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Respiratory carbon losses in a managed oak forest ecosystem

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ABSTRACT

Respiratory carbon losses from a mixed oak forest ecosystem following experimental manipulations were examined for their magnitudes and biophysical regulations. To quantify these losses, respiration measurements from chamber-based ecosystem components of sapwood, snags, down-logs, and soil, using chamber-based methods, were collected from experimental stands 8 yr after the manipulations of: non-harvest (NHM), uneven-aged (UAM), and even-aged (EAM) managements. Temperature and respiration relationships ($R = R_0 \times e^{\beta \times T}$) were used to estimate annual ecosystem respiration. The annual respiration rates were 1684 g C m^{-2} yr^{-1} in the NHM, 1787 g C m^{-2} yr^{-1} in the UAM, and 1231 g C m^{-2} yr^{-1} in the EAM stands. Harvesting reduced annual ecosystem respiration in the EAM stands by 28% compared to the NHM stands. Soil respiration was the largest component and contributed from 72% to 85% of the total respiration. The sapwood and leaf respiration were the second largest components of ecosystem respiration in both NHM and UAM stands, but down-logs were the second largest component in the EAM stands. Harvest significantly affected ecosystem respiration, with intensity driving changes in component respiration.

1. Introduction

The net ecosystem carbon (C) gain or loss is a small difference between two large fluxes: photosynthesis and respiration. In general, respiration is nearly equal to photosynthesis, and is more important than photosynthesis in determining the variability of net ecosystem productivity (Valentini et al., 2000; Yuan et al., 2009). Recent studies pointed out considerable variability regarding the role of forests in the global C budget (Houghton, 1999; Xiao et al., 2007). Also, natural and human disturbances have been proposed as a major factor causing great uncertainties in C budget estimates (Kurz et al., 2008). For forest ecosystems, the magnitudes of and changes in C fluxes vary with not only vegetation type, age, species composition, and microclimate (Tang and Baldocchi, 2005; Vogel et al., 2005; Wu et al., 2006), but also management practices such as harvesting and prescribed burning (Chen et al., 2002; Amiro et al., 2006; Noormets et al., 2008a). This study was designed to examine the changes in ecosystem respiration and its contributing components (e.g., live and dead trees) using a long-term experimental site at the Missouri Ozark Forest Ecosystem Project (MOFEP) where controlled manipulations were established in 1989 to mimic management practices for Ozark forests. Our critical question is: How do different disturbances alter the magnitude and composition of ecosystem respiration? So far, only a small number of studies have examined the contributions of these components over time (Law et al., 1999; Curtis et al., 2005; Reichstein et al., 2005).

Ecosystem respiration is regulated, and thus might be predicted, by several biophysical variables including temperature, moisture, biomass, photosynthesis, precipitation, and others. For example, soil moisture was not only an important regulator of soil respiration (Noormets et al., 2008b), but also changed the respiration–temperature relationship in the Sierra Nevada/Madre forests of California, USA (Xu and Qi, 2001b; Tang et al., 2005). Several other recent studies found that leaf photosynthesis as well as environmental variables (Högberg et al., 2001; Tang et al., 2005; Xu et al., 2011), such as precipitation frequency and duration may affect soil respiration during and after drought (Xu et al., 2004). Leaf respiration varies by species in part due to nitrogen content differences (Bolstad et al., 1999). Snowfall in the previous winter can predict total respiration in the subsequent growing season in semi-arid forests (Concilio et al., 2009). Finally, contributions by snags and down-logs may be driven by temperature, moisture, and decay class (Pyle and Brown, 1998; Wilcke et al., 2005).

The overall objective of this study was to understand how management alternatives alter ecosystem C losses by quantifying various components of ecosystem respiration for the Ozark forests, including soil, sapwood, leaf, snag, and down-log respiration. Specifically, our research tasks included: (1) conducting *in situ*

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respiration measurements, (2) estimating the changes in ecosystem respiration and the portions contributed by each component at multiple temporal scales and under different experimental treatments, and (3) exploring the underlying mechanisms of component respiration dynamics by relating them to forest stand structure and species composition.

2. Materials and methods

2.1. Study site

The study was conducted at the Missouri Ozark Forest Ecosystem Project (MOFEP), which was designed to understand the consequences of different management practices such as clear-cut and thinning on ecosystem functions and services (Brookshire and Shifley, 1997; Shifley and Brookshire, 2000; Shifley and Kabrick, 2002). MOFEP is located in the southeastern Missouri Ozarks (91°12′W and 37°06′N). This area is primarily mature (>70 yrs old) upland oak, oak-hickory and oak-pine communities; the mean canopy height is 16 m, and the mean DBH by species ranges from 4.5 to 22.8 cm (Brookshire and Shifley, 1997; Xu et al., 2004). Dominant overstory species include white oak (*Quercus alba*), black oak (*Quercus velutina*), scarlet oak (*Quercus cocinea*), shortleaf pine (*Pinus echinnata*), and hickory (*Carya* spp). MOFEP has an annual average of 1120 mm precipitation and a mean annual air temperature of 13.3 °C (Guyette and Larsen, 2000). The soils are mostly Alfisols and Ultisols (Kabrick et al., 2000).

