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Microbial growth under the snow: Implications for nutrient and allelochemical availability in temperate soils

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Abstract

Recent work has shown that plant litter inputs fuel microbial growth in autumn and winter resulting in a large increase of microbial biomass under the snow pack in tundra soils. This winter-adapted microbial community can grow at low temperatures (−5 to 3 °C) and depletes the litter of easily degraded constituents, such as simple phenolic compounds, and immobilizes nitrogen. During snowmelt there is a die-off of this winter microbial community (due to starvation and intolerance to higher soil temperature) resulting in a release of nitrogen that can be utilized by plants and the summer microbial community. The summer microbial community can tolerate higher temperatures (5 to 20 °C) and utilizes mostly plant root exudates for growth. These yearly cycles of microbial growth dynamics have profound implications for both nutrient and alleochemical availability to plants. Firstly, these results show that release (from litter) and degradation of plant phenolic compounds (potential alleochemicals) occurs before plant growth commences in the spring. Secondly, nitrogen (N) immobilized by over-winter microbial growth is released back to the soil during and after snowmelt, thus becoming available to plants. Both of these results need to be incorporated in the design of experiments to explore plant-plant interactions. Many experiments in which chemicals (or fresh litter) are incorporated during plant growth do not reflect the fact that these two events are temporally uncoupled in many natural systems.

Introduction

We know very little about how plants affect the community dynamics of microorganisms in natural systems. Such an understanding would greatly enhance our understanding of how plants and microorganisms interact to control biogeochemical cycles and how plants could potentially affect the distribution of neighboring plants through chemical means (allelopathy). Plant distribution has been shown to correlate with the spatial distribution of soil properties (Gallardo et al., 2000; Rhia et al., 1986; Stoyan et al., 2000) and microbial biomass (Herman et al., 1995; Smith et al., 1994) in many natural systems. There is also some evidence that chemistry of individual plant species can alter microbial processes (Hättenschwiler and Vitousek, 2000; Souto et al., 2001) and even select for specific microbial functional groups that can accelerate degradation of alleochemical compounds from those plants (Schmidt, 1990; Schmidt and Ley, 1999; Schmidt et al., 2000). On a slightly broader scale, it is known that plant community composition affects soil microbial community structure and function (Fisk et al., 1998; Groffman et al., 1996; Ingham, 1989). Likewise, the effects of disturbance and invasion by exotic plant species on soil microbial communities and processes have been studied (Allen et al., 1999; Ehrenfeld et al., 2001; Evans et al., 2001; Schmidt and Reeves, 1989; Zak, 1992). It is becoming apparent that these changes in the microbial community have important feedbacks at the ecosystem level (Chapin et al., 2000; Klironomos, 2002; Lipson et al., 1999a).

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Although we know little about how plants affect specific microbial groups in nature, we know even less about how microbial populations interact with plants on a seasonal basis (Wardle, 1998). Seasonal changes in microbial community composition and function have been reported elsewhere (Bardgett et al., 1999; Bossio et al., 1998; Smit et al., 2001; Zogg et al., 1997). Such information is of importance if we are to understand how microbial population dynamics affect nutrient availability (Groffman et al., 1993; Jaeger et al., 1999b; Lipson et al., 1999a; Singh et al., 1989; Zak, et al. 1990) and the chemical composition of root exudates, leaf leachates, or litter in soil. For example, in some ecosystems litter decomposition occurs mostly in the autumn and winter when most plants are dormant and thus unable to take up or interact with compounds released from litter. A better understanding of the timing of *in situ* microbial activity is needed in order to be able to predict how microbial activity affects both nutrient and carbon compound availability in natural soils.

Tundra is a good model system for understanding how plants influence microbial community dynamics and plant chemical inputs on a seasonal basis. Tundra systems exhibit profound seasonal cycles oscillating between an intense summer season of high plant productivity and the snow-covered season of no plant production. There is also a wealth of evidence that plants interact very dynamically in tundra systems and can strongly affect each other in both positive and negative ways (Chambers, 1991; Griggs, 1956; Marion, et al. 1982; Steltzer and Bowman, 1998; Theodose et al., 1996).

Recent studies have greatly enhanced our understanding of how plants influence microbial community dynamics in tundra ecosystems and how these influences change on a seasonal basis. More specifically, the yearly cycles of microbial growth dynamics have profound implications for both nutrient and alleochemical availability to plants. In terms of nutrients, the under-snow microbial community acts first as a sink (under the snow) and then a source (during snow melt) of nutrients for plant growth. With regard to allelochemicals, evidence suggests that the under-snow microbial community metabolizes alleochemicals released from plant litter in the fall and winter, before plant growth commences in the spring.

