Soil Biology & Biochemistry 40 (2008) 894–905

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Do interactions with soil organisms mediate grass responses to defoliation?

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Received 11 May 2007; received in revised form 5 November 2007; accepted 6 November 2007
Available online 3 December 2007

Abstract

Defoliation-induced changes in grass growth and C allocation are known to affect soil organisms, but how much these effects in turn mediate grass responses to defoliation is not fully understood. Here, we present results from a microcosm study that assessed the role of arbuscular mycorrhizal (AM) fungi and soil decomposers in the response of a common forage grass, *Phleum pratense* L., to defoliation at two nutrient availabilities (added inorganic nutrients or no added nutrients). We measured the growth and C and N allocations of *P. pratense* plants as well as the abundance of soil organisms in the plant rhizosphere 5 and 19 d after defoliation. To examine whether defoliation affected the availability of organic N to plants, we added ^{15}N-labelled root litter to the soil and tracked the movement of mineralized ^{15}N from the litter to the plant shoots.

When inorganic nutrients were not added, defoliation reduced *P. pratense* growth and root C allocation, but increased the shoot N concentration, shoot N yield (amount of N in clipped plus harvested shoot mass) and relative shoot N allocation. Defoliation also reduced N uptake from the litter but did not affect total plant N uptake. Among soil organisms, defoliation reduced the root colonization rates of AM fungi but did not affect soil microbial respiration or the abundance of microbe-grazing nematodes. These results indicate that interactions with soil organisms were not responsible for the increased shoot N concentration and shoot N yield of defoliated *P. pratense* plants. Instead, these effects apparently reflect a higher efficiency in N uptake per unit plant mass and increased relative allocation of N to shoots in defoliated plants. The role of soil organisms did not change when additional nutrients were available at the moment of defoliation, but the effects of defoliation on shoot N concentration and yield became negative, apparently due to the reduced ability of defoliated plants to compete for the pulse of inorganic nutrients added at the moment of defoliation.

Our results show that the typical grass responses to defoliation—increased shoot N concentration and shoot N yield—are not necessarily mediated by soil organisms. We also found that these responses followed defoliation even when the ability of plants to utilize N from organic sources, such as plant litter, was diminished, because defoliated plants showed higher N-uptake efficiency per unit plant mass and allocated relatively more N to shoots than non-defoliated plants.

Keywords: AM fungi; Clipping; Decomposer food web; Grassland; *Phleum pratense*; Plant carbon allocation; Plant nitrogen dynamics; Plant–soil interactions; Soil nematodes; ^{15}N

1. Introduction

It is increasingly recognized that soil organisms may play an important role in the response of plants to defoliation (Bardgett and Wardle, 2003; Wardle et al., 2004). For instance, defoliation typically increases the N concentration of grass shoots (Wilsey et al., 1997; Fahnestock and Detling, 1999; Green and Detling, 2000), suggesting that this is a consequence of improved availability of N in the soil following defoliation (Holland and Detling, 1990). For example, Hamilton and Frank (2001) recently showed how defoliation of smooth meadow-grass *Poa pratensis* L. increased the availability of N in the soil and led to elevated shoot N concentrations in defoliated plants. In

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doi:10.1016/j.soilbio.2007.11.004

addition, they found that the increased availability of N in the soil was associated with increased growth of decomposer microbes in the plant rhizosphere, indicating that the elevated shoot N concentrations were a result of defoliation-induced soil microbial activity. However, increased shoot N concentrations may also reflect other changes occurring after defoliation. Arbuscular mycorrhizal (AM) fungi, in addition to enhancing plant P uptake, also substantially improve uptake of N (Mäder et al., 2000). The majority of studies (reviewed by Gehring and Whitham, 1994) have reported decreases in AM colonization rates of plant roots after defoliation, but increases have also been recorded (Hartley and Amos, 1999; Hokka et al., 2004; Kula et al., 2005), which implies that elevated shoot N concentrations may in some cases also reflect enhanced AM colonization rates. Elevated shoot N concentrations can also reflect greater relative allocation of nutrients to shoots after defoliation (Ruess, 1988; Louahlia et al., 2000), and in principle they could simply result from a greater reduction in plant C assimilation than N acquisition during recovery from defoliation. There is therefore a need for studies that provide a comprehensive assessment of the role of different soil organisms, in relation to other mechanisms, in plant responses to defoliation.

