Climate Change (IPCC) expects the occurrence of extreme weather events (i.e. drought and flood) to become more frequent and/or intense (IPCC, 2007). The anticipated increase in both climate variability and extreme events is presumed to adversely affect plant growth and water availability. Everything else being constant, an increase in the number of hot days increases potential evapotranspiration leading to drought. Hence, a mechanistic understanding of how drought influences carbon exchange between ecosystems and the atmosphere is a *sine qua non* condition to anticipate possible impact of climate change scenarios. Such results can also provide the modeling community with a better basis to improve and validate their models.

The 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 (Chapin et al., 2006). The NEE can be measured directly using the eddy-covariance method (hereafter referred to as EC), which provides a spatially integrated net carbon exchange on a continuous basis with minimal disturbance to the surrounding vegetation (Aubinet et al., 2000; Baldocchi et al., 2001). With these continuous measurements, the derivation of annual sums of NEE then becomes possible. However, due to



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a combination of inherent limitations in the applicability of the measurement method and related data robustness, both data rejection and missing data are unavoidable. This data loss can be as much as 65–75% of a dataset spanning all seasons (Baldocchi et al., 2001; Falge et al., 2001; Law et al., 2002). Large resulting gaps in the dataset must be reconstructed using several methods based on varying degrees of empiricism to obtain a seasonal carbon balance. For instance, gap-filling techniques are based on a wide range of standard procedures, including linear interpolation (Falge et al., 2001), look-up tables (Falge et al., 2001), moving averages (Falge et al., 2001; Reichstein et al., 2005), non-linear regressions (Goulden, 1996; Falge et al., 2001; Suyker and Verma, 2001), artificial neural networks (Papale and Valentini, 2003; Papale et al., 2006), mechanistic models (Braswell et al., 2005; Ooba et al., 2006), and the multiple imputation method (Hui et al., 2004).

However, one of the conventional methods to replace missing data in NEE data in daytime conditions has been to resort to the use of non-linear regressions (Falge et al., 2001; Ooba et al., 2006). This approach is based on parameterized non-linear equations (e.g. Michaelis-Menten equation) to quantify the relationship between NEE and radiation (e.g. photosynthetically active radiation; hereafter referred to as PAR). While the failure using a non-linear equation to describe daytime NEE only as a function of radiation has been previously observed in various ecosystems (Li et al., 2005; Serrano-Ortiz et al., 2007; Holst et al., 2008; Wang et al., 2008), to date a mechanistic explanation 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 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 intensity, rate, duration, and the stage of plant 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; review by Reddy et al., 2003; Lauriano et al., 2004). 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 stomates to prevent further water loss through transpiration (Reddy et al., 2003). As a consequence, the CO₂ assimilation is also reduced. The long-term effect of soil water deficit on canopy assimilation is a reduction in leaf area. Drought reduces leaf area by folding, wilting, slowing leaf expansion, and shutting off the supply of carbohydrates (Clifford et al., 1993; Collino et al., 2001; Reddy et al., 2003). The consequent reduction in leaf area reduces plant's ability to capture light resources (Chapman et al., 1993a; Collino et al., 2001), resulting in a negative influence on biomass.

Measurements made in most of the above studies were conducted at the leaf scale, e.g. clamp-on leaf chambers, (Nautiyal et al., 1995; Bhagsari et al., 1976; Lauriano et al., 2004). There is still a lack of information on a continuous basis on the effect of drought stress on carbon exchange at the canopy scale. To this end, EC flux measurements were carried out 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 inadequacy of the Michaelis-Menten equation in describing the NEE-PAR relationship.

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 area is flat with a slope less than 2% and large enough to provide at least 210 m fetch in all directions. 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 g cm⁻³. The field capacity was 0.118 m³ m⁻³ and the permanent wilting point was 0.042 m³ m⁻³. Total carbon and nitrogen content of soil were 0.43 and 0.03%, respectively.

Fertilizer (N:P:K) was applied on day of year (hereafter referred to as DOY) 93 at a rate of 336 kg ha⁻¹. Peanut was planted with 6.6 kg ha⁻¹ of phorate on DOY 125. Traditional herbicides including Gramoxone (1, 1-dimethyl-4, 4 bipyridinium) at 1.75 L ha⁻¹, Storm (bentazon and acifluorfen) at 1.17 L ha⁻¹, and 2, 4-DB (4-(2, 4-dichlorophenoxy) butyric acid) at 0.44 L ha⁻¹ were applied on DOY 157 based on the typical peanut weed control program the Southeast. Leaf spot and white mold were controlled using Bravo Ultrax (on DOY 197, DOY 232, and DOY 253) and Headline 2.09EC (on DOY 1176 and DOY 211). Peanut was harvested on DOY 283 with a yield of 4783 kg ha⁻¹.

