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Spatial variation in respiration from coarse woody debris in a temperate secondary broad-leaved forest in Japan

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Abstract

We measured the rates of respiration from snags and logs (''coarse woody debris'', CWD) of Japanese red pine (*Pinus densiflora* Sieb. et Zucc.) to examine the rate of decomposition and CO_2 efflux from these materials in a temperate secondary broad-leaved forest in Japan. At this site, a high quantity of CWD of *P. densiflora* had accumulated as a result of pine wilt disease during the 1970s. Respiration rates were measured using a dynamic closed chamber method combined with an infrared gas analyzer. We measured the respiration rate of 7 samples of snags and 10 samples of logs from August 2003 to January 2004. The responses of the respiration rates of snags (R_{snag}) and logs (R_{log}) to changing temperature were both exponential and the responses to water content were quadratic, and the same function could be used to estimate annual values of both R_{snag} and R_{log}. Intensive measurements of water contents of snags and logs showed a marked difference in water content. The mean water content of snags was 20% of log water content. This difference was likely responsible for the observed difference in annual R_{snag} and R_{log}. The decay rate constants estimated from the respiration rates measurement of snags and logs were 0.019 and 0.081 year^{-1}, respectively. Despite being lower than R_{log}, R_{snag} was a significant compartment of the CWD carbon budget at this site.

Keywords: Decomposition rate; Environmental factors; Infrared gas analysis; Wood decay

1. Introduction

Coarse woody debris (CWD) plays an important role in forest ecosystems. CWD contains a large stock of carbon and nutrients, provides habitat for various microbes and invertebrates, maintains biodiversity, and affects both carbon and nutrient cycling in a forest (Harmon et al., 1986; Hammond et al., 2001; Krankina et al., 2003; Hicks et al., 2003). In recent studies, the amount and structure of CWD, its input and decomposition rates, and its contribution to the forest's heterotrophic respiration and carbon budgets have been analyzed (Daniels et al., 1997; Siitonen et al., 2000; Chambers et al., 2001; Busing, 2005; Jomura et al., 2007). In addition, studies of CWD dynamics in several forests with different ages (as a result of forest fires) and model descriptions have revealed the important contribution of CWD to long-term forest carbon cycles (Janisch and Harmon, 2002; Bond-Lamberty et al., 2003; Gower, 2003). For determination of a forest's carbon budget, rates of both production of vegetation and decomposition of organic matter must be quantified. CWD is an important component of the decomposing organic matter, so accounting for CWD respiration as a component of heterotrophic respiration is essential to determining a forest's carbon budget (Chambers et al., 2001; Bond-Lamberty et al., 2003; Howard et al., 2004).

Spatial heterogeneity is a major characteristic of CWD in forests (Harmon et al., 1986). A complex spatial distribution arises from the different positions of components of CWD, and specifically those of standing wood (''snags'', including fallen branches that remain suspended above the ground and leaning dead trees) and fallen wood on the ground (''logs''). These different positions change the environmental factors that affect CWD and, thus, affect the decomposition mechanisms (Næsset, 1999). Snag decomposition rates are usually slower than those of logs (Harmon et al., 1986; Yatskov et al., 2003). Limited

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contact with the ground and increased exposure to air circulation decrease the water content of snags (Fahey, 1983; Johnson and Greene, 1991), resulting in slower decomposition rates. Microbial invasion is also limited for snags, although the invasion rate varies considerably among tree species (Harmon et al., 1986). To elucidate the landscape-scale forest carbon cycle, the spatial heterogeneity in CWD decomposition rates must thus be examined.

CWD decomposition rates have been measured frequently in previous studies (e.g., Harmon et al., 1986; Laiho and Prescott, 2004; Mackensen et al., 2003). Most studies have used the rate of weight loss by CWD as an estimate of decomposition rates. However, weight loss of CWD includes three main processes: losses due to microbial respiration, leaching, and fragmentation. Decomposition rates based on weight loss thus evaluate the combined effects of these different biological, chemical and physical processes. However, the current emphasis on carbon cycles in forest ecosystems is on CO_2 fluxes. CWD respiration is a significant component of overall heterotrophic respiration (about 10–16% in a temperate secondary broad-leaved forest in Japan, Jomura et al., 2007) and is thus an important factor in evaluating net ecosystem production (NEP; Chambers et al., 2001) and the contribution of decomposition to CO_2 fluxes. Thus, the respiratory loss of carbon from CWD should be evaluated separately from the other two processes to permit a more precise evaluation of NEP in forest ecosystems.

