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Partitioning soil surface CO_2 efflux into autotrophic and heterotrophic components, using natural gradients in soil $\delta^{13}C$ in an undisturbed savannah soil

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ABSTRACT

We used natural gradients in soil and vegetation $\delta^{13}C$ signatures in a savannah ecosystem in Texas to partition soil respiration into the autotrophic (Ra) and heterotrophic (Rh) components. We measured soil respiration along short transects from under clusters of C_3 trees into the C_4 dominated grassland. The site chosen for the study was experiencing a prolonged drought, so an irrigation treatment was applied at two positions of each transect. Soil surface CO_2 efflux was measured along transects and CO_2 collected for analysis of the $\delta^{13}C$ signature in order to: (i) determine how soil respiration rates varied along transects and were affected by localised change in soil moisture and (ii) partition the soil surface CO_2 efflux into Ra and Rh, which required measurement of the $\delta^{13}C$ signature of root- and soil-derived CO_2 for use in a mass balance model.

The soil at the site was unusually dry, with mean volumetric soil water content of 8.2%. Soil respiration rates were fastest in the centre of the tree cluster (1.5 ± 0.18 μmol m^{-2} s^{-1}; mean ± SE) and slowest at the cluster–grassland transition (0.6 ± 0.12 μmol m^{-2} s^{-1}). Irrigation produced a 7–11 fold increase in the soil respiration rate. There were no significant differences ($p > 0.5$) between the $\delta^{13}C$ signature of root biomass and respired CO_2, but differences ($p < 0.01$) were observed between the respired CO_2 and soil when sampled at the edge of the clusters and in the grassland. Therefore, end member values were measured by root and soil incubations, with times kept constant at 30 min for roots and 2 h for soils. The $\delta^{13}C$ signature of the soil surface CO_2 efflux and the two end member values were used to calculate that, in the irrigated soils, Rh comprised $51 \pm 13.5\%$ of the soil surface CO_2 efflux at the mid canopy position and $57 \pm 7.4\%$ at the drip line. In non-irrigated soil it was not possible to partition soil respiration, because the $\delta^{13}C$ signature of the soil surface CO_2 efflux was enriched compared to both the end member values. This was probably due to a combination of the very dry porous soils at our study site (which may have been particularly susceptible to ingress of atmospheric CO_2) and the very slow respiration rates of the non-irrigated soils.

1. Introduction

Soils are the largest pool of carbon (C) in terrestrial ecosystems, globally containing more than two-thirds of their total C (Amundson, 2001) and thus storing the equivalent of about 300 times the amount of C now released each year through the burning of fossil fuels (Schimel, 1995). Understanding soil C dynamics is, therefore, important as they can have a major influence on the global C cycle, the regulation of atmospheric CO_2 concentration and climate change (Grace and Rayment, 2000; Cox et al., 2000). The rate at which C accumulates in soil is a balance between the inputs of C from vegetation (directly through rhizodeposition or via mycorrhizal fungi, or indirectly via leaf litter decomposition and root turnover) and losses due to soil respiration. Soil respiration comprises two main components: (i) autotrophic respiration, Ra, from roots and their associated mycorrhizal fungi, including respiration from other microbes in the rhizosphere directly dependent on labile C leaked from roots; (ii) heterotrophic respiration, Rh, due to the breakdown of soil organic matter (SOM). Being able to partition soil respiration into Ra and Rh is important, therefore, for understanding the processes regulating SOM turnover and, ultimately, whether soil in a particular ecosystem will become a net source or sink for C with changes in climate or land use (Millard et al., 2007).

