Forest Ecology and Management 258 (2009) 2224–2232

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Increased coniferous needle inputs accelerate decomposition of soil carbon in an old-growth forest

Susan E. Crow[a,b,*], Kate Lajtha[a], Richard D. Bowden[c], Yuriko Yano[d], Justin B. Brant[e], Bruce A. Caldwell[a], Elizabeth W. Sulzman[e]

[a] Botany and Plant Pathology Department, Oregon State University, Corvallis, OR 97330, USA
[b] ^{14}CHRONO Centre, Queen's University Belfast, BT9 6AX, UK
[c] Department of Environmental Science, Allegheny College, Meadville, PA, USA
[d] Municipality of Anchorage, Health and Human Services, Anchorage, AK 99501, USA
[e] Crop and Soil Science Department, Oregon State University, Corvallis, OR 97330, USA

ARTICLE INFO

Article history:
Received 17 July 2008
Received in revised form 15 December 2008
Accepted 8 January 2009

Keywords:
Andisol
Carbon balance
Coniferous forest
Priming effect
Soil priming

ABSTRACT

Changes in temperature, precipitation, and atmospheric carbon dioxide (CO_2) concentration that are expected in the coming decades will have profound impacts on terrestrial ecosystem net primary production (NPP). Nearly all models linking forest NPP with soil carbon (C) predict that increased NPP will result in either unchanged or increased soil C storage, and that decreased NPP will result in decreased soil C storage. However, linkages between forest productivity and soil C storage may not be so simple and direct. In an old-growth coniferous forest located in the H.J. Andrews Experimental Forest, OR, USA, we experimentally doubled needle litter inputs, and found that actual soil respiration rates exceeded those expected due to the C added by the extra needles. Here, we estimated that this 'priming effect' accounted for 11.5–21.6% of annual CO_2 efflux from litter-amended plots, or an additional 137–256 g C m^{-2} yr^{-1} loss of stored C to the atmosphere. Soil priming was seasonal, with greatest amounts occurring in June–August coincident with peaks in temperature and dry summer conditions. As a result of priming, mineral soil was more resistant to further mineralization during laboratory incubations. Soil lignin-derived phenols in the Double Litter plots were more oxidized than in the control, suggesting that the soil residue was more degraded. Our hypothesis that excess dissolved organic C produced from the added litter provided the link between the forest floor and mineral soil and a substrate for soil priming was not supported. Instead, the rhizosphere, and associated mycorrhizal fungi, likely responded directly to the added aboveground litter inputs. Our results revealed that enhanced NPP may lead to accelerated processing of some stored soil C, but that the effects of increased NPP on ecosystem C storage will be based on a net balance among all ecosystem C pools and are likely to be ecosystem-dependant. Forest C models need to include these complex linkages between forest productivity and soil C storage.

1. Introduction

Changes in ecosystem net primary productivity (NPP) and thus litterfall are predicted under climate change scenarios (Melillo et al., 1993; King et al., 1997; Raich et al., 2006). As a result, alterations of microbial (i.e. bacterial or fungal) biomass and activity also can be expected (Frey et al., 2004; Waldrop et al., 2004). Enhanced microbial respiration in response to additional plant litter inputs can release a portion of the newly added C as well as increase the rate of release of stored soil organic matter. This pattern, termed the "priming effect" was described as early as 1926 (Löhnis, 1926) and is the 'non-additive interactions between decomposition of the added substrate and of soil organic matter (SOM)' such that positive priming results in the acceleration of SOM decomposition and negative priming results in the retardation of SOM decomposition (Kuzyakov et al., 2000). Soil priming recently has received increased attention (see reviews by Kuzyakov et al. (2000) and Fontaine et al. (2003)) as the impacts of global change on terrestrial C dynamics are explored more thoroughly.

Microorganisms play a central role in determining if soil C pools increase or decrease and changes in microbial biomass or activity that resulted from alterations in inputs were frequently associated with soil priming (Kuzyakov et al., 2000). One hypothesis for the mechanism underlying the positive priming effect is that fast-growing microbes specializing in utilization of fresh inputs respond rapidly and produce extracellular enzymes that metabo-

---

* Corresponding author at: 42 Fitzwilliam Street, ^{14}CHRONO Centre, Queen's University Belfast, Belfast BT9 6AX, UK. Tel.: +44 28 9097 3085.
E-mail address: s.crow@qub.ac.uk (S.E. Crow).

0378-1127/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2009.01.014

lize not only fresh material, but also existing SOM (Fontaine et al., 2004a). Priming effects often have been attributed to enhanced microbial biomass and exoenzyme production in response to water-soluble sugar components of added litter (Schimel and Weintraub, 2003; Rasmussen et al., 2007, 2008). Alternatively, Fontaine et al. (2003) proposed a conceptual model for soil priming whereby the addition of fresh inputs establishes a competition between fast-growing species specialized in metabolizing fresh material and slow-growing species specialized in metabolizing SOM (but that also can utilize fresh material). When SOM-specialized microbes out-compete fresh litter-specialized microbes, e.g. under nutrient limiting conditions (Fontaine et al., 2004b), soil priming occurs.

In an old-growth coniferous forest at the H.J. Andrews Experimental Forest in the Pacific Northwest region of the U.S., Sulzman et al. (2005) reported that the annual CO_2 flux associated with the experimental doubling of aboveground litter increased by an additional 186 g C m^{-2} yr^{-1}, or a 34% increase, beyond what was expected based on rates of decay for the added litter. This elevated CO_2 flux suggested that positive soil priming occurred as a result of the added aboveground litter. In this region of the U.S., dry summer months are followed by a long wet season. Re-wetting of the forest floor and soil profile typically occurs in late October–November and results in a flush of dissolved organic carbon (DOC) in soil solution (Lajtha et al., 2005). Approximately one-third of water soluble leachates from fresh coniferous litter from this site were easily degradable carbohydrates (e.g., polysaccharides, and simple sugars) (Yano et al., 2004). In a seasonal experiment, Brant et al. (2006a) observed a shift in soil microbial community associated with the litter addition only in November.