The objective of our study was thus to clarify the effect of differences in the spatial positions (standing and downed) of CWD on the respiration rate. We hypothesized that the annual carbon loss from CWD would vary spatially in response to environmental factors. We constructed a function for the relationship between environmental factors and the respiration rates of snags and logs, and evaluated its ability to explain the variation in CWD respiration rates. We also evaluated the validity of the respiration measurement used to estimate decomposition rates of CWD.

2. Site and methods

2.1. Site description

The study site was located in a temperate secondary broad-leaved forest in central Japan (the Yamashiro Experimental Forest, 34°47′N, 135°50′E). More than 100 years ago, there were few trees in the area because of severe cutting of trees for firewood. Trees were planted ca. 100 years ago for soil and water conservation. Subsequently, the area was dominated by *Pinus densiflora* Sieb. et Zucc. About 30 years ago, pine wilt disease spread throughout this area; most of the *P. densiflora* died, and broad-leaved species took their place. In 1999, the living tree biomass (DBH $\geq$ 3 cm) was estimated to be 48.3 t C ha^{-1}, and deciduous broad-leaved tree species such as *Quercus serrata* Thunb. ex Murray, evergreen broad-leaved tree species such as *Ilex pedunculosa* Miq., and coniferous tree species such as *P. densiflora* accounted for 66, 28, and 6% of the total biomass, respectively (Goto et al., 2003). In 2003, the mass of dead wood (DBH $\geq$ 3 cm) was estimated to be 9.1 t C ha^{-1}, and 73% of the total was standing and downed dead wood of *P. densiflora* (Jomura et al., 2007). The annual mean air temperature was 15.5 °C, and the hourly maximum and minimum air temperatures in 2002 were observed in the summer (34.8 °C) and winter (−3.9 °C; Goto et al., 2003). Mean annual precipitation was 1449 mm; the rainy season occurred in late June and early July, and some typhoons contributed significant amounts of precipitation to the study area in the summer and fall. The study site was a 1.7 ha catchment (220 m above sea level), with a mean canopy height of 12.0 m, and mean DBH and tree height of 7.4 cm and 5.6 m, respectively, for woody vegetation with DBH $\geq$ 3 cm. The stand density averaged 3209 trees ha^{-1} and the total basal area averaged 20.7 m^2 ha^{-1} (Goto et al., 2003). The forest soil was immature and sandy, was derived from weathered granite, and had thin O and A layers.

3. Methods

Because the majority of the CWD at our study site was *P. densiflora* materials, we focused our analysis on these materials. Samples were obtained from standing *P. densiflora* (snags, $n = 7$) and downed dead wood of this species (logs, $n = 10$). All samples were of similar age (judged based on the fact that the bark remained attached), so we did not attempt to estimate the age of the samples. The diameter and length of each sample were measured and volumes were calculated based on an assumption that samples were regular cylinders. Subsamples were also obtained to estimate the oven-dry wood density. The dry weight of each sample was calculated by multiplying the sample volume by the wood density of the subsample. Snags and logs had similar mean wood densities (0.29 ± 0.05 and 0.30 ± 0.11 g cm^{-3}, respectively; $P = 0.803$) and diameters (16.9 ± 5.6 and 15.4 ± 6.2 cm, respectively, $P = 0.785$). Samples were cut to a mean length of 69 ± 2 cm to fit within the sample chamber (described below). Cut surfaces of the samples were sealed with a silicone sealant to prevent the invasion of microbes and emission of CO_2 at these surfaces. All samples were retained at the study site. Snag samples were stood vertically against a steel frame and were isolated from the ground by a vinyl sheet spread under the frame. Log samples lay directly on the ground.

Respiration rates of snag and log samples were measured in a dynamic closed chamber connected to an infrared gas analyzer (IRGA). The system was composed of an LI-800 IRGA meter (LI-COR Inc., Lincoln, NE, USA), a chamber made of acrylic resin (W 30 cm × D 80 cm × H 30 cm inner diameter; 72 000 cm^3), polyethylene tubes, a pump (GS-3EA, Enomoto Micro-Pump, Tokyo, Japan), filters, and a flow meter (Fig. 1). The temperature in the chamber (T_c) was measured using a copper-constantan thermocouple. We enclosed individual snag and log samples in the chamber, and measured the CO_2 concentration in the chamber for 10 min. The CO_2 concentration and temperature in the chamber were recorded each second using a datalogger (NR-1000, Keyence, Osaka, Japan). To avoid the effects of air disturbance caused by opening the chamber cover, the data for the 60-s period after the