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Fire interacts with season to influence soil respiration in tropical savannas

Anna E. Richards [a,*], Josefine Dathe [b], Garry D. Cook [a]

[a] CSIRO Ecosystem Sciences, PMB 44, Winnellie, Northern Territory 0822, Australia
[b] University of Applied Science, Eberswalde 16225, Germany

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ABSTRACT

Soil respiration (R_s) is the second-largest source of CO_2 to the atmosphere in terrestrial systems. In tropical savannas seasonal moisture availability and frequent fires drive ecosystem dynamics and may have a considerable impact on soil carbon (C) cycling, including R_s. In order to test the effect of fire on soil C cycling we measured R_s in annually burnt and unburnt plots in wet and dry seasons at a long-term fire experiment established in savanna woodlands of northern Australia. There was a significant interaction between season and fire, with highest rates of daily R_s (722 mmol CO_2 m^{-2} d^{-1}) observed in the wet season on unburnt, leaf litter patches. The three fold higher R_s rate on unburnt plots in the wet season was due to greater root-derived respiration (R_{root}: 356 mmol CO_2 m^{-2} d^{-1}), while smaller changes to soil-derived respiration (R_{soil}: 51 mmol CO_2 m^{-2} d^{-1}) were simply the result of C moving through decomposition rather than combustion pathways. Relationships between instantaneous R_s and soil temperature showed hysteresis with variable direction, suggesting that season and fire treatment also influence the soil depth at which CO_2 is produced. We suggest that (1) changes to fire regimes, through active management or climate change, in tropical savannas could have an impact on R_s, and (2) the direct effect of fire on soil C cycling is limited to the removal of aboveground litter inputs.

1. Introduction

Soil respiration (R_s), which refers to the flux of CO_2 from soils to the atmosphere, is the second-largest terrestrial source of CO_2 and an important part of the global carbon (C) cycle (Raich et al., 2002; Raich and Schlesinger, 1992). CO_2 is produced from several sources; (1) microbial decomposition of soil organic matter in root free soil without undecomposed plant material (basal respiration), (2) microbial decomposition of soil organic matter in root or plant residue affected soil (termed the 'rhizosphere priming effect'), (3) microbial decomposition of dead plant material, (4) microbial decomposition of rhizodeposits (rhizomicrobial respiration), and (5) root respiration (Kuzyakov, 2006). These sources can be grouped into soil-derived CO_2 (first and second sources) and the remaining sources as plant-derived CO_2.

The main physical drivers of R_s are temperature and moisture. Numerous studies have shown a positive relationship between temperature and R_s (e.g. Fang et al., 2005; Raich and Potter, 1995). Moisture availability also impacts R_s, with dry soils having lower R_s than wet soils (Conant et al., 2004). However, due to, high spatial variability and cost of measurement, R_s is the least understood component of the terrestrial C cycle, and this hampers efforts to model and predict changes to R_s, particularly under future climate changes (Bond-Lamberty and Thomson, 2010; Trumbore, 2006).

Savannas are a large and important biome in tropical regions, store a significant proportion (*ca.* 80%: Dalal and Allen, 2008) of their terrestrial C stocks in soil pools and have high CO_2 efflux rates (tropical ecosystem R_s rates 1286 ± 633 g C m^{-2} y^{-1}: Bond-Lamberty and Thomson, 2010). Savannas are also some of the most flammable ecosystems on the planet, with *ca.* 20% of their land area burnt annually (Chuvieco et al., 2008; Dwyer et al., 2000), and are characterised by distinct wet and dry seasons, such that seasonally available moisture dramatically influences productivity (Hutley and Setterfield, 2008). These characteristics of moisture and disturbance driven dynamics may have a considerable impact on soil C cycling in tropical savannas. Consistent with this premise, a previous study that measured R_s in tropical savannas of northern Australia found rates were highest in the wet season (5.37 mol CO_2 m^{-2} s^{-1}) and only positively correlated with temperature in the wet season (Chen et al., 2002). However, this study did not look at the effect of fire on R_s.

In a system without fire, C enters via photosynthesis and then returns to the atmosphere through above- and below-ground autotrophic and heterotrophic (herbivore, carnivore, detritivore, microbial) respiration. In flammable ecosystems, such as tropical savannas, it has been suggested that fire consumes aboveground C much like herbivores (Bond and Keeley, 2005), removing C from

* Corresponding author. Tel.: +61 8 8944 8437; fax: +61 8 8944 8444.
E-mail address: Anna.Richards@csiro.au (A.E. Richards).

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other consumption pathways, including R_s. If the reduction in R_s in regularly burnt ecosystems, as has been observed elsewhere (García-Oliva et al., 1999; Liu et al., 2010; Mills and Fey, 2004), is equivalent to the consumption of C by fire, then the direct effect of fire is to simply modify the pathway through which C is returned to the atmosphere. However, if fire modifies other processes, such as microbial biomass and community composition (Campbell et al., 2008), soil physical properties (Certini, 2005; Mills and Fey, 2004), plant root activity and the quality and quantity of subsequent soil organic matter inputs (Cook, 2001; Hernandez and Hobbie, 2008; Johnson and Matchett, 2001; Ojima et al., 1994; Reich et al., 2001), then the effect of fire on soil C cycling, including R_s, may be much greater than alteration of consumption pathways.

