

Seasonal changes in net ecosystem exchange of CO₂ and respiration of *Cenchrus ciliaris* L. grassland ecosystem in semi-arid tropics: an eddy covariance measurement

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The daily net ecosystem CO₂ exchange, diurnal pattern of net CO₂ exchange and ecosystem respiration of *Cenchrus ciliaris* grassland in semi-arid region were studied during July 2008–June 2009 using eddy covariance measurement. The active season during which daily net CO₂ uptake was observed corresponded with the wet season which lasted for 7 months. High CO₂ uptake was observed during September to December. Pulses in CO₂ release occurred with the rewetting of the soil by summer rain events during dry period. The amplitude of daytime and nocturnal ecosystem CO₂ exchange increase by many folds during the active season when compared with the dry season. Ecosystem respiration exhibits strong positive relationship with soil moisture ($r^2 = 0.768$) but negatively correlated with soil temperature ($r^2 = 0.498$). The seasonal changes in net ecosystem exchange and ecosystem respiration were strongly regulated by soil moisture, therefore, the phase of the net uptake and release of CO₂ by the ecosystem depend on the balance between the wet season and the dry season.

Keywords. Ecosystem respiration, grassland ecosystem, net ecosystem CO₂ exchange, soil temperature, soil moisture.

GRASSLANDS cover approximately one-third of the earth's terrestrial surface area and play an important role in global carbon cycling¹ as they store between 10% and 30% of the world's soil carbon^{2–4}. *Cenchrus ciliaris* L. (Buffel grass), also known as Anjan grass, is one of the most important forage crops of India and other tropical and semitropical regions of the world⁵ due to its low water demand, high nutrition content and ability to recover from grazing. As grasslands cannot extract water from deep soil profile⁶ due to their shallow root system⁷, they are sensitive to seasonal and interannual changes in environmental factors. Seasonal and interannual variability in plant and soil processes is largely a function of changes in soil moisture and temperature^{8,9}. Grasslands in semi-

arid regions of the southern part of India experience hot and dry summer which adversely affects the physiology of the plants. Semi-arid tropics are likely to undergo changes in future due to the critical environmental conditions of changing temperature and precipitation pattern^{10,11}. Since arid and semi-arid ecosystems occupy two-fifths of the Earth's terrestrial surface¹², understanding of the temporal variations in ecosystem CO₂ exchange in these regions will give better insight into the estimation of global carbon budgets. So far, there is no report of the long-term continuous measurement of CO₂ fluxes in grassland ecosystem of semi-arid regions of India. This lack of information necessitates the continuous study of ecosystem CO₂ exchange and to assess the effect of environmental constraints on ecosystem CO₂ exchange.

The eddy covariance (EC) measurement technique has been widely used in various parts of the world and such research has recently commenced in India. This is the first report of net ecosystem exchange (NEE) of CO₂ using EC system in India. Seasonal variations in ecosystem CO₂ exchange with the atmosphere occur in response to meteorological conditions and physiological activity of plants¹³. By using EC method, which is a micro-meteorological technique, direct continuous measurement of carbon, water and energy fluxes between vegetated canopies and the atmosphere for a short period or even for several years can be obtained with minimal disturbance to the vegetation^{14–16}. Another attribute of this method is its ability to sample a relatively large area of land¹⁷. The NEE of CO₂ between the biosphere and the atmosphere is the balance between fluxes associated with photosynthetic assimilation by the foliage (gross ecosystem production (GEP)) and respiratory effluxes from autotrophs (roots) and heterotrophs (microbial and soil fauna)¹⁸.

NEE provides information about the length of the active season and the strength of the component processes, photosynthesis and respiration¹³. Ecosystem respiration is the efflux of CO₂ from the ecosystem to the atmosphere due to autotrophic (vegetation respiration) and heterotrophic (soil respiration excluding root respiration) activi-

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ties. Ecosystem respiration contributes significantly to the NEE and varies with changing environmental factors. The ecosystem respiration measured using chamber technique and in laboratory is limited to measurement over short period or at a particular time of a small area with disturbance of the ecosystem¹⁹. The EC system enables the continuous measurement of nighttime ecosystem CO₂ fluxes unlike most of the chamber measurements. These nighttime CO₂ flux measurements corrected with the wind turbulence can be used to estimate ecosystem respiration^{20–22}.

