



Modeling pulsed soil respiration in an African savanna ecosystem



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ARTICLE INFO

Article history:

Received 14 August 2014

Received in revised form 15 October 2014

Accepted 19 October 2014

Keywords:

DOC

Birch effect

Microbial

Precipitation

Drying

Wetting

ABSTRACT

Savannas cover 60% of the African continent and play an important role in the global carbon (C) emissions from fire and land use. To better characterize the biophysical controls over soil respiration in these settings, half-hourly observations of volumetric soil–water content, temperature, and the concentration of carbon dioxide (CO₂) at different soil depths were continually measured from 2005 to 2007 under trees (“sub-canopy”) and between trees (“inter-canopy”) in a savanna vegetation near Skukuza, Kruger National Park, South Africa. The measured soil climate and CO₂ concentration data were assimilated into a process-based model that estimates the CO₂ production and flux with coupled dynamics of dissolved organic C (DOC) and microbial biomass C. Our results show that temporal and spatial variations in CO₂ flux were strongly influenced by precipitation and vegetation cover, with two times greater CO₂ flux in the sub-canopy plots (~2421 g CO₂ m⁻² yr⁻¹) than in the inter-canopy plots (~1290 g CO₂ m⁻² yr⁻¹). Precipitation influenced soil respiration by changing soil temperature and moisture; however, our modeling analysis suggests that the pulsed response of soil respiration to precipitation events (known as “Birch effect”) is a key control on soil fluxes at this site. At this site, “Birch effect” contributed to approximately 50% and 65% of heterotrophic respiration or 20% and 39% of soil respiration in the sub-canopy and inter-canopy plots, respectively. These results suggest that pulsed response of respiration to precipitation events is an important component of the C cycle of savannas and should be considered in both measurement and modeling studies of carbon exchange in similar ecosystems.

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1. Introduction

Savannas are an important contributor to the Earth's biogeochemical cycles. These regions cover approximately 17–23% of world's land surface area, store approximately 15% of world's terrestrial carbon (C), and contribute to approximately 30% of the world's terrestrial net primary productivity (NPP; Grace et al., 2006; Peel et al., 2007). These systems may also be vulnerable to increasing atmospheric carbon dioxide (CO₂) concentration, which could cause a vegetation transition from grassland to woody-plant in the savanna regions (Bond, 2008; Higgins and Scheiter, 2012). Such a change would also lead to changes in savanna biomass and productivity, and associated impacts on global C cycle and climate (Beringer et al., 2011).

The savannas of Africa cover over half the continent and are the world's largest example of this biome (Grace et al., 2006). The

combination of C₃ tree species with C₄ grasses in tropical savannas creates potential spatial variability in soil C flux patterns and represents one of the primary scales of organization in these ecosystems. The variation in vegetation cover also introduces significant uncertainty into estimates of landscape scale fluxes of mass and energy (Baldocchi et al., 2004) and numerous studies suggest that there is variation in nutrient cycling and water use under tree canopies compared to grass-dominated inter-canopy sites (Dohn et al., 2013; Ludwig et al., 2003; Oren et al., 2006; Wang et al., 2009).

The savannas of Africa are also characterized by distinct wet and dry seasons as well as a high degree of inter-annual variance in precipitation. For these reasons, the dynamics of savanna ecosystems are significantly influenced by variations in both precipitation and temperature (Brummer et al., 2008), causing strong inter-annual and seasonal variations in savanna C exchange and primary productivity (Williams et al., 2007). In addition, the drying–wetting cycles due to isolated precipitation events can produce pulsed inputs of moisture, resulting in pulse-response C flux characteristics that are common to similar semi-arid ecosystems (Fierer and Schimel, 2003; Ma et al., 2012; Williams et al., 2009; Xu et al., 2004) and is

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known as “Birch effect” (BE) (Birch, 1964). Therefore, the system response to moisture is not a negligible control on net ecosystem exchange at the ecosystem scale (Williams et al., 2007).

In studies of Mediterranean ecosystems, the response of soil respiration to moisture exhibited strong nonlinear dynamics, suggesting a relatively complex relation between soil moisture availability and decomposition (Almagro et al., 2009; Jarvis et al., 2007; Schmidt et al., 2007). In addition to the impact of pulsed inputs of moisture on soil respiration by directly changing soil temperature and moisture, there are a number of other reasons why moisture and decomposition flux are not linearly coupled in semi-arid ecosystems. Pulsed inputs of moisture due to precipitation events could introduce the easily decomposable exogenous substances (e.g., fresh and/or labile C derived from plant residues or litter) into soil (Qualls et al., 1991) or release microbe-available labile C (e.g., derived from microbial cell death) that are previously inaccessible to microbes (Manzoni et al., 2014). This would significantly change substrate supply kinetics and the subsequent microbial dynamics (e.g., microbial biomass and activity) and soil respiration. Many studies indicated that microbial dynamics was the key factor responsible for the pulsed response of soil respiration to precipitation events (e.g., Blazewicz et al., 2014; Jarvis et al., 2007; Liu et al., 2006; Meisner et al., 2013; Turner et al., 2003).