Australian savannas cover 2 million km^2 and are mostly structurally intact landscapes that have undergone relatively little land-use modification (Woinarski et al., 2007). However, changes to fire management in the last 50–100 years, particularly in northern, mesic savannas, have led to more frequent and intense fires (Russell-Smith et al., 2007). Approximately 55% of mesic (>1000 mm annual rainfall) tropical savannas in the Northern Territory currently burn at least once every two to three years. In response to this, there has been a recent effort to implement greenhouse gas emissions (methane and nitrous oxide only) abatement programs that undertake fire management to reduce the extent and frequency of intense fires in Australia's tropical savannas (Russell-Smith et al., 2009; Whitehead et al., 2008). However, there is increasing interest in understanding the impact of these programs on all greenhouse gas dynamics by measuring the additional effect of fire management on above- and below-ground C dynamics (Richards et al., 2011).

Our objective in this study was to understand the impact of fire on soil C cycling by using frequent, automated measurements of R_s in regularly burnt and unburnt tropical savanna. In order to understand how other abiotic factors may interact with fire to influence R_s and its components; root- and soil-derived CO_2, we undertook measurements in the late dry season and early wet season and concurrently recorded soil temperature and soil moisture. Analysis of the interaction between disturbance and physical factors and their impacts on R_s should improve our understanding of the drivers of C cycling in tropical savannas.

2. Materials and methods

2.1. Study site

R_s measurements were made at a fire experiment established in 2004 at the Territory Wildlife Park, Northern Territory, Australia (12°41′42″S, 131°58′50″E). The vegetation at the site is open-forest and woodland savanna dominated by *Eucalyptus miniata* A.Cunn. ex Shauer, *Eucalyptus tetrodonta* F.Muell. and *Corymbia bleeseri* (Blakely) K.D.Hill & L.A.S.Johnson, with a grassy understorey dominated by *Sarga intrans* (F.Muell.) Spangler, *Pseudopogonatherum contortum* (Brongn.) A.Camus. and *Eriachne triseta* Nees ex Steud (Scott, 2008). The soils are relatively shallow (0.5–1 m deep) gravelly red earths (Petroferric Red Kandosol: Isbell, 2002) of the Kay land system within the Koolpinyah land surface group, developed predominantly from deeply weathered sandstones, siltstones and shales (Wood et al., 1985). The climate is wet–dry tropical with greater than 90% of annual rainfall (1401 mm) falling in the wet season from November to April, and average annual monthly maximum and minimum temperatures of 34.3 °C ± 1.9 °C and 20.6 °C ± 3.9 °C, respectively (Bureau of Meteorology, Commonwealth of Australia).

The fire experiment at the Territory Wildlife Park consists of 18 one hectare plots grouped into 3 blocks arranged along a north-south transect (for further details see Richards et al., in press). Six fire treatments were randomly assigned to each block and included unburnt, plots burnt at fire return intervals of 1, 2, 3 and 5 y in the early dry season (low intensity fires) and every 2 y in the late dry season (higher intensity fires). Prior to implementation of the burning treatments in 2004 all areas had experienced a low fire frequency (approximately one fire every 7 years) for at least 14 years. R_s measurements were made on the unburnt and annually burnt plots only.

2.2. Soil measurements

An automated R_s system with eight long-term observation chambers connected to an infra-red gas analyser and multiplexer (LI-8100, LI-COR Inc., Lincoln, Nebraska, USA) was used to record soil CO_2 fluxes. Each measurement took 90 s with an initial 20 s delay prior to logging data. Chambers automatically opened between measurements allowing soil to be exposed to ambient environmental conditions. Measurements were made every hour over 48 h on each plot. Observation chambers were placed over PVC soil collars (11.4 cm high and covering a 324 cm^2 area) that were inserted into the soil to a depth of approximately 3 cm in each plot at least 48 h prior to measurements. Plots were measured consecutively over a four week period in October 2009 (late dry season) and a two week period in January 2010 (early wet season). The total rainfall and average maximum air temperature during the two measurement months was 20 mm and 38 °C in October, and 704 mm and 33 °C in January.

At each plot the 8 measurement chambers were placed on 4 patches covered in leaf litter (only 3 leaf litter patches were measured during the wet season), and 4 patches that were bare (burnt plots) or covered in grass litter (unburnt plots). Note that the leaf litter on the burnt plots was made up of scorched leaves that had been shed from tree canopies following the experimental fires in June, while the leaf litter on unburnt plots had presumably accumulated over several seasons. Chambers were a maximum distance of 30 m apart on any plot. Following measurements, litter in each soil collar was collected, oven dried (70 °C) and weighed. Daily R_s was calculated by integrating instantaneous fluxes over each consecutive hour across a 24 h period.

Soil temperature was logged concurrently with soil CO_2 flux measurements using small thermocouple i-buttons enclosed in waterproof cases and buried next to each chamber 2.5 cm below the soil surface (Maxim Integrated Products Inc., California, USA). Volumetric soil water content (6 cm depth) was also recorded at three points near each chamber at the start and end of the 48 h measurement period using a hand-held theta probe (Delta-T Devices Ltd., Cambridge, England). A soil-specific calibration was implemented for the theta probe to convert raw readings in volts to volumetric soil moisture content (%vol.) using soil similar to that found at the study site and equations listed in the theta probe user manual (Delta-T Devices 1999). Briefly, 5 soil cores (244 cm^3) were collected and rewetted to field capacity, soil moisture was measured with the theta probe and the soil cores were weighed. The cores were then oven dried for 48 h (105 °C), weighed and re-measured with the theta probe.

In order to scale R_s measurements to a flux per hectare, the percentage cover of leaf litter and grass litter or bare patches on each plot was quantified using the transect intercept method. Two 80 m transects were laid down on each plot and the presence of a grass, bare or leaf litter patch was recorded every 0.5 m along each transect. On burnt plots bare patches made up on average 38 ± 18% and leaf litter patches 62 ± 18% of the plot area, while on unburnt plots grass litter patches made up 51 ± 10% and leaf litter patches 49 ± 10% of the plot area.