The main objective of this research was to continuously measure CO₂ exchange between the grassland ecosystem and the atmosphere and to elucidate seasonal changes in NEE and ecosystem respiration in semi-arid grassland.

Materials and method

Site information

The study was carried out at undisturbed and protected 20-year-old *Cenchrus ciliaris* grassland at Botanical Garden (lat. 10°00'N; long. 78°10'E; alt. 133 m above msl), Madurai Kamaraj University, Madurai, India. The topography of the site is flat land. The mean annual precipitation is 600 mm and the wet season occurs from August to December with high rainfall during October–December. The dry season starts by February and lasts till June, and July is the transition between dry season and wet season. Brief summer rains are received mostly in March and June. The average mean ambient temperature ranges

between 20.3°C (min) and 38.6°C (max). The soil type is laetrite loam with pH 8.5, bulk density of 1.54 g/cm³ and water holding capacity of 34.34%.

Eddy flux measurements

EC measurement was taken from 6 July 2008 to 21 June 2009. Eddy covariance sensors were mounted 2 m above the ground on a portable CM10 tripod (Figure 1) as described by Baldocchi *et al.*⁶. The fetch area is estimated to be 200 m diameter. The EC system consists of open path infrared gas analyser (LI-7500, LICOR, Lincoln, NE, USA), three-dimensional sonic anemometer (CSAT3), net radiometer (Q 7.1) mounted at 2 m from the ground, self-calibrating soil heat flux plate (HFP01SC-L50) placed at 8 cm from the soil surface, water content reflectometer (CS616-L50) placed horizontally at 2.5 cm from the soil surface, averaging soil temperature probe (TCAV-L50) placed at 2 and 6 cm from the soil surface, and a data logger (CR3000) which are all obtained from Campbell Scientific, Inc., Logan, Utah, USA. The datalogger recorded the signal from all the sensors every 0.2 s and calculated every half hourly average which was used as raw data. Out of the study period of one year, the data coverage accounted for 83.5%. This is higher than the typical percentage of 65–75 of data coverage from EC measurement in a year as reported by Falge *et al.*¹³.

Diurnal and daily NEE

The CO₂ flux data corrected according to Webb *et al.* were used as NEE^{23–25}. The average of half an hour flux

