PROTIST NEWS

Soil Respiration, Climate Change and the Role of Microbial Communities

Introduction

Although this contribution is not intended to be a comprehensive perspective on current knowledge of soil respiration, a brief overview of some pertinent research on global patterns of soil respiration is presented first as a context for the more focused discussion of the role of microbial communities in soil carbon budgets and net respiratory flux to the atmosphere. Major reviews, and relevant broad research studies of current knowledge about regional and global respiratory flux patterns, are available from other sources. These include reviews of terrestrial respiration in broad geographical regions (e.g. Raich and Schlesinger 1992; Schlesinger 1997; Schimel 1995; Peng and Apps 2000; Luo and Zhou 2006); in particular geographic regimes and biomes (e.g. Townsend et al. 1992; Bekku et al. 2003; Bond-Lamberty and Thomson 2010; Anderson 2010a); and in relation to soil decomposition processes (e.g. Tate 1995; Adl 2003). With increasing evidence of global climate change, including increasing global temperature and likely major changes in patterns of precipitation, effects on soil microbial communities are likely to be significant, especially at higher latitudes where thawing of the permafrost may release substantial stored-up carbon compounds, thus increasing microbial respiration and efflux of CO_2 to the atmosphere. Some perspectives on emerging evidence of the effects of climate change, especially precipitation patterns and soil moisture on the dynamics of microbial communities and respiratory CO_2 emissions, are presented in a subsequent section of this paper. Finally, some of the prospects and challenges for future research on the role of bacterial and protist soil microbial communities in terrestrial carbon budgets and CO_2 efflux are discussed in relation to emerging research themes and new methodological approaches.

Factors Influencing Soil Respiration

At the beginning of the twentieth century, some of the major factors that influence soil respiration had been established. These included the role of soil moisture in microbial activity (Greaves and Carter 1920), the primary role of bacterial decomposition as a source of CO_2 efflux (Turpin 1920), importance of soil diffusion kinetics in determining efflux (Lundegårdh 1927) and the correlation of CO_2 production with the rate of diffusion through the soil (Smith and Brown 1933). More recently, estimates of global terrestrial CO_2 flux to the atmosphere have improved substantially, in accuracy and number, especially in relation to different biomes (e.g. Bond-Lamberty and Thomson 2010). The mean rates of soil respiration (g C m^{-2} yr^{-1}) for a variety of vegetation-based, global biomes have been tabulated by Raich and Schlesinger (1992). Examples include Tundra (60 ± 6), northern bogs and mires (94 ± 16), desert scrub (224 ± 38), temperate grasslands (442 ± 78), temperate deciduous forests (647 ± 51), and tropical moist forests (1,260 ± 57). With increasing climate change, current evidence indicates there has been a substantial increase in terrestrial CO_2 flux to the atmosphere during the period of 1960 to present, especially for temperate and tropical biomes compared to high latitude biomes. Based on data analyzed by Bond-Lamberty and Thomson (2010), the recent annual global soil respiration (R_s) is estimated to be 98 ± 12 Pg C; or if agricultural areas are excluded, 85 Pg C. The contribution to total R_s by boreal, temperate and tropical biomes is 13%, 20% and 67%, respectively. Although the largest contribution is from temperate and tropical biomes, the most significant relative change in recent years (7%) has been in the polar biomes. There are less dramatic increases (2-3%) in lower latitudes. This is further supported by meta-analyses of large networks of data sources (e.g. Rustad et al. 2001). Furthermore, as may be expected, the Bond-Lamberty and Thomson (2010) analyses indicate increasing R_s can be partially attributed to increasing global climate change. Laboratory studies of the effects of warming on soil respiration also indicate that the response of microbial respiration to warming as assessed by Q_{10} measurements may differ substantially for soils from different latitudes (Bekku et al. 2003). As climate patterns change, including variations in temperature and precipitation patterns, major shifts in biome boundaries are expected to occur. Among these are likely transitions between grasslands and