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A range of methods has been used to partition the soil surface CO_2 efflux into Ra and Rh (Hanson et al., 2000; Trumbore, 2005; Kuzyakov, 2006; Subke et al., 2006). These have included experiments to exclude root respiration and so eliminate Ra, by girdling trees (Bhupinderpal-Singh et al., 2003; Subke et al., 2004; Scott-Denton et al., 2006), or trenching to remove roots (Jiang et al., 2005; Sulzman et al., 2005; Tang et al., 2005). Alternatively, elevated CO_2 supplied with its own unique $\delta^{13}C$ signature has been used as a tracer in labelling experiments (Andrews et al., 1999; Lin et al., 1999; Pendall et al., 2001; Søe et al., 2004; Trueman and Gonzalez-Meler, 2005) or at ambient concentrations in short term experiments with small trees (Lin et al., 1999; Phillips and Fahey, 2005). All of these approaches introduce a significant disturbance into the system (Hanson et al., 2000; Kuzyakov, 2006), which can affect soil respiration directly. This is particularly the case for elevated CO_2 studies, which accelerate soil respiration due to priming of the ecosystem with additional C (King et al., 2004). An alternative isotopic approach has been the use of ^{13}C natural abundance discrimination, utilising differences in the $\delta^{13}C$ signature of SOM and plant roots to partition the soil surface CO_2 efflux into Ra and Rh. Using this approach C_3 plants have been grown in pots with soil originating from under C_4 vegetation (Fu and Cheng, 2002) or by transplanting C_4 soil into a forest (Susfalk et al., 2002). In agricultural systems a C_4 crop (maize) has been grown in soil from under C_3 vegetation (C_3 soil) in the field to produce the necessary isotopic differences (Rochette and Flanagan, 1997).

Use of ^{13}C natural abundance discrimination to partition soil respiration in undisturbed ecosystems relies on the presence of a natural difference in the $\delta^{13}C$ signature of SOM and plant roots, which Kuzyakov (2006) and Hanson et al. (2000) have suggested is unusual in natural ecosystems and, therefore, a limitation to the use of the technique. However, savannah ecosystems comprise a dynamic mixture of C_3 trees and C_4 grassland and at the global scale cover an area of some 33 million km^2 (Beerling and Osborne, 2006). In these biomes woody cover is a main determinant of ecosystem properties (Sankaran et al., 2005) and, depending on the precipitation, can either decrease (at wetter sites) or increase (at dryer sites) the amount of SOM when woody vegetation invades grassland (Jackson et al., 2002). For example, in the subtropical Rio Grande Plains of Southern Texas, during the last 150 years C_3 trees and shrubs have invaded areas previously dominated by C_4 grasses, to produce a savannah ecosystem (Archer, 1995). This has resulted in significant changes in soil biogeochemistry, with an increase in SOM (McCully et al., 2004) and depletion in the soil $\delta^{13}C$ signature under the trees compared with the grassland (Boutton et al., 1998, 1999). This makes the ecosystem ideal for using the differences in natural gradients in soil $\delta^{13}C$ signature of Ra and Rh to partition their contribution to total soil surface CO_2 efflux.

The approach taken was to measure soil respiration along a short transect from under C_3 trees into the C_4 dominated grassland in a savannah ecosystem in Texas. Because soil respiration rate can vary considerably in relation to soil moisture (Tedeschi et al., 2006) and the site chosen for the study was experiencing a prolonged drought, an irrigation treatment was applied at two positions in the transect. Soil surface CO_2 efflux was measured along the transect and respired CO_2 collected for analysis of the $\delta^{13}C$ signature in order to: (i) determine how soil respiration rates varied along the transect and were affected by localised change in soil moisture and (ii) partition the soil surface CO_2 efflux into Ra and Rh using a mass balance model (Lin et al., 1999), which required measurement of the $\delta^{13}C$ signature of root- and soil-derived CO_2. The $\delta^{13}CO_2$ value of soil (Ehleringer et al., 2000) and root (Klump et al., 2005) respiration can differ from that of the solid material and can also vary with the length of incubation (Klump et al., 2005). Therefore, as a preliminary to partitioning the soil surface CO_2 efflux, it was also necessary to determine if there was a difference between the $\delta^{13}C$ signature of respired CO_2 and solid samples of soil and roots and establish the conditions for measuring their $\delta^{13}C$ signature.