Seasonal dynamics of tundra systems

Tundra ecosystems exhibit striking seasonal cycles. Plant growing seasons are short but intense, and winters are long. Tundra plants are adapted to take advantage of the short growing season, but until recently it was unclear as to how plants obtained enough nutrients from cold tundra soils. For example, in alpine tundra common indexes of nitrogen (N) availability indicated that there is not enough net N mineralization to account for observed plant N demands (Fisk and Schmidt, 1995). Explanations for how some tundra plants obtain enough N have come from studies of organic nitrogen uptake by mycorrhizal and non-mycorrhizal plants (Lipson and Näsholm, 2001; Lipson et al., 1999b) and from studies that have shown that turnover and re-assimilation of microbial N is much faster than was previously thought (Fisk et al., 1998; Lipson et al., 2001). Even more surprising is the recent observation of a large pulse of available N during snowmelt in many tundra soils (Brooks et al., 1998; Lipson et al., 1999a) which can be exploited by several tundra plant species (Jaeger et al., 1999b; Mullen et al., 1998).

Observation of the seasonality of N availability led to more detailed studies to quantify and characterize microbial biomass under winter snow packs in tundra. Past work in tundra and other systems also hinted at the possibility that there is much microbial activity under winter snows. For example, gas accumulation (e.g., CO_2, CH_4, N_2O) and litter decomposition occur under winter snow packs in a broad array of temperate ecosystems (Bleak, 1970; Hobbie and Chapin, 1996; Moore, 1983; Penny and Pruitt, 1984; Sommerfeld et al., 1993; Zimov et al., 1993). However, many early authors and some recent authors attributed much of these observations to unexplained abiotic phenomena. It has only been recently that direct measurements of microorganisms, their enzyme activities and DNA levels have shown that microbial biomass is very high and active under snow packs (Brooks et al., 1998; Lipson et al., 1999a, 2002; Schmidt et al., 2003). Studies of the seasonality of microbial population dynamics also revealed that the microbial community undergoes a shift in function and genetic structure between winter and summer (Lipson et al., 2002) corresponding with the pulse of N discussed previously.

Microbial growth in autumn and winter

Recent research shows that water availability, rather than temperature *per se*, limits life in cold systems (Fisk et al., 1998; Kennedy, 1993; Mazur, 1980). Microscopic films of unfrozen water exist on the surface of soil particles at temperatures well below 0 °C and there is sufficient available water for psychrophilic and psychrotrophic soil microbes at temperatures down to at least −5 °C (Anderson, 1970). Temperatures above −5 °C are common late in the winter under snowpacks due to the insulating effects of the snow (Brooks et al., 1998) and significant microbial respiration has been measured at temperatures down to −5 °C in tundra soils (Brooks et al., 1997; Clein and Schimel, 1995).

Even at very extreme high altitude sites (3700 m) temperatures under the snow can remain around 0 °C for many months, allowing the proliferation of a large and diverse cold-adapted microbial community (Ley et al., 2004). In addition, inorganic nutrients are plentiful in under-snow soils due to high levels of nitrogen mineralization and a lack of plant activity (Brooks et al., 1998). Thus, the under-snow environment can be an ideal incubator for microbial growth and activity in tundra and other systems.

The carbon and energy to power the under-snow proliferation of microbes comes from plant litter inputs. Most of the litter input in temperate systems occurs in the autumn when biomass senesces or goes dormant above ground and many fine roots die below ground. This autumnal input of carbon is especially important in tundra systems where most of the above ground biomass dies back to the ground in winter and there is a large dieback of roots below ground (Fisk et al., 1998). This pulse of litter results in high concentrations of cellulose and the hot-water soluble fraction of soil carbon compounds (proteins, starch and tannins) in the fall and winter compared to very low levels of these compounds in summer soils (Lipson et al., 2000). Thus, there are large pools of available carbon compounds to support microbial growth in the winter and the microbial populations that develop under the snow mineralize much of this carbon during the course of the winter. Lipson et al. (2000) showed that soil microbes became carbon limited in late winter and early spring and this was a factor that contributed to the decline of the cold-adapted microbial biomass during snowmelt.