2.2 Field measurements and data processing

Fluxes of carbon dioxide, water vapor, heat and momentum were continuously measured using 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 3-dimensional sonic anemometer (CSAT3, Campbell Scientific, Logan, UT) and a fast response open-path CO₂/H₂O infrared gas analyzer (IRGA, Li 7500, Li-Cor Inc., Lincoln, NE). The IRGA was placed with a 30° tilt angle to minimize accumulation of dust and water droplets on the windows. Calibration of the IRGA was done prior to the experiment campaign using nitrogen gas and 600 ppm CO₂ gas to calibrate the CO₂ and water vapor zeros and the span of CO₂, respectively. The span of water vapor was calibrated with dew point generator (Li 610, 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.

Along with the EC tower, standard meteorological and soil parameters were measured continuously with an array of sensors. Net radiation (R_n) 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. The canopy temperature was measured at canopy height using a precision infrared thermocouple sensor with an accuracy of $\pm 0.4^\circ\text{C}$ (IRTS-P5, Apogee Instrument Inc., Logan, UT). Belowground measurements were 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 was measured using time domain reflectometry sensors (CS615, Campbell Scientific, Logan, UT) at depths of 0.02 and 0.02 to 0.05 m. The soil heat flux (G) was determined using the averaging of two soil heat plates measurements (HFT-3, Campbell Scientific, Logan, UT). The plates were buried at a depth of 0.08 m in two distinct locations; one was between peanut rows and the other was within a row. The average temperature of the soil layer above the plate was measured using 4 parallel thermocouples (TCAV, Campbell Scientific, Logan, UT). The thermocouples were placed at the depths of 0.02 and 0.06 m to obtain the average temperature of the soil layer above each heat flux plate. The total heat flux at the soil surface is then calculated by adding the heat flux measured by the plate to the energy stored in the soil layer. Storage of heat in the soil above the soil heat flux plate was calculated by multiplying the change in soil temperature over the averaging period by the soil heat capacity. The value used for the heat capacity of dry soil was $0.84 \times 10^{-3} \text{ J kg}^{-1} \text{ K}^{-1}$.

An automatic weather station (ET106, Campbell Scientific, Logan, UT) with 30-min average data output was installed 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 Ahr sealed-rechargeable battery that was charged with a 1000 W solar panel. All meteorological and belowground measurements were averaged over 30-min periods and stored to a datalogger (CR10X, Campbell Scientific, Logan, UT). In addition, the leaf area index (hereafter referred to as LAI) was determined at intervals of 7 to 10 days with an electronic leaf area meter (LAI-2000, Li-Cor Inc., Lincoln, NE) throughout the season. The canopy temperature sensor was replaced on DOY 180. Gaps in solar radiation, temperature, and precipitation data were filled with data

from a nearby meteorological station located approximately 8 km. Incident PAR was estimated from solar radiation.

2.3 Data analysis

The raw 10 Hz data from the sonic anemometer and the infrared gas analyzer were checked for spikes before calculating eddy-covariance fluxes. This was done following Vickers and Mahrt (1997). Each individual data point of the three-velocity components from the sonic anemometer was also rotated according to a planar fit rotation to virtually align the sonic anemometer axis along the long-term streamlines (Wilczak et al., 2001). Before half-hourly fluxes of CO₂ (NEE), latent heat (λE), and sensible heat (H) were calculated, the time series were linearly detrended. Finally, the flux data were corrected for variations in air density due to fluctuations in water vapor and heat fluxes, i.e. using the Webb, Pearman and Leuning correction (Webb et al., 1980). Data collected during periods with rain or dew was rejected. The analyses were conducted using a C++ program written in-house.

It has been recognized for some time by the flux monitoring community that the EC technique is likely to underestimate eddy fluxes in calm conditions at night, but there is no consensus on how to correct the problem. Most researchers screen nighttime data using a friction velocity (u_*) threshold (Goulden et al., 1997; Aubinet et al., 2000; Reichstein et al., 2005; Papale et al., 2006). Estimation of u_* threshold values followed Reichstein et al. (2005) using the online calculation software found at <http://gaia.agraria.unitus.it/database/eddyproc>. In calm nights, 78.68% of the carbon flux data was rejected so nighttime flux data are not presented in this study.

In this study, daytime is defined as the period with solar radiation $> 20 \text{ W m}^{-2}$. 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 ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) on solar PAR ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$):

$$\text{NEE} = \frac{\alpha \cdot \text{PAR} \cdot \text{NEE}_{\text{sat}}}{\alpha \cdot \text{PAR} + \text{NEE}_{\text{sat}}} + R_e, \quad (1)$$

where α is the apparent quantum yield or the initial slope of the light response curve ($\mu\text{mol CO}_2 \mu\text{mol}^{-1} \text{ photons}$), NEE_{sat} is the saturation value of NEE at an infinite light level, and R_e is the ecosystem respiration in daytime conditions.