2.2. Experimental treatments

The MOFEP sites were treated in the fall of 1996 according to Missouri Department of Conservation (MDC) forest land management guidelines for even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM) treatments (Missouri Department of Conservation, 1986). The three treatments were randomly assigned to nine sites, ranging in size from 266 to 527 ha, using a randomized complete block design (Brookshire and Shifley, 1997; Sheriff and He, 1997). Each site was subdivided into stands, averaging 4 ha in size, of similar ecological land types (ELTs) defined by slope, aspect, vegetation composition, and soil type. A system of 648 permanent forest vegetation plots (0.2 ha) was distributed across the nine MOFEP sites to document forest vegetation response to treatments (Li et al., 2007). These plots were allocated among stands based on stand size with the constraint that each stand receives at least one plot (Brookshire and Shifley, 1997). In this study, twelve replicates were sampled of each treatment type (EAM, UAM, and NHM) among the permanent forest vegetation plots with similar soil types, species composition, and ELT for a total of 36 plots. Although EAM included a combination of clear-cutting and intermediate thinning, our sampling points were only located within the clear-cut area. UAM consisted of harvesting by both single-tree selection and group selection, but our plots were all located in areas of single-tree selection.

2.3. Field data collection

Soil respiration (R_{soil}, g CO_2 m^{-2} h^{-1}) was measured using an EGM4 (PP Systems, Amesbury, MA, USA) at each of 36 plots. Six soil collars, each with a height of 4.4 cm and a diameter of 10 cm, were inserted into the soil at each plot in three random clusters, and each cluster had two collars. Surface efflux was measured during the summer and fall 2003, summer 2004, and early spring and summer 2005. Soil temperature at 5 cm was measured adjacent to each respiration collar with a portable temperature probe (Fig. 1). Soil water content was measured from TDR rods that were installed near each cluster of soil collars by a time domain reflectometer (TDR100, Campbell Scientific In., Logan, UT). Both temperature and soil water measurements were made every 2–4 weeks in the 2003–2005 growing season, late fall of 2003, and early spring of 2005. However, the soil water content did not appear to be a constraint to soils and plants throughout the growing season (see data analysis) so that further details are not presented in this study.

In addition to the periodic measurements of soil temperature coinciding with respiration measurements, continuous soil temperature was measured at 5 cm by three HOBO thermostats per plot (Fig. 1) and averaged every hour using a HOBO data-logger (Onset computer Corporation, Pocasset, MA, USA), starting at November 11, 2002. The following exponential equation was used to develop an empirical model to predict respiration from soil temperature:

$$R = R_0 \times e^{\beta \times T} \quad (1)$$

where R is component respiration, T is temperature, R_0 and β are empirically estimated coefficients for each component model (soil, down dead wood, snag, sapwood, or leaf; Table 1). The Q_{10} can be derived from $Q_{10} = \exp(10 \times \beta)$. Estimated coefficients were used to predict respiration at an hourly scale over the 3-yr study period.

Down-log decay classes were defined according to Shifley and Brookshire (2000) as: (I) recently downed material with tissue and bark intact throughout; (II) sapwood beginning to decay or mostly present, bark beginning to crack, and heartwood tissue intact; and (III) sapwood and bark mostly gone or gone, heartwood beginning to decay or with substantial decay. Down-log respiration was measured on three down-logs for each decay class for a total of nine down-logs per plot and for a total of 108 down-logs per treatment. The collars were inserted into randomly selected, large-diameter down-logs and sealed with silicon. We used the same measurements protocols as for soil respiration. Three plots per treatment were randomly selected for continuous temperature measurement. Each measured log in a selected plot had a HOBO thermostat installed near the collar at 5 cm depth for a total of 27 down-logs per treatment; hourly mean temperature was recorded during the study period. The volume of down-logs was estimated according to (Wagner, 1964; Martin, 1976). Basically, we laid out a 100-m transect in each plot for a total of 36 transects. Along each transect, every down-log greater than 5 cm in diameter touching the transect line was recorded by decay classes, length, and diameter. The volume of the total down-logs was estimated as:

$$V = \frac{\pi^2 \sum d^2}{8L} \quad (2)$$

where V is volume per unit area (m^3 ha^{-1}), d is diameter of the log intersected with transect (cm), and L is the length of the transect (m).

Snag decay classes were defined according to Shifley and Brookshire (2000) as: (I) dead trees with most of the bark and branches present; (II) sapwood and bark completely gone. Snag respiration was measured on three snags of each decay class for a total of six snags per plot and for a total of 72 snags per treatment. The measurement collars were mounted on each snag with silicon at approximately 137 cm height above ground and at random azimuths. These respiration measurements were also taken at 2–4 week intervals. The chamber measurements were scaled up to the stand level by estimating snag surface area/volume based on (Martin et al., 1998):

$$\log_{10} Y = a + b \times \log_{10} x \quad (3)$$

where x is the stem DBH (cm), Y is the snag surface area/volume, and a and b are species specific parameters. The mean surface area