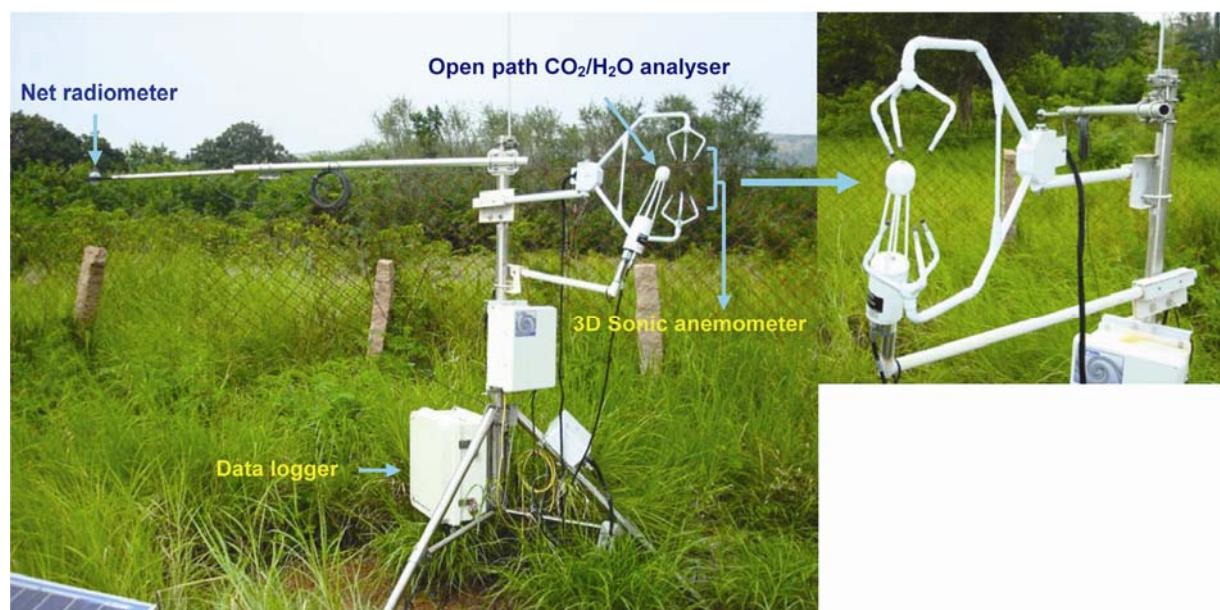


Figure 1. Eddy covariance system installed on *Cenchrus ciliaris* grassland at Madurai Kamaraj University, Madurai.

data in units of $\text{CO}_2 \text{ mg m}^{-2} \text{ s}^{-1}$ was multiplied by 1800 to give the total CO_2 flux in 30 min duration. Daily diurnal (from midnight to midnight) NEE and the average of every half an hour NEE were calculated. Positive NEE indicated that CO_2 was released and negative values represented uptake of CO_2 . The duration of the active season or the growing season was determined by the week that was the first of two or more consecutive weeks with negative NEE as described by Falge *et al.*¹³ and Law *et al.*¹⁸.

Ecosystem respiration

The night CO_2 flux is taken as an estimate of ecosystem respiration as the GEP is zero²⁴ due to absence of assimilation or photosynthesis at night. The night respiration was determined by taking the average of half an hour fluxes during the period when the net radiation was negative. The relationship between ecosystem respiration (Reco) and volumetric soil moisture; and Reco and soil temperature was determined by plotting regression graph.

Friction velocity

Underestimation of the nighttime CO_2 fluxes can occur due to low wind turbulence. According to previous reports^{26–29}, the cut-off value of the vertical wind velocity (friction velocity denoted as u^*) depends upon the site and vegetation. Arneth *et al.*²⁶ report that the cut-off value or threshold of u^* is $>0.2 \text{ m s}^{-1}$ at birch forest, $>0.1 \text{ m s}^{-1}$ at the Mopane woodland in northern Botswana, 0.055 m s^{-1} at the wetland and 0.15 m s^{-1} at the pine forest. We observed underestimation of CO_2

fluxes at u^* below 0.05 m s^{-1} . To avoid nocturnal underestimation of CO_2 fluxes, the CO_2 flux data U^* below 0.05 m s^{-1} were corrected.

Results

Seasonal pattern of daily NEE

The daily NEE showed marked seasonal variation (Figure 2). NEE and soil moisture content showed similar pattern. The early part of July showed positive NEE which indicated that CO_2 was released by the grassland ecosystem. Ecosystem CO_2 uptake was observed soon after the rainfall during late July that indicates the starting of the growing season which lasted till mid-January. The high CO_2 uptake during September to December corresponded with the rainy season during which high soil moisture content was observed. Maximum average CO_2 uptake of $-18.73 \text{ g m}^{-2} \text{ day}^{-1}$ was observed in November. Soil moisture content showed minimum of $0.022 \text{ m}^3 \text{ m}^{-3}$ in July and maximum value of $0.275 \text{ m}^3 \text{ m}^{-3}$ in October. The gradual decrease in soil moisture from late December corresponded with the gradual decrease in CO_2 uptake and eventually the release of CO_2 by the ecosystem. Positive NEE from late January to June except few days after summer rains in April and May, indicated that the ecosystem was a source of CO_2 in the dry season during which soil moisture was below $0.08 \text{ m}^3 \text{ m}^{-3}$. Positive pulses in NEE were observed in the first rainfall events (evident from the soil moisture content) after prolonged drought. The pulse or sharp increase in CO_2 release was caused by the rewetting of soil and dropped down to stable value after one or two days. The light summer rain events