forests. Some current evidence (McCulley et al. 2004) suggests that mean soil organic carbon in forested sites can be as much as two-times larger than in remnant grasslands (e.g. 3,382 vs. 1,737 gC m^{-2}), including increased R_s in forested sites compared to grasslands (745 vs. 611 gC m^{-2} yr^{-1}). Microbial biomass carbon was also higher in the woodlands compared to grasslands (444 vs. 311 mg C kg^{-1} soil, respectively). Transitions between grasslands and woodland ecosystems can occur in either direction, depending on climatic factors, particularly changes in precipitation patterns, with less precipitation favoring transitions from woodland to grassland regimes.

Soil Respiration, Precipitation Patterns and Soil Moisture

Among major climatic variables, patterns of precipitation and soil moisture are likely to have significant effects on soil microbial communities and their respiratory responses. Therefore, a survey of some pertinent published research on the response of soil respiration to variations in precipitation is presented as background for the more focused analysis of the role of microbial communities in soil respiration presented later. A recent review of relationships between soil respiration and soil moisture, including an historical analysis of the phases of research in the field in recent decades, has been presented by Cook and Orchard (2008). Soil microbial communities have adapted to the stringent environmental conditions of terrestrial life, where stress from repeated cycles of precipitation and drying have created strong selection pressures to adapt to these highly unpredictable environments. Microbial activity is reduced or ceases below critical levels of soil moisture, resulting in desiccation-resistant dormant stages such as spores or cysts in some species. Soil fungi, with extensive multicellular networks of hyphae, produce hyphal strands that bridge across air-filled pores and are active at a water potential as low as -15 MPa; whereas, bacteria are inactive below -1.0 to -1.5 MPa (Swift et al 1979). Naked amoebae, one of the more common protists in soils, encyst at low levels of soil moisture, but rapidly excyst under favorable conditions when sufficient moisture is present. Based on one estimate from temperate soil, the percent active (P) is linearly related to the weight-based percent water content (M) of the soil, i.e. $P = 2.84\ M - 5.59$, $r^2 = 0.95$, based on samples from a Northeastern U. S. site

(Anderson 2000). A cubic polynomial regression equation relating water potential (W) in bars to soil percent moisture (M) is: $W = 21.45 (P) – 1.285 (P)^2 + 0.025 (P)^3 – 117.41$.

Overall, global soil respiration (g C m^{-2} yr^{-1}) is linearly related to mean annual precipitation (mm), with a slope of ~ 0.5 (Raich and Schlesinger 1992). The relationship of soil respiration to soil moisture content is complex, however, owing in part to the variations in soil porosity, amount of aeration of the soil in relation to soil water content, and of course the differential physiological responses of the microbial community (e.g. Lou and Zhou 2006, p. 92-93). Field observations indicate that soil CO_2 efflux is curvilinear related to soil moisture. CO_2 efflux is limited mainly at the lowest and highest moisture levels with a maximum plateau in the optimum soil moisture range (Bowden et al.1998; Xu et al. 2004), consistent with earlier experimental reports (e.g. Ino and Monsi 1969). A review of current research on the relationship of soil respiration to soil moisture in some major biomes (Polar Regions, grasslands, and meadows and woodlands) is presented as further background information for the subsequent major section on “Soil Respiration, Carbon Budget and Microbial Communities”.

In tundra, moss-rich surface soil that has thawed, and is sufficiently moist to support microbial activity, the CO_2 efflux is higher for mesic sites compared to wet sites where water-logging and anaerobic conditions can suppress aerobic respiration (e.g., Oberbauer et al. 1991; Illeris et al. 2004; Anderson 2010b). Illeris et al. (2004), working with subarctic heath soil, report that optimum moisture content for CO_2 efflux was in the moderate range of 240% soil dry weight, consistent with a range between 200 and 500% reported by Heal et al. (1981). Laboratory measurements of tundra soil respiration from a mesic upslope location compared to a wetter downslope location (Anderson 2010b) also supported the conclusion that respiratory efflux (nmol min^{-1} cm^{-3}) was greater at the mesic site relative to the wetter site when measured at two different temperatures of 15^o C (9.1 ± 0.6 vs. 4.1 ± 0.7) and 25^o C (21.4 ± 0.2 vs. 7.8 ± 0.5). With increased evidence of global warming, and increasing annual temperatures in polar regions, substantial stores of organic compounds in the permafrost may be released supporting microbial respiratory growth and CO_2 efflux to the atmosphere. There are millions of square kilometers of circumpolar tundra, and estimates of respiratory CO_2 emissions can become as high as 5 to 10 kmol km^{-2} h^{-1}, assuming continued climate