Detailed ecophysiological studies of microbial populations support the idea that microbes are very active in breakdown of plant structural and allelochemicals over the winter. For example, Lipson et al. (2002) showed that the winter microbial community has a higher specific activity (activity per unit microbial biomass carbon) of cellulase, and the use of the phenolic compound vanillic acid was higher in the winter than in the summer. Likewise Schmidt et al. (2003) found the largest populations of microbes that can mineralize phenol and salicylic acid in the autumn and winter in tundra soils. These results are consistent with our idea that the winter community is utilizing plant litter and phenolic carbon sources in the winter.

Evidence from traditional litter decomposition studies also support the idea that microbial populations are very active in the winter and are supplied with carbon and nutrients from plant litter laid down at the end of the previous growing season. Hobbie and Chapin (1996) noted that litter mass losses were very high in the winter under Arctic tundra snow packs. Likewise Bleak (1970) found higher mass losses in winter than in summer, with up to 51% of litter mass loss over the winter at high elevation (3000 m) sites in Utah. As a result, Bleak (1970) theorized that these losses were mostly due to activity of fungi and bacteria beneath the snow, although he made no measurements of microbial populations. Studies of litter decomposition in forested systems also indicate substantial microbial activity under winter snow packs. Taylor and Jones (1990) reviewed the results of 17 studies of litter decomposition and concluded that over-winter decomposition usually constitutes 40–60% of mass loss during the first year of study. Their compilation of results also strongly suggested that under-snow decomposition resulted in the microbial consumption of all ‘leachable or labile material’ from litter of forbs, grasses, hardwood leaves and conifer needles during the first winter of the studies reviewed (Taylor and Jones, 1990). All of these studies support our contention that microorganisms are actively degrading plant-produced allelochemicals in cold soils over the winter.

Microbial growth in the summer

In contrast to the winter and autumn when compounds from moribund plant material feeds most microbial population growth, root inputs of carbon compounds drive summer microbial community dynamics. Growing plants contribute carbon compounds to soil from sloughing of root cells and exudation of many organic compounds into the rhizosphere (Rovira, 1969). Due

to this carbon input, rhizosphere soils usually support 10–20 times higher populations of bacteria and fungi than do bulk soils (Dandurand and Knudsen, 2002). This bloom of microbial growth in the rhizosphere is especially pronounced near growing root tips where exudation of sugars and amino acids is greatest (Jaeger et al., 1999a). In turn the prolific growth of microorganisms attracts protozoa and other predators to the rhizosphere resulting in increased turnover and nutrient release from microbial biomass (Clarholm, 1985; Elliott et al., 1984).

Further evidence that plant rhizosphere inputs are the primary control over heterotrophic microbes during the growing season is made apparent by considering the magnitude and types of carbon inputs into the rhisosphere. As one example, Norton et al. (1990) estimated that 35% of carbon fixed by pine seedlings flowed to mycorrhizal fungi and other rhizosphere inhabitants. There is a wide array of chemicals released into the rhizosphere by plants (Jaeger et al., 1999a; Marschner et al., 1987; Römheld, 1991), but probably the most important for microbial growth are amino acids and sugars which can constitute the majority of root exudates (Uselman et al., 2000). Uselman et al. (2000) and Rattray et al. (1995) showed rapid turnover of a high proportion of compounds deposited in the rhizosphere with turnover times of hours as opposed to days for more complex compounds in soils.

That compounds deposited in the rhizosphere can support rapid microbial growth is not doubted, even under less than optimal conditions encountered in tundra soils. For example, Lipson et al. (2002) showed that the summer microbial community in tundra had a higher proportion of individuals that could use the simple amino acid glycine than the winter microbial community at the same site. These results were backed up by DNA cross-hybridization studies and direct microbial counts that showed a radical shift in microbial community composition between winter and summer at the same site. Fungi dominated the winter community whereas faster growing bacteria dominated in the summer (Lipson et al., 2002).

Implications for plant ecological studies

One of the most important implications of the profound seasonality of microbial community dynamics is how it affects nutrient availability in soil (Figure 1). Traditional growing season estimates of nitrogen fluxes in tundra soils gave baffling results in that the fluxes observed during the growing season were much too low to account for plant demands for N (Fisk and Schmidt, 1995). It was not until fluxes were measured during the transition from winter to summer that large enough fluxes were observed to partially explain plant N dynamics in tundra soils. The decline in the cold–adapted microbial biomass during snowmelt coincides with a large increase in soil proteins and microbial protease activity in soil, which in turn results in a pulse of N availability early in the plant growing season (Lipson et al., 1999a). A number of tundra plants can take advantage of this early season pulse of N (Jaeger et al., 1999b) and this uptake is enhanced by mycorrhizal fungi associated with these plants (Lipson et al., 1999b; Mullen et al., 1998). Other tundra plants seem to have a different strategy wherein they take advantage of the transient microbial turnover of N later in the growing season (Bowman and Bilbrough, 2001; Fisk et al., 1998).