The canopy conductance was used to assess stomatal control on CO₂ 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 EC measurements. Therefore, half-hourly surface conductance (hereafter referred to

as g_s) was calculated by rearranging the Penman-Monteith equation (Monteith and Unsworth, 1990):

$$\frac{1}{g_s} = \left[\left(\frac{\Delta}{\gamma} \right) \beta - 1 \right] \left(\frac{1}{g_a} \right) + \frac{\rho \cdot C_p \cdot \text{VPD}}{\gamma \cdot \lambda \cdot E}, \quad (2)$$

where Δ is the rate of change of saturation vapor pressure with temperature, γ the psychrometric constant, β the Bowen ratio which is $H/\lambda E$, ρ and C_p 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 aerodynamic conductance was obtained from sonic anemometer output as (Monteith and Unsworth, 1990):

$$\frac{1}{g_a} = \frac{u}{u_*^2} + 6.2 \cdot u_*^{-0.67}, \quad (3)$$

where u is the mean wind speed.

We examined the energy balance closure which is often considered to be an independent method to assess the reliability of the EC measurements (Wilson, 2002; Aires, 2008). The energy balance closure was tested using a linear regression between the amount of the available energy ($Rn - G$) and the sum of sensible heat and latent heat fluxes ($H + \lambda E$) using half-hourly data collected during the experiment. The relationship we found was: $(H + \lambda E) = 0.74(Rn - G) + 7.22$, with $R^2 = 0.96$. This result suggests that the EC measurements underestimate $H + \lambda E$ by 26%. Although, the energy balance closure is not perfect, it is typical of the range found at other flux sites. In a comparison of the energy balance closure of 22 FLUXNET sites, Wilson et al. (2002) reported slope, intercept and R^2 ranging, respectively, between 0.53 and 0.99, -32.9 and 36.9 W m^{-2} , and 0.64 and 0.36 without any effect of vegetation height. In the present study, one of the apparent causes for the imbalance may relate to different source scales of measurements in Rn and G compared to H and λE (Schmid, 1994; Wilson, 2002). The net radiometer and soil heat flux plates measure radiation exchange from a relatively small portion of the landscape near the measurement tower, while EC measurements represents an area hundreds of meters square in area (Schmid, 1994). Other possible source of errors lie in the contribution of sub-mesoscale eddies to sensible and latent heat fluxes, choice of the u_* threshold, and non-inclusion of the heat storage between the measurement level and the ground. Meyers and Hollinger (2004) found that including the heat storage between the measurement level and the ground, as well as the ground heat storage above the plate in the energy balance of a maize crop and a soybean crop, increase the regression slopes of 3% to 6%.

3 Results and discussion

3.1 Seasonal variation in environmental conditions and leaf area index

Over the study period, seasonal trends of soil and canopy temperatures 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 19.4 to 31.2 °C, respectively. The canopy temperature was slightly higher than the soil and air temperatures. However, maximum values were observed on DOY 222 (Fig. 1a). The total rainfall at the 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 ($0.042 \text{ m}^3 \text{ m}^{-3}$) 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 $7.81 \text{ m}^2 \text{ m}^{-2}$ around DOY 210. While the minimum LAI of $2.92 \text{ m}^2 \text{ m}^{-2}$ was found during periods of stress (DOY 217–228), the corresponding LAI reduction is due to either drought-induced limitation of leaf area expansion or temporary leaf wilting or rolling during periods of severe stress (Chapman et al., 1993b; Clifford et al., 1993). With 52 mm of total precipitation on DOY 235, LAI subsequently recovers reaching the values of $5.06 \text{ m}^2 \text{ m}^{-2}$ 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 function (Eq. 1) to describe the response of NEE averaged over a 30-min period (Fig. 3). In general, peanuts are fast growing so that the functional response of NEE to PAR was determined separately for each growing stage using bins of 7 to 10 consecutive days of data (Table 1). 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 (2.00 ± 1.18 and 2.06 ± 1.19 kPa, respectively) were high and SWC (0.037 ± 0.002 and $0.048 \pm 0.020 \text{ m}^3 \text{ m}^{-3}$, respectively) was low (Table 1), the Michaelis-Menten function succeeded in describing the NEE-PAR relationship. Figure 3 shows the large scatter of the data points during these periods should be noted, highlighting the dependence of NEE-PAR relationship on other environmental factors. This will be discussed in greater detail later.

