Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Soil C and N cycling in three semiarid vegetation types: Response to an in situ pulse of plant detritus

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A R T I C L E I N F O

Article history: Received 11 April 2008 Received in revised form 9 July 2008 Accepted 17 July 2008 Available online 13 August 2008

Keywords: Carbon availability Detritus In situ pulse Microbial substrate C:N N immobilization Organic matter fraction Semiarid

ABSTRACT

Plant detritus is an important source of labile C that drives soil microbial growth and regulates the balance of N mineralization and immobilization. In semiarid ecosystems, timing of plant detrital inputs may be especially important in regulating microbial C and N cycling because of the relatively short window of time when moisture is available. Low soil moisture in early-summer may inhibit microbial colonization of recently released detritus, resulting in C-limitations to microbial growth, and this may explain the NO₃ accumulation commonly observed in semiarid, and Mediterranean ecosystems. We examined linkages between soil C availability and gross N cycling rates during summer in three common semiarid vegetation types: sagebrush, crested wheatgrass, and cheatgrass. To determine whether dry soils inhibit microbial colonization of plant detrital inputs, we stimulated soil C availability in situ by killing plant biomass shortly before the summer dry-season with herbicide (detrital-pulse treatment). Soil C and gross N cycling rates were determined during field incubations of intact soil cores from untreated soils on three occasions from late-spring to late summer, and from detrital-pulse treated soils on two occasions in summer. We hypothesized that greater C availability, resulting in increased microbial biomass and C mineralization rates, would translate to greater N immobilization rates, and this would inhibit the accumulation of inorganic N during summer months.

There were few differences in soil C and N cycling among vegetation types. In all vegetation types, the in situ detrital-pulse stimulated soil C mineralization and gross N cycling rates compared to untreated soils; however, this treatment did not inhibit the summertime accumulation of NO_3 . Instead, elevated N cycling rates and large labile N pools in detrital-pulse soils persisted throughout the summer. Our results combined with a model of microbial C–N dynamics indicate that microbes in detrital-pulse soils were utilizing substrates with C:N ratios 27% lower than in untreated soils (p < 0.04), and much lower than expected based on the C:N of plant detritus. This suggests that substrates released by senescing plants had much lower C:N than would be predicted based on the overall C:N of plant tissue. In addition, appearance of ¹⁵N in different soil density fractions showed that the detrital-pulse treatment stimulated microbial N immobilization in both C-rich and N-rich soil microsial. Greater N immobilization associated with light fraction organic matter is consistent with greater microbial growth due to earlier input of plant detritus. Interestingly, heavy fraction organic matter was also an important sink for immobilized N and was strongly stimulated by the detrital-pulse treatment, indicating that this fraction is not as recalcitrant as formerly thought.

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1. Introduction

The supply of plant carbon (C) inputs to soil, through leaf and root turnover, is an important source of labile C substrate that drives the growth and activity of heterotrophic soil microorganisms. The activity of heterotrophic microbes is a key linkage between soil C and nitrogen (N) cycling. Consumption of labile C

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results in microbial growth and immobilization of available N (Hart et al., 1994; Gallardo and Schlelsinger, 1995; Schaeffer and Evans, 2005). Simultaneously, in comparatively N-rich microsites, microbial intra- and extracellular enzyme activity and biomass turnover result in the release (or mineralization) of actively cycled N (Bengtsson et al., 2003; Schimel and Weintraub, 2003; Saetre and Stark, 2005). The size of microbial biomass pools and rates of N immobilization have been linked to soil C availability across broad climate gradients (Barrett and Burke, 2000; Booth et al., 2005), beneath plant canopies versus plant-interspaces (Barrett and Burke, 2000; Chen and Stark, 2000), and after experimental





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additions of plant detritus (Recous et al., 1999; Whalen et al., 2001; Luxhoi et al., 2006).

Shifts in the dominant vegetation type may alter soil C availability through differences in the quantity and quality of plant detrital inputs (Vinton and Burke, 1995; Evans et al., 2001; Carrera et al., 2003), particularly in semiarid ecosystems where soil organic C and N pools are small (Schlesinger, 1997). Increased C inputs, through differences in foliage and root turnover among different vegetation types (Caldwell et al., 1977; Gill and Jackson, 2000; Belnap and Phillips, 2001; Schenk and Jackson, 2002), may increase microbial N demand and reduce N available for plant uptake (Hart et al., 1994). By contrast, increased quality of plant detrital inputs (i.e. lower litter C:N ratios) may result in greater N availability due to decreased microbial demand for inorganic N per unit organic C consumed (Hart et al., 1994; Chen and Stark, 2000; Carrera et al., 2003; Saetre and Stark, 2005).

The simultaneous occurrence of N mineralization and N immobilization in bulk soils suggests that microbes are distributed among distinct microsites dominated by N-rich (C-limited) and C-rich (N-limited) substrates (Chen and Stark, 2000). While the source of mineralizable N is believed to be derived predominantly from older, more highly decomposed mineral-associated organic matter with narrow C:N ratios, such as the heavy fraction (HF), C-rich microsites with high rates of microbial N consumption are likely to be associated with particulate organic matter derived from plant detritus, such as the light fraction (LF) (Sollins et al., 1984; Boone, 1994; Crow et al., 2007). Immobilization of added ¹⁵N into soil organic matter fractions, in combination with determination of gross N cycling rates, may better reveal the effects of small changes in the quantity or quality of plant detrital inputs to soil compared to rates estimated for bulk soils alone.