The other main effect of over-winter microbial activity is that it profoundly modifies the chemical composition of plant litter laid down the previous fall. Microbial attack on allelochemicals and other substrates is vigorous under tundra snow packs resulting in litter that is depleted in such compounds by the time plant growth commences. The two main consequences of this are: (1) allelopathically active substances are mostly metabolized before plant growth begins the following year, (2) the potential for nutrient immobilization caused by microbial growth on high C:N substrates is minimized by the time plant growth begins (Figure 1).

The consequences of over-winter microbial activity can inform researchers in designing realistic ecological experiments. For example, experiments in which fresh or dried plant material (or extracts from such litter) is applied to actively growing plants should be avoided because such treatments represent conditions that would not occur under natural conditions. Even in agricultural settings it is rare for crop residues to be incorporated into the soil immediately before a new crop is planted. Traditional farmers from many cultures have long understood the idea that planting too soon after the incorporation of crop residues results in stunted plant growth. This is especially true for substrates containing low levels of nitrogen (less than approx. 2%) which can result in significant microbial immobilization of N during the initial stages of decomposition (Alexander, 1977).

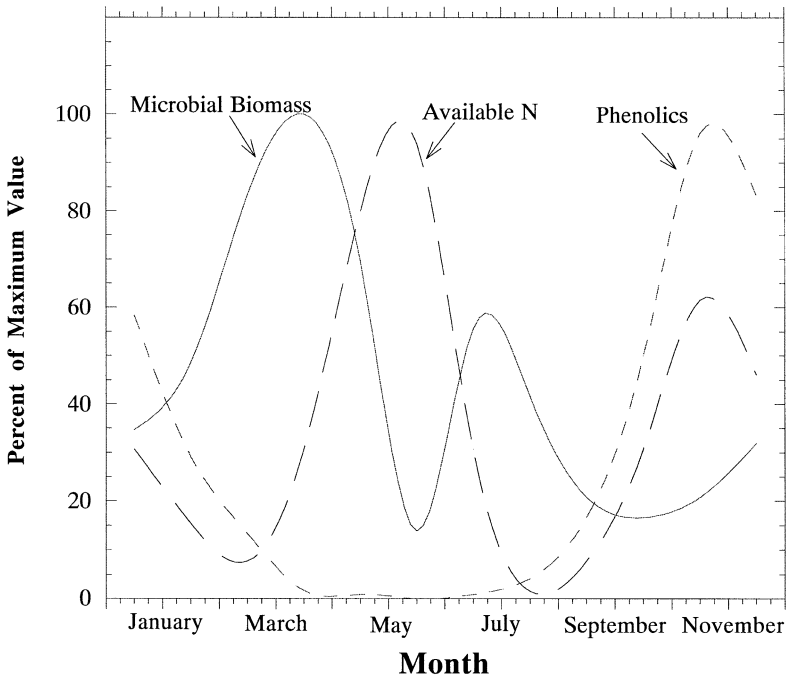

Figure 1. Yearly cycles of microbial biomass, available N, and simple phenolic compounds in soil of alpine tundra. Microbial biomass increases to maximal levels in late winter under the snow and then declines during snowmelt (Lipson et al., 1999a, 2000; Schmidt et al., 2003). This crash results in a pulse of N availability that is used by plants and the developing summer microbial community (Brooks et al., 1998; Lipson et al., 1999a). There are also transient inputs of available N associated with summer rainstorms but, for simplicity, these are not shown. Potential allelochemicals, such as simple phenolic compounds, are released from fresh litter in the autumn and are a carbon and energy source for the microbial community that develops in the autumn and winter (Lipson et al., 2000, 2002). Thus, these potential alleochemiclas are consumed before plant growth commences in the spring.

Conclusion

Our understanding of the dynamics of microbial communities and activity has expanded enormously in the last decade. One consequence of this explosion in knowledge has been a rethinking of the environmental constraints on nutrient cycles and plant-plant interactions. Work reviewed in this paper shows that degradation of potential alleochemicals from litter occurs in the autumn and winter before plant growth commences in the spring. In addition, nitrogen immobilized by over-winter microbial growth on litter can be released back to the soil during and after snowmelt, and is an important pool of temporally available nitrogen in nitrogen-limited systems such as tundra. This new knowledge of the temporal variation in microbial population dynamics should help researchers design more realistic experiments to explore plant-plant interactions in nature.

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