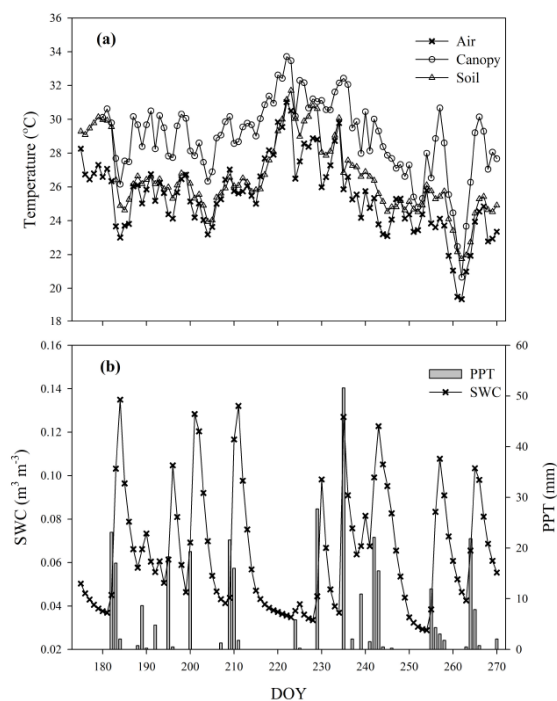


Fig. 1. Seasonal variation in (a) daily average of air temperature, canopy temperature, and soil temperature at the depth of 2 cm; (b) daily average soil water content (SWC) at the depth of 2–5 cm and daily total precipitation (PTT) over the course of the study. DOY 1 means days of year.

Based on the statistical analysis using Eq. (1), the regression coefficients indicated that the change in PAR accounted for 67 to 89% of the variations in NEE. The α values varied from -0.0183 to $-0.0438 \mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photons. This value was well within the range of α reported for crops and grasslands (-0.008 to $-0.465 \mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photons; Ruimy et al., 1995; Valentini et al., 1995; Suyker and Verma, 2001; Suyker et al., 2004). The low α at the end of the study was most likely due to late life cycle of the peanut plant, then in its 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 separated into three T_a classes ($T_a < 28^\circ\text{C}$, $28 < T_a < 32^\circ\text{C}$, and $T_a > 32^\circ\text{C}$), three VPD classes ($\text{VPD} < 1.0 \text{ kPa}$, $1.0 < \text{VPD} < 2.0 \text{ kPa}$, and $\text{VPD} > 2.0 \text{ kPa}$), and three SWC classes ($\text{SWC} < 0.04 \text{ m}^3 \text{ m}^{-3}$, $0.04 < \text{SWC} < 0.07 \text{ m}^3 \text{ m}^{-3}$, and $\text{SWC} > 0.07 \text{ m}^3 \text{ m}^{-3}$) (Fig. 4a–c). Within each group, the NEE data were further subdivided by PAR into $200 \mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photons increments ranging from 0 to $2200 \mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photons and then were bin averaged for each PAR subgroup.

Results showed NEE increased as PAR increased for all temperature conditions (Fig. 4a). These results are in general agreement with previous findings suggesting that peanuts

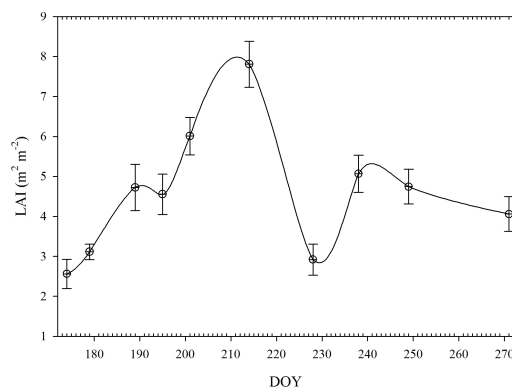


Fig. 2. Seasonal variation in leaf area index (LAI) \pm standard error over the course of the study.

perform well in the temperature range between 24 to 33°C (Saxena et al., 1983). However, at high temperature ($T_a > 32^\circ\text{C}$), the 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 $\text{VPD} < 1.0 \text{ kPa}$ and $1.0 < \text{VPD} < 2.0 \text{ kPa}$ 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 ($> 2.0 \text{ kPa}$), 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 ($\text{SWC} > 0.04 \text{ m}^3 \text{ m}^{-3}$), NEE increased with PAR and there was no indication of canopy light saturation. For very low SWC ($< 0.04 \text{ m}^3 \text{ m}^{-3}$), 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 $1300 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. A reduction in NEE in dry conditions has been observed in different ecosystems (Sims and Bradford, 2001; Hastings et al., 2005; Li et al., 2005; Fu et al., 2006; Aires et al., 2008b; Holst et al., 2008; Wang et al., 2008) and caused by midday stomata closure when irradiance, temperature, and VPD are all high, when the SWC is low (Sims and Bradford, 2001; Li et al., 2005; Aires et al., 2008b) or 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 results from several factors, including PAR, LAI, T_a , 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 depression of NEE, we investigated the diurnal course of NEE

Table 1. Values of parameters in the Michaelis-Menten function (Eq. 1).