The complexity of soil water relations and microbiological responses to soil water content in semi-arid soils may translate into difficult prediction and/or simulation of soil C flux in response to changing environmental conditions. Although it is possible to simulate the pulse–response dynamics of soil respiration by empirically fitting existing models to data (e.g., Li et al., 2006, 2010), the absence of adequate mechanistic representations of soil microbial processes can lead to substantial over- or under-estimation of soil flux under variable moisture conditions (Lawrence et al., 2009). In modeling laboratory drying–wetting experiments, traditional first order soil organic matter models consistently underperformed more mechanistic complex models that included explicit representation of soil microbial processes (Lawrence et al., 2009). For prediction of responses of soil respiration to variability in short-term precipitation or longer-term climatic parameters, the failure to quantify the impacts of precipitation on soil respiration flux has implications for prediction of ecosystem scale C exchange and soil C storage (Hanan et al., 1998).

In this study, we combine high temporal frequency field measurements with a data assimilation/modeling approach to examine soil respiration dynamics in an African Savanna. The overall goal of our study was to evaluate the importance of precipitation-induced soil respiration pulses on the savanna C cycle. Our study has several components. First, to evaluate seasonal and landscape-scale variation in soil CO₂ flux, we measured soil flux on an approximately monthly basis across a series of plots distributed in sub-canopy and inter-canopy plots in a *Combretum* savanna. Secondly, we installed two profiles of in situ soil CO₂ sensors that measured soil CO₂ concentrations continuously for a period of nearly two years. These sensors were used to examine short time scale pulse–response dynamics of soil respiration at these sites. Lastly, to place these fluxes in a mechanistic and quantitative context, we used a newly created, process-based soil diffusion and soil carbon cycling model to simulate the production and transport of CO₂.

2. Methods

2.1. Site and study description

Our study was conducted within a 300 m × 300 m plot near the Skukuza camp of Kruger National Park, South Africa (latitude:

–25.02; longitude: 31.496) at an elevation of 370 m. Skukuza has a mean annual precipitation of 550 mm with the majority (~90%) of the precipitation falling in the wet season (between November and April). The study area is a savanna ecosystem with shallow soil (~0.6 m deep) and 28% tree cover (Scholes, 1999). The grassy and herbaceous understory of this savanna is primarily comprised of *Panicum maximum*, *Digitaria eriantha*, *Eragrostis rigidor*, and *Pogonarthria squarrosa* (see Scholes, 1999 for detailed site descriptions).

2.2. Soil CO₂ flux measurements

Chamber based soil CO₂ flux measurements were performed with an infra-red gas analyzer (IRGA) (SRC-1 chamber and EGM-2 IRGA, PP-Systems, Haverhill, MA). Measurements were taken at each sub-canopy and inter-canopy plot one to two times a month from November 2004 to July 2006 except for during the dry season (August, September, and October) of 2005. A 200 m transect was established along a 2% slope consisting of eight sub-canopy plots and eight adjacent inter-canopy plots (eight sub-canopy/inter-canopy pairs). Each paired set of plots was separated by a distance of approximately 20 m. We inserted a 10.2 cm diameter soil respiration collar 2.5 cm into the ground in the beginning of the study and this collar was used for all subsequent soil CO₂ flux measurements.

2.3. Soil CO₂ concentration, temperature, and water content measurements

To develop near-continuous time-series data for soil CO₂ concentrations, we installed two profiles of Vaisala GMP 220 solid state CO₂ sensors (Vaisala, Helsinki, Finland) within one of our canopy/inter-canopy plot pairs. The Vaisala sensors were installed below the ground at 5, 10, and 20 cm in a sub-canopy plot and at 5 and 10 cm in an inter-canopy plot. These sensors were located within 2 m of Campbell CS615 Time Domain Reflectometer probes and thermocouples that were installed at 5, 13, 29, and 61 cm depths for soil water content and temperature measurements, respectively. To avoid moisture damage to the Vaisala sensors, the probes were housed in PVC tubes inserted, at an angle, into the soil with an opening at the desired measurement depth. The PVC tubes were sealed at the top with a Silicone sealant that was tested prior to installation to ensure no reaction with headspace CO₂. Prior to installation, each probe was evaluated for consistent responses to changing CO₂ concentrations and probe calibrations were conducted as needed to ensure similarity among the probes.

2.4. Soil physical and chemical analysis

In each sub-canopy and inter-canopy site, we collected 0–5 cm, 10–15 cm, and 20–25 cm deep soil cores with a soil auger. Each soil core was analyzed for organic C (OC) and soil texture. Prior to soil analysis, soil cores were oven dried at 60 °C, weighed, and passed through a 2-mm sieve. The less than 2-mm soil size fraction was homogenized and divided into 1 g aliquots for OC and texture analyses with a soil splitter (model SP-171X, Gilson Company, Inc., Lewis Center, OH). Once the 1 g aliquots were collected, the remaining soil was recombined and divided in half with the soil splitter. One half of the soil was archived. The other half was weighed and removed of roots in order to determine root mass within the soil and determine root OC content. Bulk density was determined for each site using volumetric sampling of soil samples that were subsequently dried and weighed.

Soil and root OC content was measured at the University of Colorado with an EA 1110 CNS combustion analyzer (Thermo Electron

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