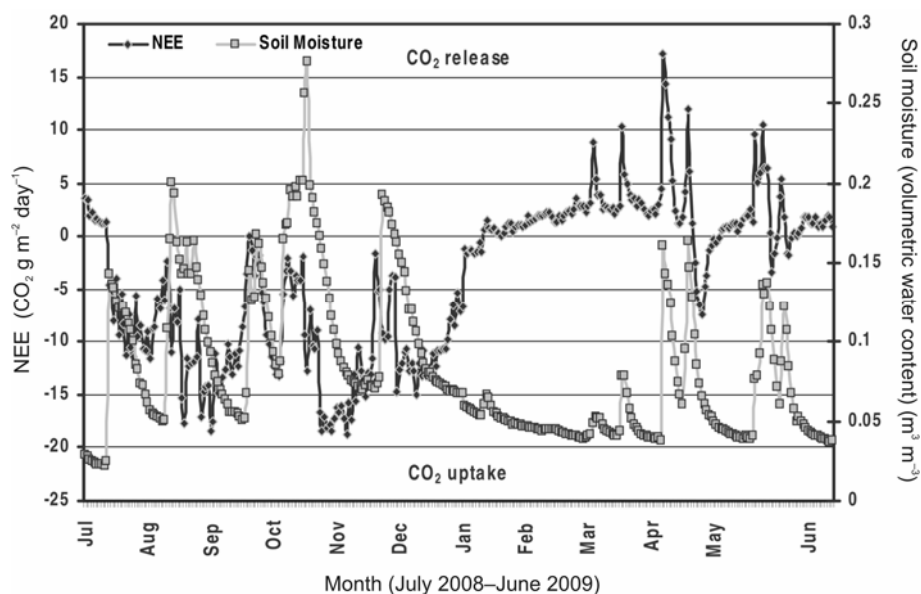


Figure 2. Seasonal pattern of daily net of ecosystem exchange of CO_2 and soil moisture content of *Cenchrus ciliaris* grassland. Positive points indicate CO_2 release and negative points indicate CO_2 uptake by the ecosystem.

during March and May caused pulses in CO₂ and soil water content. Short duration of CO₂ uptake was observed after the rewetting during April and May. The amplitude of daily CO₂ uptake during the active season was much higher than the CO₂ released during the dormant season, which was below 5 g of CO₂ m⁻¹ day⁻¹ except few pulses due to rewetting.

Diurnal NEE

The variation in diurnal NEE was strongly regulated by seasonal changes during the study period. During the wet season from August to December, high daytime and nighttime CO₂ fluxes in comparison with the dry season were observed (Figure 3). In this wet season, although

