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Effects of above-ground herbivory on soil microbial biomass in conventional and no-tillage agroecosystems

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Abstract

The effects of above-ground herbivory on soil microbial biomass associated with maize (*Zea mays*) roots were measured in field experiments. Different grazing intensities were established by placing grasshoppers (0, 5, 10 and 20) in cages around individual maize plants, and allowing them to graze for 5 days. Soil samples were taken 12 days later at a depth of between 8 and 12 cm. Soil microbial biomass was measured using the chloroform fumigation direct extraction method. Results indicated that intermediate levels of herbivory increased soil microbial biomass in the no-tillage system. However, in a conventional tillage system no significant differences were found among the grazing treatments. It is hypothesized that increases in soil microbial biomass in the no-tillage system were attributable to increases in root exudates resulting from above-ground herbivory.

Keywords: Soil microbial biomass; Herbivory; Maize; Root exudates; Conventional tillage; No-tillage

1. Introduction

The primary carbon sources for below-ground microbial populations are root biomass (Fogel, 1985) and root-derived exudates (Warembourg and Billes, 1979; Helal and Sauerbeck, 1986; Martin and Kemp, 1986; Keith et al., 1986; Van Veen et al., 1989). Plant detritus provides the most abundant microbial resource, but root exudates, such as sugars and amino acids, provide higher quality carbon substrates for microbial growth (Warembourg and Billes, 1979; Kraffczyk et al., 1984). Root exudates are primarily composed of carbohydrates (Martens, 1990); up to 65% of maize root exudates are sugars (Kraffczyk et al., 1984). Using $^{14}CO_2$, researchers have traced the flux of carbon fixed by plants to roots and soil microbes (Helal and Sauerbeck, 1986; Van Veen et al., 1989; Martens, 1990). During early stages of plant growth, 16 – 41% of photosynthate is released into the soil (Van Veen et al., 1989; Martens, 1990). Helal and Sauerbeck (1986) reported that 68% of microbial growth was attributable to maize photosynthate released into the soil, whereas soil carbon accounted for only 32% of the increased microbial growth.

In the extensive review on factors influencing root exudates by Hale and Moore (1979), only two papers addressed the effect of above-ground herbivory on root exudates. Both Smith (1972) and Bokhari and Singh (1974) found an increase in root exudates in defoliated, compared with non-defoliated, plants; however, neither study examined the effects of increased root exudates on microbial populations. Smith (1972) and Dyer and Bokhari (1976) hypothesized that an increase in root exudates due to defoliation may have a significant

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impact on rhizosphere microbes. Ruess and McNaughton (1987) reported that soil microbial biomass was correlated with the intensity of above-ground grazing by mammalian herbivores on a Serengeti grassland.

Research comparing conventional tillage (CT) and no-tillage (NT) agroecosystems has emphasized differences in below-ground patterns and processes, while little emphasis has been placed on above-ground interactions (e.g. herbivory) that may affect below-ground processes (e.g. carbon flux). NT surface soil (0 – 7.5 cm) contains greater microbial populations, root density, and root biomass when compared with CT surface soil, while the lower depth (7.5–15 cm) in CT soil contains greater microbial populations, root density and root biomass than NT soil (Doran, 1980; Linn and Doran, 1984; Cheng et al., 1990). Although the effects of herbivory on root demography, growth, and biomass remain controversial, studies have shown that herbivory does not affect root distribution (Ganskopp, 1988) and may cause a decrease in root biomass and growth (Richards, 1984; Ganskopp, 1988; Oesterheld, 1992). The objectives of the research reported here were (1) to examine influences of varying above-ground herbivore intensities on soil microbial biomass associated with individual maize plants, and (2) to compare the relative effects of above-ground herbivory between conventional tillage and no-tillage systems.

2. Materials and methods

The study was conducted at the University of Georgia's Horseshoe Bend experimental area, located near Athens, Georgia. Both the conventional tillage and no-tillage plots (0.3 ha) used in the study have been maintained under tillage treatment since 1978. The soil is characterized as a well-drained moderately acidic, fine loamy, mixed, thermic Rhodic Kanhapludult. Maize (*Zea mays*) was grown as a summer crop, following wheat (*Triticum aestivum*) and clover (*Trifolium incarnatum*) cover crops during winter months. Further descriptions of the site are given by Beare et al. (1992).

The lubber grasshopper, *Romalea guttata* (Houttuyn), was used as the herbivore because it is a flightless, general feeder, and herbivory is easily controlled with this species. Grasshoppers were collected in Athens, Georgia and maintained on lettuce and water in a greenhouse. The grasshoppers were starved for 48 h before the experiment to increase the likelihood of the grasshoppers feeding at similar rates. Different grazing intensity treatments were established by caging 0 (control), five, ten, or 20 grasshoppers around individual maize plants. Cages (120 cm tall, 37 cm diameter) were constructed of 2 mm mesh metal window screen stapled to a fence stake.