Treatment	LAI ($\text{m}^2 \text{m}^{-2}$)	SWC ($\text{m}^3 \text{m}^{-3}$)	T_a ($^{\circ}\text{C}$)	VPD (kPa)	α ($\mu\text{mol} \mu\text{mol}^{-1}$)	NEE_{sat} ($\mu\text{mol} \text{CO}_2 \text{m}^{-2} \text{s}^{-1}$)	R_e ($\mu\text{mol} \text{CO}_2 \text{m}^{-2} \text{s}^{-1}$)	n	R^2
DOY 181–190	4.72	0.073 ± 0.026	27.1 ± 3.3	1.22 ± 0.71	-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	1.20 ± 0.70	-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	1.23 ± 0.69	-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	1.28 ± 0.73	-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	2.00 ± 1.18	$-0.4306 \pm 0.9883^*$	$-24.02 \pm 21.67^*$	$16.68 \pm 22.17^*$	188	0.10
DOY 227–234	2.92	0.048 ± 0.020	31.5 ± 4.1	2.06 ± 1.19	$-0.0921 \pm 0.1226^*$	-18.71 ± 6.92	$8.60 \pm 7.96^*$	183	0.16
DOY 235–244	5.06	0.088 ± 0.025	26.8 ± 3.0	0.70 ± 0.52	-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	1.31 ± 0.70	-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	0.80 ± 0.50	-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	0.89 ± 0.64	-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 $P \leq 0.05$.

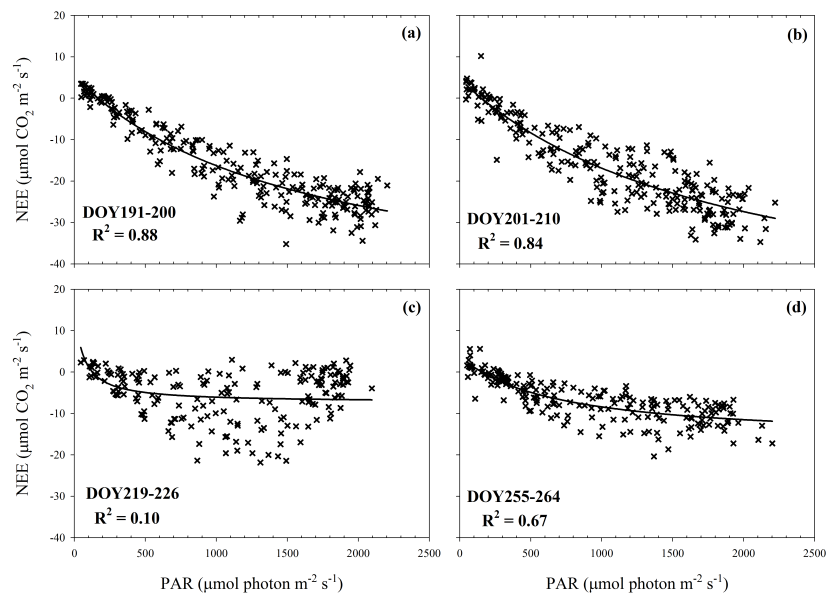


Fig. 3. Example of light-response curves at different growth stages during the study period. The Michaelis-Menten equation as described in Eq. (1) was used to fit the data, and the regression coefficients (R^2) are presented.

and g_s on clear days in two contrasting conditions. During non-stress days, corresponding to an average of SWC of $0.075 \pm 0.026 \text{ m}^3 \text{m}^{-3}$, similar trends were observed for T_a and VPD. T_a and VPD increased during the daytime reaching the maximum at $31.7 \pm 1.4 ^{\circ}\text{C}$ and $2.05 \pm 0.39 \text{ kPa}$, respectively, in the late afternoon (Fig. 5a). NEE increased to a maximum of $26.71 \pm 5.72 \mu\text{mol} \text{CO}_2 \text{m}^{-2} \text{s}^{-1}$ 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). During periods with water stress, 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 ($36.9 \pm 1.6 ^{\circ}\text{C}$ for T_a , $3.93 \pm 0.83 \text{ kPa}$ 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 , which increased to a maximum ($15.98 \pm 3.16 \mu\text{mol} \text{CO}_2 \text{m}^{-2} \text{s}^{-1}$ for NEE, $0.0107 \pm 0.0074 \text{ m} \text{s}^{-1}$ for g_s) around mid-morning and then rapidly declined as VPD increased (Fig. 5d). In the late afternoon when VPD decreased, the NEE and g_s decreased and recovered slightly approaching conditions seen earlier during