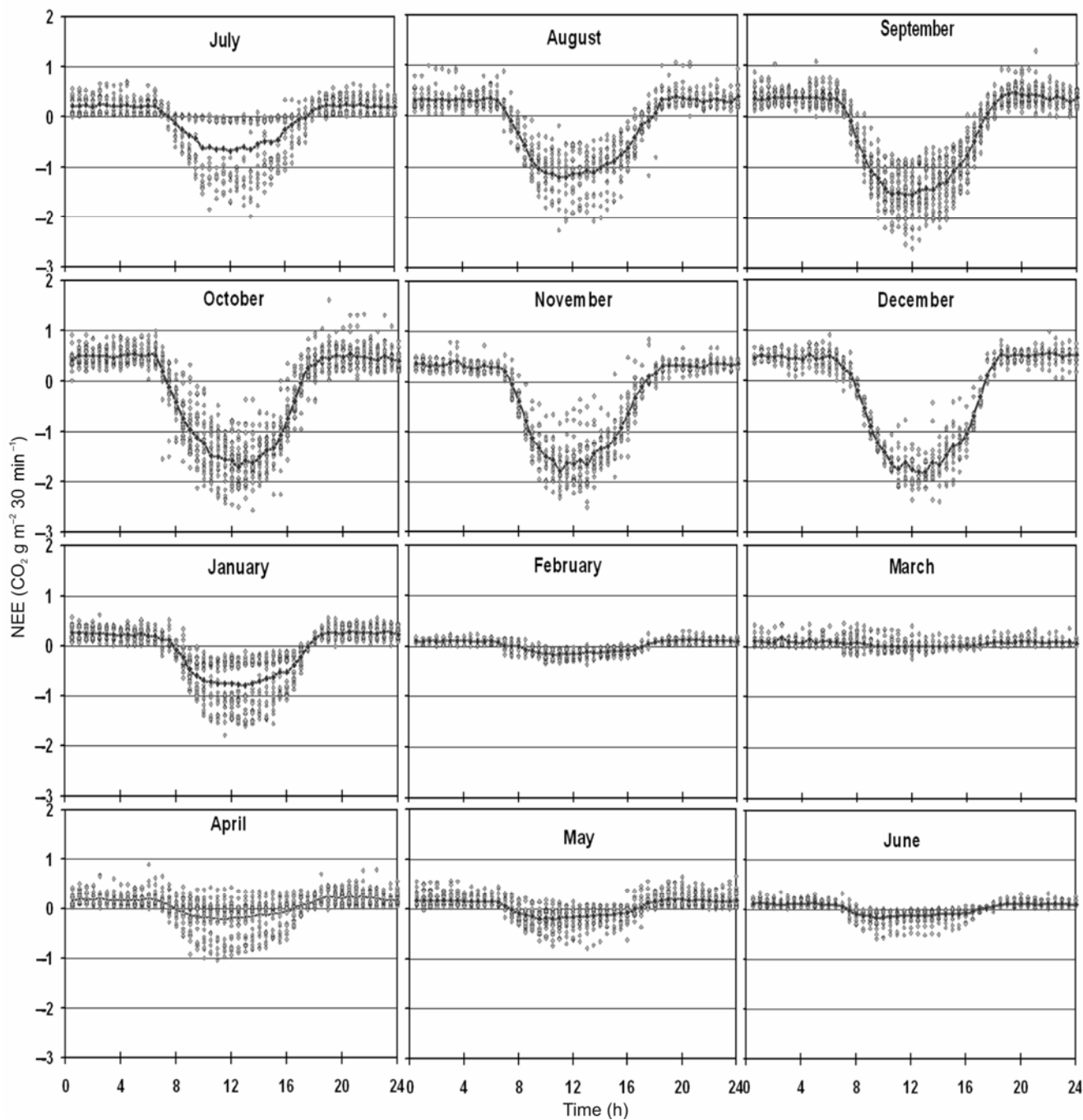


Figure 3. Monthly diurnal net ecosystem exchange of CO₂ of *Cenchrus ciliaris* grassland. Each point is the half hourly average and dark line is the average of all the points of that particular time of a day. Positive value denotes release of CO₂ and negative value denotes uptake of CO₂ by the ecosystem.