2. Materials and methods

2.1. Site description and transect layout

The soil respiration measurements were made at the Texas Agricultural Experimental Station La Copita Research Area (lat. 27°40′N, long. 98°12′W, elevation 75 m) in southern Texas. The site is a subtropical savannah ecosystem that has been described extensively before (Boutton et al., 1998, 1999; Hibbard et al., 2001; Liao et al., 2006). The mean annual temperature is 22.4 °C and the mean annual precipitation is 716 mm, with rainfall peaks in May–June and September. The soil is a sandy-loam (Typic and Pachic Argiustolls) and the current vegetation is C_4 grassland (dominated by *Paspalum*, *Bouteloua*, *Chloris* and *Eragrotis* species, but also containing a number of C_3 forbs (Boutton et al., 1999)), interspersed with small, discrete clusters of woody, C_3 plants. The N_2-fixing tree legume, *Prosopis glandulosa* (Torr.) var. *glandulosa* (honey mesquite), is the first woody plant to colonise and subsequently facilitates recruitment of other woody plants beneath its canopy (such as *Condalia hookeri* (M.C. Johnst.), *Celtis pallida* (Torr.), *Zanthoxylum fagara* (L.), *Diospyros texana* (Scheele.), and *Mahonia trifoliolata* (Moric.) (Fedde)) (Boutton et al., 1999). These thorny clusters expand laterally to form larger groves of woody vegetation, producing a mosaic of woody vegetation within the grassland. As a result, there is a variation in the $\delta^{13}C$ signature of the soil, which under the woody clusters reflects the C_3 vegetation, but in the grassland is intermediate between a typical C_3 and C_4 signature (Boutton et al., 1999).

In June 2006 six replicate tree clusters were selected on the basis of the similarity of their age (as assessed by the basal diameter of the *P. glandulosa* trunk). For each cluster a series of six soil respiration collars were positioned as shown in Fig. 1. Each transect had four positions, which were: (i) adjacent to the trunk of the *P. glandulosa* tree (bole); (ii) half way between the tree trunk and the edge of the tree canopy (mid canopy); (iii) at the edge of the tree canopy, adjacent to the grassland (drip line); and (iv) in the grassland. The length of each transect varied from 4.5 to 9.0 m, depending upon the size and shape of the tree canopy and the nearby presence of grassland with C_4 species. At both the mid canopy and drip line positions an additional ring was positioned for irrigation, by applying 792 cm^3 of water to a collar, the equivalent of 50 mm of rain, to simulate a subtropical rainstorm. Irrigation was applied 6 h before the respiration measurements commenced, to allow for the physical displacement of CO_2 from soil pores as water moved down the soil profile. Preliminary measurements showed that this occurred as a peak in CO_2 efflux from the soil surface for up to some 2–3 h after irrigation (Boutton, personal communication).

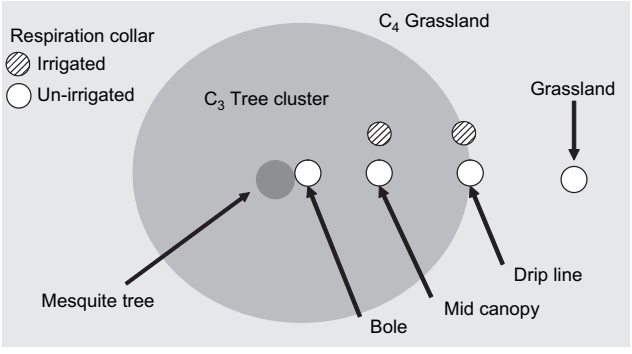

Fig. 1. The positioning of the soil respiration collars (○) in a transect from the central tree bole of a cluster into the surrounding grassland, including the two collars in each transect that were irrigated (▨).