On 29 June 1993 grazing treatments were applied to maize plants that were 30 days old and in early stages of growth. Three replicates of each of the four grazing treatments were randomly assigned to plants in both CT and NT plots. Plants visibly different from mean field plant size were not used. The grasshoppers were allowed to graze the plants for 5 days to establish a grazing gradient that represented a continuum of low to high leaf area removed. After 5 days, cages and grasshoppers were removed. Samples were taken 12 days later in order to allow plants adequate time to respond to grazing. The phytomass was cut and removed at the point where prop roots began to emerge from the maize stalk. Fresh and dry weights of above-ground plant biomass were measured. The soil–root system was removed using a shovel. One soil sample per plant was taken from within the root system directly underneath the maize stalk at a depth of between 8 and 12 cm.

Soil samples were stored at 4°C for 5 days and then analyzed for microbial biomass using the chloroform fumigation direct extraction method (CFEM) (Vance et al., 1987; Jordan and Beare, 1991). Gravimetric moisture was determined for each soil sample from a 10 g subsample. Soil samples were sieved (2 mm mesh) to remove roots. Two subsamples, a fumigation (F) and non-fumigation (NF), of 20 g dry weight equivalents were taken from each field soil sample. F and NF subsamples were brought to 25% moisture content to improve extraction efficiency (W. Cheng, personal communication). F subsamples were fumigated with distilled chloroform for 24 h. F and NF subsamples were extracted with 60 ml of 0.5 M K_2SO_4. Extracts were analyzed for carbon using a Shimadzu Total Organic Carbon Analyzer (TOC-500). Total microbial biomass carbon (TMBC) was calculated as: $TMBC = F_{TOC} - NF_{TOC}/k_c$. The k_c used was 0.33 after Sparling and West (1988).

Analyses of variance (ANOVA) were used to analyze for grazing treatment effects on soil microbial bio-

mass. A Student–Newman–Keuls test was used to compare means of the different grazing treatments. Analyses were performed using the Statistical Analysis System for microcomputers (Statistical Analysis Systems Institute, 1988).

3. Results

Above-ground grazing treatments had a significant effect on soil microbial biomass carbon in the no-tillage field ($F_{3,8} = 8.17$; $P = 0.0081$), but no significant effect in the conventional tillage field ($F_{3,8} = 3.85$; $P = 0.06$) (Fig. 1). Grazing treatments produced no trend in plant weight in CT. However, there was a trend for decreasing plant weight with increasing herbivore intensity in NT. In CT, no significant differences were observed in soil microbial biomasses between the different grazing treatments and the control (Fig. 1). In NT, the low level of herbivory treatment (five grasshoppers per plant) had significantly greater soil microbial biomass carbon than control, medium, and high grazing intensity (Fig. 1). Soil microbial biomass for the low grazing intensity was 35% greater than soil microbial biomass for the control and high herbivory (20 grasshoppers per plant), and 20% greater than the grazing treatment with ten grasshoppers per plant. Soil microbial biomass carbon for the grazing treatment with ten grasshoppers per plant was 19% greater than soil microbial biomass of the control and high herbivory.

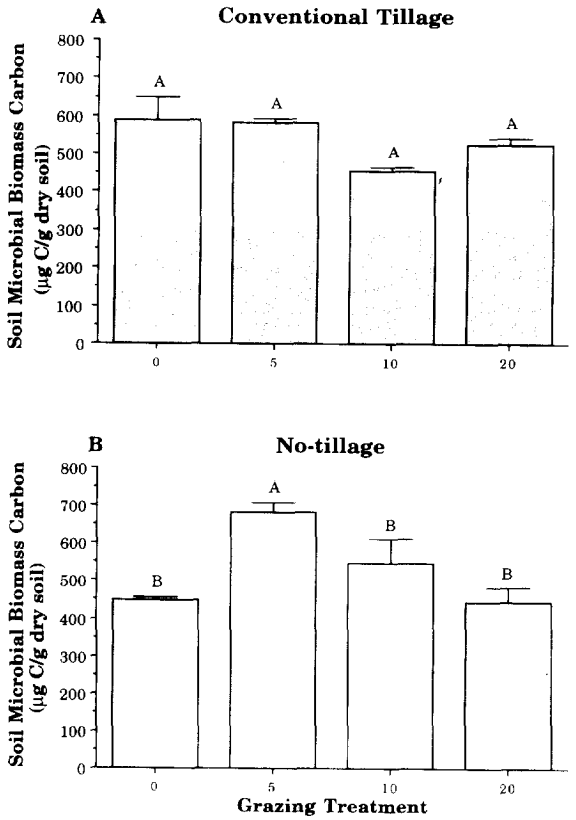

Fig. 1. Mean (±1 SE) soil microbial biomass carbon for each grazing treatment (0, 5, 10, and 20 grasshoppers per treatment for 5 days) for conventional tillage (A) and no-tillage (B) agroecosystems. Treatments with the same letters are not significantly different using Student–Newman–Keuls test (d.f. = 8, $P < 0.05$). Statistical analyses of treatment means among fields were not performed.