The potential role of soil organisms in the response of plants to defoliation stems from the fact that defoliation induces changes in plant C allocation that can affect the availability of labile C in the soil. For instance, defoliation can increase photosynthate allocation to roots (Holland et al., 1996) or increase the concentrations of soluble C in roots (Paterson and Sim, 1999), which in turn may increase C exudation from roots to soil and stimulate soil microbes (Mawdsley and Bardgett, 1997). Similarly, increased allocation of C to roots after defoliation may induce greater AM infection rates of roots (Gehring and Whitham, 1994). However, a stimulated soil microbial community does not necessarily improve soil nutrient supply for plants. Soil microbes compete effectively with plants for available nutrients (Van Veen et al., 1989; Kaye and Hart, 1997; Bardgett et al., 2003), and C addition and the resulting microbial growth may, in contrast, reduce plant nutrient uptake (Diaz et al., 1993; Jonasson et al., 1996; Schmidt et al., 1997). Microbe-feeding animals, such as protists and nematodes, that release nutrients from microbial biomass when consuming it are therefore necessary for maintaining the availability of nutrients for plants (Clarholm, 1985; Paterson, 2003). When microbial grazers are present, increased root C release can potentially improve plant N availability if it induces microbes to increase utilization of dead organic matter, because part of the organic N assimilated into the microbial biomass at this stage will subsequently be released by microbial grazers for plant uptake. To understand how trophic interactions in soil are affected by defoliation and what consequences this may have on N mineralization are therefore crucial to assessing the role of soil organisms in plant responses to defoliation, such as elevated shoot N concentrations. Although evidence has long been accumulating of soil decomposers being affected by plant defoliation (Stanton, 1983; Seastedt et al., 1988; Mawdsley and Bardgett, 1997; Fu et al., 2001; Mikola et al., 2001, 2005a; Techau et al., 2004), no study has so far experimentally linked the multitrophic level effects of defoliation in soil food webs to soil N availability and plant N uptake.

Here, we present a greenhouse study that was aimed at assessing the role of soil organisms in grass responses to defoliation. We established controlled microcosms consisting of natural soil communities and seedlings of timothy *Phleum pratense* L., an important forage grass in northern pastures (Berg et al., 1996). We defoliated the seedlings and followed their growth and C and N allocations as well as the abundances of soil organisms in the plant rhizosphere. We also added ^{15}N-labelled litter in the soil before defoliation and tracked the movement of ^{15}N from litter to plant shoots to examine whether defoliation affected the availability of soil organic N to plants. We predict that if interactions with soil organisms mediate *P. pratense* responses to defoliation and especially the expected increase in shoot N concentrations, (1) the activity and abundance of soil decomposers and/or rates of root AM colonization will increase after defoliation, and as a result (2) transfer of N from the added litter to *P. pratense* plants will be higher for defoliated than for non-defoliated plants. Since we reasoned that the availability of easily utilizable inorganic forms of N in the soil at the moment of defoliation may determine whether defoliation induces microbes to increase utilization of N from the litter added, we further measured the effects of defoliation in systems with and without additional inorganic nutrients. This experimental approach allowed us to compare a comprehensive and previously unexplored set of mechanisms potentially able to mediate and modify grass responses to defoliation.

2. Materials and methods

2.1. Establishment of the microcosms

Soil with a sandy texture, total C content of 2.5%, total N content of $1.5\,g\,kg^{-1}$, total P content of $1.2\,g\,kg^{-1}$ and pH (water) of 6.4 was collected from a pasture in central Finland (62°N, 26°E) in September 2003. The soil was sieved (1 cm) and homogenized, and 950 g (dry weight equivalent) was added to each of 68 plant pots (height 9 cm, diameter 11–13 cm, with holes in the base to allow free drainage of water). No organisms were removed from or added to the soil during this procedure. To allow later addition of ^{15}N-labelled litter into the soil, three plastic tubes (diameter 1.6 cm, height 13 cm) were placed vertically into the full depth of the soil in a triangle in the middle of each pot, 3.5 cm apart. One 5-wk-old *P. pratense* seedling, sprouted in vermiculite, was then planted in each pot in the middle of the triangle.