In semiarid ecosystems, soil C and N cycling may also be affected by the timing of plant biomass turnover relative to seasonal patterns of temperature and soil moisture. As the summer dry-season develops, perennial plants reduce growth rates, increase litterfall (West and Fareed, 1973; Comstock and Ehleringer, 1992; Evans and Black, 1993), and shift the distribution of active roots to deeper soil depths (Fernandez and Caldwell, 1975). By contrast, annual grasses senesce with the onset of the summer dry-season (Stewart and Hull, 1949; Harris, 1967). In these soils, soil C availability would be expected to increase during the early-summer due to the pulse of high C:N leaf and root litter inputs. In spite of this, surface soils of semiarid ecosystems tend to accumulate NO_3^- during the summer (Jones and Woodmansee, 1979; Jackson et al., 1988; Davidson et al., 1990; Augustine and McNaughton, 2004), particularly in annual grass soils (Booth et al., 2003; Sperry et al., 2006; Hooker et al., in review). This NO3 accumulation suggests that microbial N immobilization is limited by C availability, which is inconsistent with the expectation that plant detrital inputs stimulate soil C availability. One explanation for this inconsistency is that by the time annual grasses senesce in late-spring (late-May-early-June), the soil may already be too dry for microbes to colonize the newly released detritus. Thus, there may be a time-lag in N immobilization because microbes are unable to colonize plant detritus until soil moisture increases in autumn.

In this study we investigated whether the apparent summertime C limitation in semiarid soils, evidenced by NO₃ accumulation, was due to a time-lag in microbial colonization and decomposition of recently released plant detritus. Gross N cycling rates and soil C availability were compared among three distinct vegetation types common to the Great Basin: Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), introduced perennial crested wheatgrass (*Agropyron desertorum*), and invasive annual cheatgrass (*Bromus tectorum*) communities. We stimulated soil C availability in situ by releasing plant biomass to the soil detrital pool 3 weeks prior to the summer dry-season, using large soil cylinders and herbicide at peak biomass; this is referred to as the detrital-pulse treatment. Since only a fraction of perennial plant root biomass turns over annually (Gill and Jackson, 2000), the detrital-pulse treatment likely increased the quantity of plant detrital inputs in perennial plant-dominated systems, but only the timing of plant detrital inputs should be affected in the annual grass system. We hypothesized that the detrital-pulse treatment would stimulate C availability and increase microbial biomass and C mineralization rates, and thus result in higher gross N immobilization rates compared to untreated soils. This study is novel in that we investigated the response of soil microbial C and N dynamics to an in situ pulse of plant detritus, and used ¹⁵N to link gross N immobilization rates to organic matter density fractions.

2. Materials and methods

2.1. Study site

This study was carried out on a Great Basin sagebrush rangeland in Rush Valley (Tooele County), Utah (112° 28'W, 40° 17'N, elev. 1610 m). The site contains extensive, nearly monodominant stands of Wyoming big sagebrush (A. tridentata Nutt. ssp. wyomingensis Beetle and Young), crested wheatgrass (A. desertorum (Fisch. ex. Link), var. 'Nordan'), and cheatgrass (B. tectorum L.). Mean annual precipitation and temperature measured on-site over a 5-year period were 240 mm and 8.3 °C, respectively. The summer dryseason begins in early June as mean monthly precipitation declines from spring (29.4 mm for a 5-year average) to summer (15.7 mm). Most summer precipitation occurs as small events (>75% of summer precipitation events are <5 mm), while larger, more biologically effective pulses are uncommon (>5 mm occur approximately 1.0 ± 0.1 days/month; >15 mm events occur 0.2 ± 0.2 days/ month). Soils at the site are derived from lacustrine and alluvial sediments of primarily limestone deposits, and classified as Erda silt loam, very deep, well drained, mixed, superactive, mesic Aridic Calcixerolls (A. Mitchell personal communication; Trickler et al., 2000). Soils contain approximately 10 g CO_3 -C kg⁻¹ soil in the surface 0–10 cm, and are non-saline (EC < 2.0 dS/m).

Stands of crested wheatgrass and cheatgrass were established in 1992 on areas formerly dominated by sagebrush. Crested wheatgrass was established to improve rangeland quality by disking to remove shrubs and drill-seeding (30-cm row spacing). Cheatgrass established naturally with the onset of autumn rains after a summer wildfire consumed several large areas of sagebrush. In late 1998, four 22×22 m permanent plots were created in each vegetation type. Permanent plots were randomly located along two north–south and two east–west transects that crossed all three vegetation types.

2.2. Installation of the detrital-pulse treatment and field sampling

On May 4, 2003, approximately 3 weeks prior to the onset of the summer dry-season, 10 random locations within each plot were permanently marked. The detrital-pulse treatment was initiated at five of the sampling points by inserting a 30-cm diameter \times 25-cm long cylinder into the soil, severing all roots. An area within and around (0.5-m radius) the cylinder was sprayed with herbicide (Roundup, Monsanto) to kill the vegetation and release plant biomass to the soil as detritus. The remaining five sampling points at each plot were left as untreated soils, and were at least 2 m from a detrital-pulse treatment. For sagebrush plots, we used only areas beneath shrub canopies; untreated and detrital-pulse plots were placed beneath separate shrubs, but with similar aspect in relation to the shrub stem. All aboveground vegetation appeared to be dead within the detrital-pulse plots approximately 10 days after

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