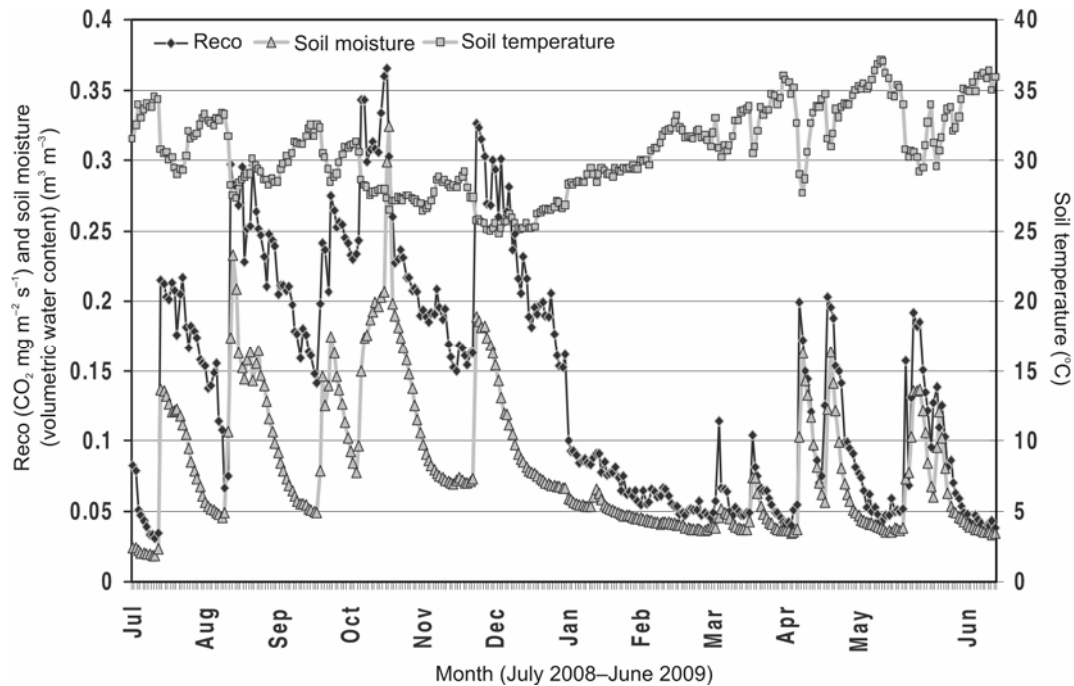


Figure 4. Seasonal pattern of ecosystem respiration (Reco), soil moisture and soil temperature. Each point represents the average of half hourly data of one night.

there was high nocturnal CO₂ efflux from the ecosystem, the daytime uptake of CO₂ was comparatively much higher, here the NEE became more negative (Figure 2). Maximum daytime CO₂ uptake was observed around midday (11:00 h to 13:00 h). Maximum average uptake of $-1.809 \text{ g m}^{-2} \text{ 30 min}^{-1}$ was observed during December at 12:30 h. During the dry season from February to June, there was a significant reduction in daytime and nighttime CO₂ fluxes and in February, March and June, the average CO₂ fluxes were close to zero. In March, positive average NEE was observed during daytime which implies that the ecosystem respiration rate exceeded the assimilation rate due to the drying up of the aerial parts of the plant.

Ecosystem respiration

Reco showed similar pattern of seasonal variation with soil moisture (Figure 4). Reco ranged from $0.0309 \text{ CO}_2 \text{ mg m}^{-2} \text{ s}^{-1}$ in July to $0.365 \text{ CO}_2 \text{ mg m}^{-2} \text{ s}^{-1}$ in October, which corresponded to the minimum soil moisture of $0.018 \text{ m}^3 \text{ m}^{-3}$ in July and maximum soil moisture of $0.324 \text{ m}^3 \text{ m}^{-3}$ in October. According to Austin *et al.*³⁰ and Huxman *et al.*³¹, microbes have the capacity to respond rapidly to wetting events in highly seasonal and dry land. Chou *et al.*³² reported that large positive pulses of CO₂ from the ecosystem occurred in wet-up events and the combined wet-up events contributed to 8–18% of the total carbon respired per year in annual grassland in California. Borken *et al.*³³ reported that a strong decrease in microbial respiration with decreasing soil water content

and the low summer water content restrict the microbial decomposition of organic matter. Unlike the pattern of CO₂ uptake, where there was a lag between the maximum soil moisture content and the time of high CO₂ uptake, the maximum Reco occurred when the soil moisture content was maximum and decreased gradually with the gradual depletion of soil moisture. This finding supported the report of Arneeth *et al.*¹¹ that the instantaneous increase in respiration was caused by the first rainfall in Mopane woodland and that assimilation was observed about 10 days later. Reco and volumetric soil water content showed strong positive correlation of coefficient of determination, $R^2 = 0.768$ (Figure 5). Soil temperature decreased with the increased soil moisture, reaching minimum of 24.74°C during December and increased toward the summer and reached maximum of 37.14°C in May. Negative correlation of $R^2 = 0.498$ was observed between Reco and soil temperature (Figure 6). Low Reco was observed during the dry season from February to June.

Discussion

NEE of the grassland ecosystem showed a cyclic pattern of active season (ecosystem CO₂ uptake) and dormant season during which CO₂ was released by the ecosystem. This cyclic pattern strongly corresponds with the wet and dry season based on the rainfall pattern of the year. This showed that the physiological condition and productivity of the plant as well as the biogeochemistry of the soil strongly depend on the soil moisture dynamics. The active season when uptake of CO₂ exceeded the ecosystem