The mean (±1 SE) value for NT control microbial biomass carbon was 447 ± 8 μg C g^{-1} dry soil at a depth of 8–12 cm. Jordan and Beare (1991) used the CFEM to estimate NT microbial biomass carbon in HSB soils. They reported mean (±1 SE) microbial biomass carbon as 521 ± 19 μg and 203 ± 9 μg C g^{-1} dry soil for soil depths of 0–5 cm and 5–15 cm, respectively. The control microbial biomass carbon for this study fell within the range reported by Jordan and Beare (1991). Published data are limited for CFEM measurements of CT microbial biomass in HSB soils.

4. Discussion

The quantity of photosynthate released into the soil as root exudates is variable and depends on plant species, plant age, plant physiology, water stress, and soil environmental factors (Hale and Moore, 1979; Heal and Dighton, 1985; Martin and Kemp, 1986; Van Veen et al., 1989). Above-ground herbivory alters plant physiology by affecting plant growth rates and carbon allocation (Dyer et al., 1991). Different grazing intensities induce different growth rates for roots and shoots (Oesterheld, 1992). I attribute the observed differences in microbial biomass carbon in the NT field to increases in soil carbon substrates through root exudates, which resulted from above-ground herbivory. I hypothesize that at low levels of herbivory an increase in carbon allocation to roots results in an increase in root exudates, while at high levels of herbivory shoots are carbon sinks. An alternative explanation to increases in root exudates is that grasshopper frass inputs stimulated

soil microbial growth. Frass may increase soil surface microbial growth, but in this study much of the frass never reached the soil surface because it was intercepted by the maize leaves. Frass inputs to soil were small and an observable effect at the 8–12 cm sampling depth is unlikely. If microbial responses were produced by frass inputs, then a linear increase in microbial biomass would be expected due to a linear increase in frass with grazing intensities. Microbial biomass in this study did not vary linearly with grazing intensity.

In the no-tillage agroecosystem, microbial biomass was highest at low levels of grazing and then decreased as grazing intensity increased (Fig. 1(B)). Ruess and McNaughton (1987) reported similar results for a multi-site transect grazed by mammalian herbivores in Serengeti grasslands. They found that soil microbial biomass increased as grazing intensity increased, but then decreased at high grazing intensities. Furthermore, they reported that microbial biomass varied as a function of grazing intensity ($P < 0.05$), which agrees with the results reported here ($P = 0.0081$). Ruess and McNaughton (1987) hypothesized that increased dung inputs by mammalian grazers may have induced the microbial responses. This would account for the increases in microbial growth, but not the decrease observed at the higher grazing intensity as the dung was both carbon and nutrient rich. Herbivore mediated root exudation is an alternative explanation. Smith (1972) and Bokhari and Singh (1974) reported that root exudates increased for defoliated plants. Kinsinger and Hopkins (1961) found that grasses with low levels of defoliation had greater quantities of root carbohydrates compared with controls and heavily defoliated grasses. Using a hydroponic medium, Dyer and Bokhari (1976) investigated effects of grasshopper grazing on grass and found that pH changes in root media varied with grazing. They hypothesized that above-ground grazing may increase below-ground respiration and root exudation, thus having a significant impact on below-ground food webs.

Different microbial responses to above-ground herbivory in the CT and NT agroecosystems suggest tillage practice may play a role in herbivore–plant–soil–microbe interactions. Mixing of plant detritus in CT may provide more carbon resources, which are available for soil microbial communities, at lower soil depths than those seen in NT, in which plant detritus remains on the soil surface. Thus, if carbon resources below ground were more abundant, then an increase in CT microbial biomass may not be observed. Alternatively, the observed differences between CT and NT fields may have resulted from grazing treatments not being effectively established in the CT field. A trend for decreasing plant weight with increasing herbivore intensity was produced in the NT field, but not in the CT field. However, plant weights should not be directly compared with effectiveness of grazing intensity establishment, since the plants had 12 days for regrowth.

This study demonstrates that above-ground herbivory can stimulate an increase in soil microbial biomass. Future studies may enhance our understanding of herbivore–plant–soil–microbe interactions by using ^{14}C-technology to trace plant fixed carbon to roots and soil microbes associated with plants with varying levels of herbivory.

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