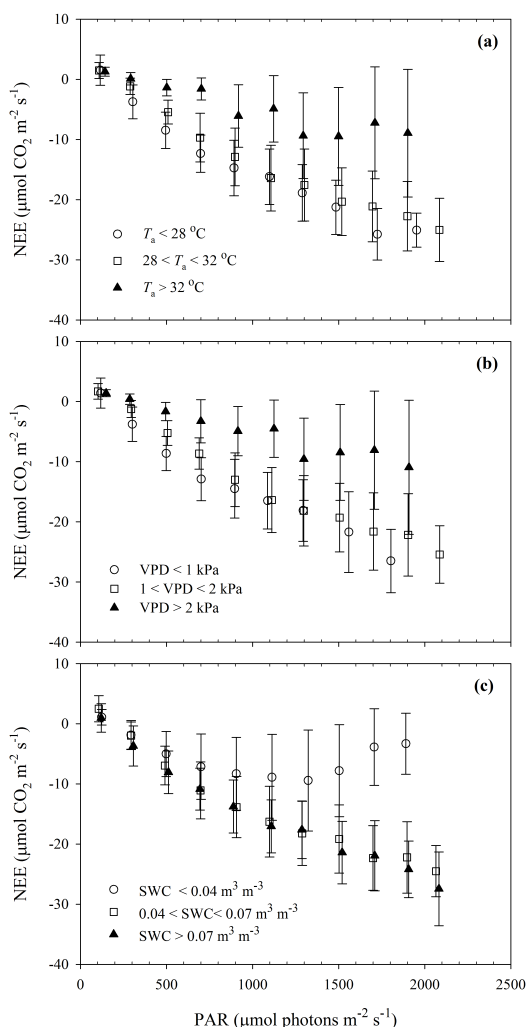


Fig. 4. Relationship between net ecosystem CO_2 exchange (NEE) and photosynthetically active radiation (PAR) under (a) different air temperature (T_a), (b) different vapor pressure deficit (VPD), and (c) under different soil water content (SWC) during the peak growing stages (DOY 201–240). NEE data were averaged with PAR bins. Bin width is $200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. Bars indicate standard deviations.

the day (Fig. 5d). The recovery of g_s was small because of the reduced plant transpiration and soil evaporation as both of these were limited by low soil water content (Fu et al., 2006). Early daytime peaks in NEE have been observed previously at Metolius (Anthoni et al., 1999) and in a California grassland (Valentini et al., 1995). Valentini (1995) indicated that afternoon stomatal closure can have a dramatic impact on the diurnal cycle of assimilation, resulting in an early morning peak in NEE, i.e. a response often enhanced during periods of low soil water content. This is consistent with theoretical studies of optimal stomatal control suggesting that afternoon CO_2 uptake should be suppressed as soil drying progresses (Cowan, 1982)

The distinct hysteresis loop was evident in the relationship between NEE and PAR for both non-stress and water-stress days (Fig. 6a, b). However, the hysteresis loop was much reduced in area on the non-stress days when compared to water-stress days. On non-stress days, as PAR increased in the morning, NEE increased (gets more negative) reaching the peak value at the highest PAR of $2080 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ and as PAR decreased in the afternoon, NEE declined (Fig. 6a). The result suggests that T_a , VPD, and SWC are not the limiting factors in the NEE–PAR response. During water-stress conditions, as PAR increased in the morning, NEE increased, reaching the peak value at PAR of $1100 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ and then rapidly decreased, reaching almost zero at the end of morning. As PAR decreased, NEE remained constant nearly zero throughout the afternoon (Fig. 6b). Zeppel et al. (2004) explained that 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. 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 diurnal pattern of NEE depends on the interaction between the atmosphere and physiological response. Körner (1995) attributed the asymmetric (hysteresis) shape of the diurnal cycle of NEE during dry periods with high VPD to a limitation of photosynthesis due to stomatal closure at high VPD or to enhanced respiration induced by high temperatures. Moreover, a wide range of studies have shown that ecosystem respiration also exhibits hysteresis. This may be attributed either to the fact that temperature is out of phase between the different levels from leaf to deep soil (Gaumont-Guay et al., 2006; Graf et al., 2008; Pingintha et al., 2010), to a lagged response of root respiration to light (Tang et al., 2005), or both (Bahn et al., 2008). In the present study, the daytime NEE data obtained during non-stress and water-stress days was compiled using different bins of T_a and VPD. Bin width was 2°C for T_a and 0.5 kPa for VPD, respectively. The NEE data were averaged over each bin regardless of PAR, and then were plotted against T_a and VPD in Fig. 7a and Fig. 7b, respectively. Clearly, under non-stress conditions, NEE almost linearly increased as T_a (Fig. 7a) and VPD (Fig. 7b) increased. In contrast, under water-stress conditions, NEE increased with T_a until approximately 29°C , then decreased with any additional increase in T_a (Fig. 7a). Similarly, NEE also increased with increasing VPD and decreased as VPD above 1.2 kPa (Fig. 7b).