Based on these collective observations at H.J. Andrews, we hypothesized that if fast-growing microbes specializing in the utilization of fresh inputs responded rapidly to added litter and resulted in overall positive soil priming, then the observed priming effect would be greatest in the fall when a flush of DOC from the forest floor provided an easily-accessible substrate for soil microbes and was associated with the shift in microbial community observed when extra litter was added to the forest floor. By this conceptual model, we expected DOC transport to provide the link between forest floor litter and mineral soil priming. To refine the relationships among increased CO_2 efflux, altered microbial communities, and DOC transport, we synthesized previously collected data in a novel analysis to investigate the potential impact of increased aboveground NPP on old-growth coniferous forest soil dynamics.

2. Methods

2.1. Field site

Plant litter inputs were manipulated as part of the on-going Detritus Input Removal and Transfer (DIRT) Experiment in the H.J. Andrews Experimental Forest in OR, USA (44°13′N, 122°13′W, 531 m elevation) since 1997. The H.J. Andrews DIRT site was established in an undisturbed old-growth (>500 yr) western hemlock [*Tsuga heterophylla* (Rafinesque) Sargent] and Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] stand. Other significant tree species at the site include vine maple (*Acer circinatum* Pursh.) and western red cedar (*Thuja plicata* D. Don). Mean annual temperature is 8.7 °C and annual precipitation is 2370 mm yr^{-1}(average from 1973 to 2002), which occurs mostly as rain. Over 70% of the precipitation occurs during a wet season between November and March (Sollins et al., 1980). Nitrogen deposition to this area is ~0.2 g N m^{-2} yr^{-1} (Vanderbilt et al., 2003). Soils are derived from volcanic parent materials and classified as coarse loamy mixed mesic Typic Hapludands. The soil C/N ratio is 35, 19, and 16 for the 0–5, 5–10, and 10–20 cm increments of the mineral soil (Keirstead, 2004). In the A horizon, the bulk density is 0.82 Mg/ha), the texture is loamy with 13% clay, and the pH is 5.4 (Dixon, 2003). Mean annual soil temperature for 2001–2003 was 9.5 °C at 5 cm and mean annual soil moisture for 2001–2003 was 29% (Sulzman et al., 2005).

The DIRT Experiment treatments include the addition or removal of above- and belowground litter inputs with the goal of understanding long-term controls on soil organic matter formation and stability (Nadelhoffer et al., 2004). Six litter input/exclusion treatments, replicated three times, were randomly assigned to the plots. Plots are approximately 10 m × 15 m and include trees; there is a small range in plot sizes due to available space and obstacles. Litter manipulation treatments include combinations of aboveground litter addition, screens placed atop the soil surface to collect aboveground litter, and use of trenches and root barriers to remove roots (Table 1).

In this study, we utilized data from the Control, Double Litter, No Litter, and No Roots treatments, but focus on the Control and Double Litter treatments. To obtain a doubled needle and fine litter inputs for the Double Litter treatment, we used litter obtained from the No Litter plots; litter was excluded with 1-mm-mesh screens, and was transferred to Double Litter plots 2–5 times per year. Large branches and stems or lichen/moss masses that fell on screens were discarded. Over the first six years, 490 g C m^{-2} of additional litter has been added to the double needle plots; in 2005, the O-horizon depth was 1.9 cm on the Double Litter plots compared to 1.5 cm on the Control plots (Lajtha et al., 2005). In 2003, litter transfers were made on April 25 and July 17, but flux measurements for those months were taken before the litter addition occurred.

Daily precipitation totals and mean air temperature for 2003 were taken from the H.J. Andrews primary meteorological station (PRIMET) which is located at the nearby Experimental Forest headquarters (44°21′N, 122°26′W, 430 m elevation). Soil moisture was measured at the DIRT site at 10 cm in the A horizon at 30-min intervals (Onset Tidbit Temperature Data Logger, Onset Computer Corporation, Bourne, MA).

2.2. Field CO_2 flux and priming estimation

Soil CO_2 efflux was measured at least monthly in 2003 with a portable infrared gas analyzer (Li-6250, LI-COR Inc., Lincoln, NE) incorporated into a photosynthesis system (Li-6200), and attached to a closed, dynamic soil respiration chamber (LI-6200-09) designed for use with the Li-6200. For each measurement, the soil respiration chamber was placed on a 10 cm diameter by 5 cm height polyvinyl chloride (PVC) collar that was installed permanently 2 cm into the mineral soil. The forest floor and O-horizon was left intact within each PVC collar. There are five permanently

Table 1
Treatments and methods of the Detritus Input Removal and Transfer (DIRT) Experiment.

Treatment	Method
Control	Normal litter inputs are allowed.
No Litter	Aboveground inputs are excluded from plots with netting.
Double Litter	Aboveground leaf/needle inputs are doubled by adding litter removed from No Litter plots.
Double Wood	Aboveground wood inputs are doubled by adding large shredded wood pieces, both fresh and highly decayed, based on measured input rates of woody debris fall.
No Roots	Roots are excluded with impermeable plastic barriers extending from the soil surface to the top of the C horizon.
No Inputs	Aboveground inputs are prevented as in No Litter plots; belowground inputs are prevented as in No Roots plots.