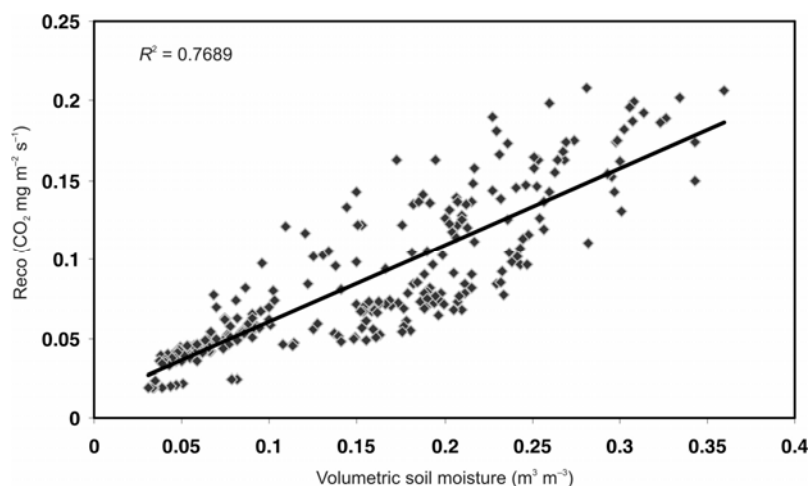


Figure 5. Relationship between Reco and volumetric soil moisture content in *Cenchrus ciliaris* grassland. Each Reco point is an average of one night's half hourly data.

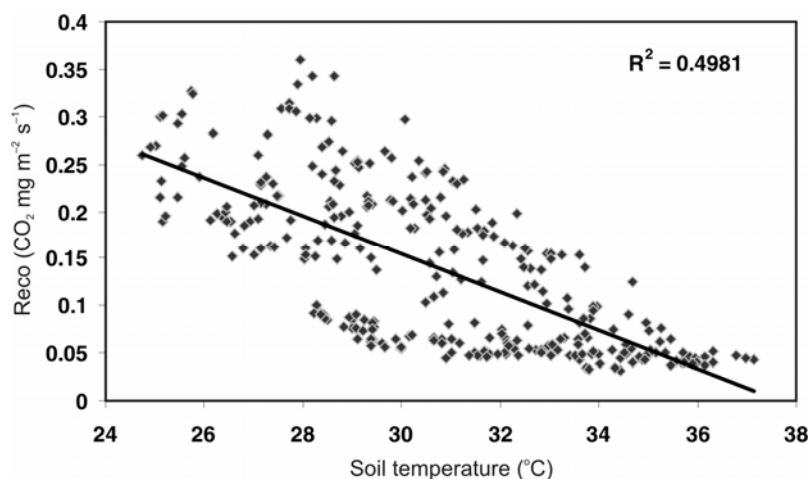


Figure 6. Relationship between ecosystem respiration (Reco) and soil temperature in *Cenchrus ciliaris* grassland. Each Reco point is an average of one night's half hourly data.

respiration accounted for 7 months of the year. The longer duration of the active season and comparatively much higher amplitude of the net ecosystem CO₂ uptake in the wet season to the duration and amplitude of CO₂ released in the dry season is an indication of the high potential of the grassland ecosystem in sequestering atmospheric carbon. Characterization of seasonal phasing and amplitudes of ecosystem CO₂ fluxes is important in understanding the factors that govern the interplay between respiratory and assimilation processes and in assessment of regional and global carbon sequestration potentials¹³. From this observation, it is apparent that the grassland ecosystem is a carbon sink during the wet season and a source during the dry season. Fay *et al.*³⁴ and Chou *et al.*³² reported that the ecosystem-scale carbon cycling in annual grasslands was more sensitive to seasonal distribution of rainfall than to total amount of rainfall in any given year. Porporato *et al.*³⁵ also suggested that even under the same amount total rainfall, variation in the intensity and frequency of rainfall events will affect the soil moisture dynamics and plant conditions to

an extent that depends on the soil and plant physiological characteristics at the site. Therefore, accounting only for changes in mean responses to climatic variability is not sufficient in elucidating the impact of climate change on ecosystems. The pulse in positive NEE in rewetting is because of the outburst of CO₂ from the ecosystem due to the filling of soil pore spaces by the percolating water, the release of carbon held as inorganic carbonates^{36,37}, and the rapid decomposition and microbial activity³⁰. Previous report stated that the ability of microorganisms to respond within a few minutes of wetting³³ and the duration of the post-wetting CO₂ pulse may depend on the duration of drought and the amount of water added³⁸. The CO₂ pulse following wetting of dried soil has been related to the amount of easily decomposable C due to the death of microorganisms or exposure of easily decomposable carbon on drying³⁹. The pulses in CO₂ released due to rewetting of the soil were comparatively smaller in March than the pulses in April and May. The rewetting in April and May was sufficient to revive the plant for short period, thereby causing net ecosystem CO₂ uptake for