Bhagsari et al. (1976) observed large reductions in photosynthesis and stomatal conductance as the relative water content of peanut leaves decreased from 80 to 75%. They further concluded that the main effect of a soil water deficit on leaf carbon exchange rate is exerted through stomatal closure. Reddy et al. (2003) reported also a decrease in leaf mesophyll conductance during water stress. This feature has been suggested to be of importance as water stress increases,

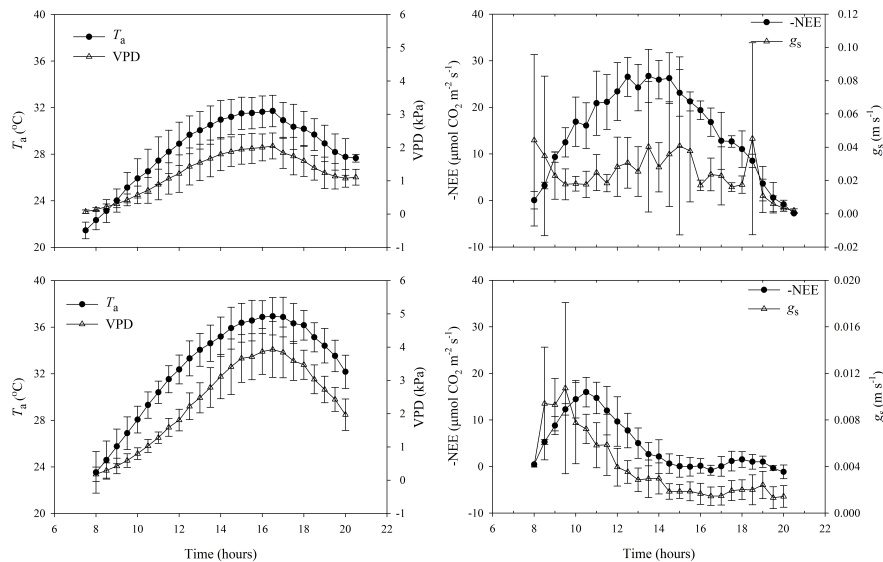


Fig. 5. Diurnal variations of negative net ecosystem CO₂ exchange (-NEE), surface conductance (g_s) and correspondingly environmental factors of air temperature (T_a) and vapor pressure deficit (VPD) on clear days under non-stress conditions (**a** and **b**, measured on DOY 210, 212, 213, 214, and 216) and water-stress conditions (**c** and **d**, measured on DOY 220, 222, 225, 226, and 227). Bars indicate standard deviations.

because it limits the transfer of CO₂ from the intercellular air spaces to the carboxylation sites (Bogi and Loreto, 1989) results in a reduction in photosynthesis. It is evident that the reduction of photosynthesis was related to the variation of g_s with water-stress (Anthoni et al., 2002; Aires et al., 2008b). In our case, under water-stress days without the limitation of PAR ($>1000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), decreasing in g_s with increasing VPD was observed ($R^2 = 0.95$; Fig. 8). Considering the consequences of water stress, Oguntunde (2005) also found a strong correlation between canopy conductance and VPD in stressed cassava at non-limiting solar radiation. The observed decrease in g_s with increasing VPD corresponds to a decrease in carbon uptake, indicating strong stomatal control. These results inferred that during times when plants were subject to water stress, the afternoon NEE decreased caused by a limitation of photosynthesis due to stomatal closure at high VPD. Furthermore, since ecosystem respiration, a significant fraction of NEE, typically increases with temperature (e.g. Reichstein et al., 2005; Fu et al., 2006; Wang et al., 2008), the higher afternoon temperatures may have led to a decrease in NEE during that time of day (Fu et al., 2006). We can then infer that the suppression of NEE in the peanut ecosystem during periods of water stress resulting from a limitation of photosynthesis attributed to stomatal closure at high VPD and enhanced respiration due to high temperature, is responsible for a large of hysteresis loop. The consistent presence of hysteresis appears to limit the ability of the Michaelis-Menten function to adequately predict daytime NEE as a function of PAR. Future work should be done to construct a gap-filling model that takes into account temperature and vapor pressure deficit, both variables of significance

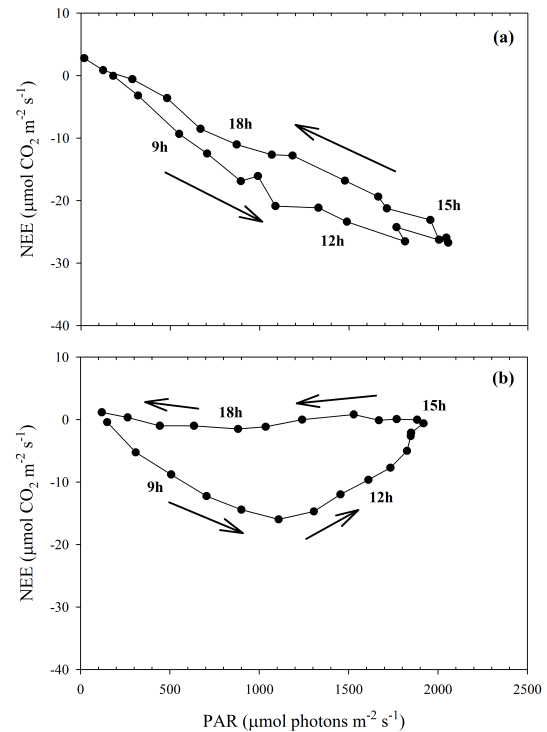


Fig. 6. The relationship between photosynthetically active radiation (PAR) and net ecosystem CO₂ exchange (NEE) on clear days under (**a**) non-stress conditions (measured on DOY 210, 212, 213, 214, and 216) and (**b**) water-stress conditions (measured on DOY 220, 222, 225, 226, and 227). The arrows indicate the direction of the hysteresis effect.