few days after the rain. This showed the sensitivity of the *C. ciliaris* grassland to soil moisture dynamics in semi-arid regions and the ability of the plant to quickly recover with slight increase in soil moisture content even after a long dry period. Although the rewetting in March resulted in pulses in CO₂ release but not in CO₂ uptake in successive days, it may be however crucial for the plant to withstand the dry season and to respond to larger rewetting as observed during April and May. Yan *et al.*⁴⁰ reported that duration of interpulse and severity of drought stress determine the rate of recovery of photosynthesis and transpiration, and small pulses due to rewetting help plant to survive or maintain leaf area, which increases their capacity to respond to larger events.

The amplitude of the diurnal cycle of daytime and nighttime CO₂ fluxes increased by many folds during the wet season when compared to dry season which is attributed to the active assimilation and respiration rate. This is in agreement with the findings of Furger *et al.*⁴¹ that during period of maximum assimilation, the amplitude of the CO₂ variation (CO₂ uptake and respiration) is about twice as large as that of low assimilation in late autumn in grassland in the Swiss Alps. The observations in different ecosystems studied under FLUXNET, EUROFLUX and Ameriflux also exhibit similar trends of high uptake corresponding with high release and low uptake with low releases¹³. The diurnal NEE indicated that the studied ecosystem is a source of CO₂ in dry season not because of increased ecosystem respiration but due to the sharp decline in daytime CO₂ uptake or even release of CO₂ in daytime as observed in March. This result supports the previous report by Mateus *et al.*⁴² that the depression in NEE in summer is mostly due to the carbon uptake than the increase in respiration. Even though there was a high rate of ecosystem respiration at night, the CO₂ uptake during daytime was much higher. This showed that considering only the ecosystem respiration or the soil respiration could be misleading in evaluating CO₂ fluxes of an ecosystem as the high CO₂ efflux coincides with the comparatively higher rate of CO₂ uptake.

The strong relationship between soil moisture and Reco showed the regulation of Reco by soil moisture. Similar results were reported in soil respiration of tree plantations at this study site by Saraswathi *et al.*⁴³. Although the role of soil temperature on Reco was difficult to assess as soil temperature decreased with increase in soil moisture, it is apparent from their negative correlation that soil temperature is not the determinant of Reco in semi-arid tropics unlike most of the ecosystems of temperate regions where strong positive correlation exists.

Conclusion

This is the first study of NEE of CO₂ and ecosystem respiration of grassland ecosystem in semi-arid tropics of

India using EC system. The grassland ecosystem in semi-arid region showed high seasonal changes in NEE and ecosystem respiration rates. Severe reduction in soil moisture is the main limiting factor of carbon uptake in grasslands of semi-arid tropics and the phase of net ecosystem uptake (carbon sink) and release (carbon source) of CO₂ depends on the balance between wet season and dry season. The active season was discerned by the high amplitude of daytime net CO₂ uptake and nocturnal CO₂ release. The much higher amplitude of daytime CO₂ uptake when compared with nocturnal CO₂ release resulted in the high daily net CO₂ uptake despite high nocturnal CO₂ release in this season. Ecosystem respiration is strongly determined by the soil moisture rather than the soil temperature.

From this preliminary study, it is evident that grassland ecosystems in semi-arid tropics are highly sensitive to changes in environmental factors. The immediate response (in carbon uptake) to the increase in soil water content by rainfall and the high carbon uptake in the wet season proved that grasslands have high carbon sequestration capacity. The grassland being a carbon source during the dry season implies that grasslands in semi-arid regions are in a critical state under the global climate change where prolonged drought has been predicted in arid and semi-arid regions. The effect of changes in inter-annual total rainfall and rainfall distribution on the assimilation and respiration processes, and the rejuvenation capacity of grassland in semi-arid regions have to be studied for a longer period for model prediction of carbon budget of grassland ecosystems.

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