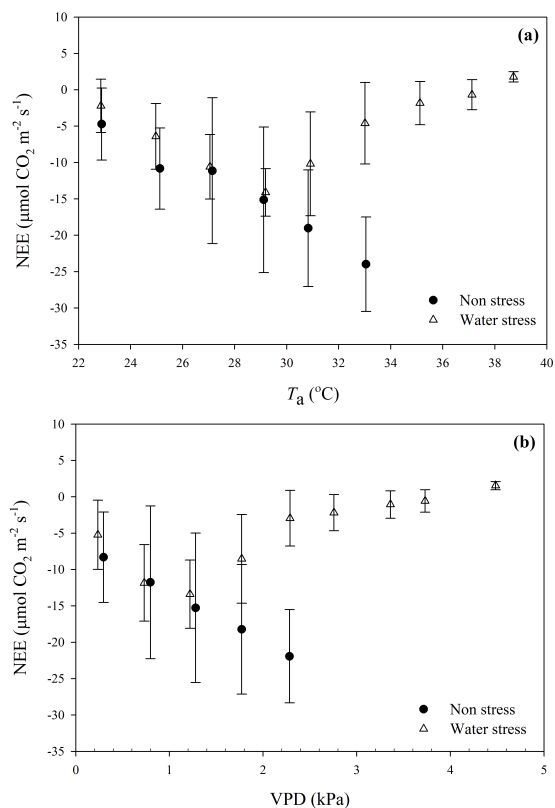


Fig. 7. The response of net ecosystem CO₂ exchange (NEE) to (a) air Temperature (T_a) and (b) vapor pressure deficit (VPD) on clear days under non-stress conditions (measured on DOY 210, 212, 213, 214, and 216) and water-stress conditions (measured on DOY 220, 222, 225, 226, and 227). NEE was bin averaged. Bin size was 2 °C for T_a and 0.5 kPa for VPD, respectively. Bars indicate standard deviations.

in water-stressed conditions, and apply these finding to other ecosystems.

4 Conclusions

We quantified NEE and its response to drought stress over a rainfed peanut field during the growing season using the eddy-covariance method. PAR was the primary driver controlling daytime NEE, accounting for 67 to 89% of the variations in NEE during the peanut growing season. However, Michaelis-Menten model describing NEE during daytime as a function of PAR could not be used during portions of the peak growing stage, indicating that other environmental variables became proportionally more important in controlling NEE during these periods. We found that, for very low soil water content conditions ($SWC < 0.04 \text{ m}^3 \text{ m}^{-3}$), NEE significantly decreased when PAR values exceeded $1300 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. Results suggest that soil water content was the dominant factor limiting the NEE-PAR response of peanut during the peak growing stage.

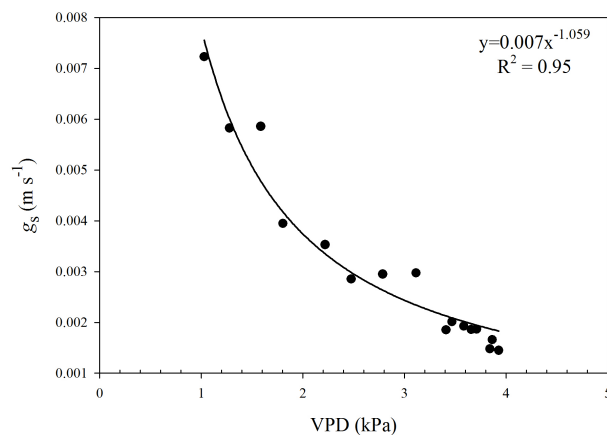


Fig. 8. Response of half-hourly surface conductance (g_s) to vapor pressure deficit (VPD) during water-stress condition (measured on DOY 220, 222, 225, 226, and 227) when $PAR > 1000 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$.

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 much larger during water-stress days than non-stress days. NEE was suppressed under high air temperature and vapor pressure deficit during periods of water stress due to higher ecosystem respiration at high temperatures and stomatal limitation of photosynthesis at high vapor pressure deficit.

The resultant large hysteresis loop leads to the failure of the Michaelis-Menten function in describing the NEE-PAR relationship. Previous studies have described the effect of high vapor pressure deficit and temperature on net ecosystem CO₂ exchange, but the characterization of these variables impact being linked through hysteresis is largely unexplored. This research will aid in developing more robust gap filling methodologies. Further studies of water-limited ecosystems are needed to develop improved models during these extreme environmental conditions to more reliably predict long-term NEE. This in turn should lead to improvements in our estimation of the global carbon balance.

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