change warming, a 10-cm thaw depth, and suitable patterns of precipitation (e.g. Anderson 2008; 2010a,b). This is based, however, on a model that assumes only bacterial and protist contributions - estimates could change substantially in the future, depending on differences in soil physical characteristics, percent active bacteria, and a better estimate of contributions by fungi. However, the above estimates are consistent with current evidence based on field sampling (e.g. Oberbauer et al. 2007). In addition to estimates of tundra protist contributions to respiratory CO_2, the carbon content of the protist community can be as much as 25% of the amount in the bacteria in the sampled Alaskan tundra soil (e.g. Anderson 2008).

Risch and Frank (2006) studying a temperate grassland in North America reported seasonal soil respiration (μmol m^{-2} s^{-1}) in relation to soil moisture. Their data indicate a positive relationship between respiration and soil moisture. For example, at an ungrazed site varying in soil moisture, the respiration (% soil moisture) measurements were 0.8 ± 0.2 (15.8 ± 6.6), 2.6 ± 0.9 (17.4 ± 5.0) and 3.8 ± 0.8 (25.1 ± 13.1). An analysis of their entire set of data (N = 12) shows a positive correlation between soil respiration and seasonal moisture ($r = 0.65$, $p < 0.05$). McCulley et al. (2007) examined soil respiration (g CO_2 m^{-2} d^{-1}) at a subtropical savanna for a control and irrigated site. The respiration data reported in relation to moisture content (m^3 m^{-3}) are: control site 7.9 ± 6.2 (0.063 ± 0.055) and irrigated site 11.7 ± 7.4 (0.179 ± 0.057). The respiration rate of soil from lowland (Japan) and alpine (China) meadow soils in relation to soil moisture content was assessed by Suh et al. (2009). They found a curvilinear positive relationship between respiration (mg CO_2 $(kgsdw)^{-1}$ h^{-1}) and percent soil moisture with an optimum in the 50% to 60% soil moisture range. The maximum respiration at 60% moisture in the alpine meadow was in the range of 0.6 mg CO_2 $(kgsdw)^{-1}$ h^{-1} for surface or deeper layers. It was less 0.2 mg CO_2 $(kgsdw)^{-1}$ h^{-1} at an intermediate depth of 10-15 cm. Comparable depth data for the lowland meadow indicated maximum respiration of 0.4 mg CO_2 $(kgsdw)^{-1}$ h^{-1} at the shallow and deeper soil layers and ~ 0.2 mg CO_2 $(kgsdw)^{-1}$ h^{-1} for the intermediate soil depth.

Wang et al. (2010a) reported the soil respiration rate (μmol CO_2 m^{-2} s^{-1}) at 5 cm depth for three forest locales in China: 1) old-growth mixed coniferous and broad-leaved (MN), 2) middle-aged broad-leaved (BL), and 3) young conifer plantation (CP). The

respiration rates related to moisture (m^3 m^{-3}) for the three sites were: MN, 4.74 ± 0.41 (50.83 ± 2.05); BL, 5.98 ± 0.54 (40.28 ± 1.82); and CP 3.50 ± 0.37 (48.03 ± 2.85). For a subtropical locale, McCulley et al. (2007) reported soil respiration (g CO_2 m^{-2} d^{-1}) for a grove (G) and drainage woodland (W). The respiration rates related to moisture (m^3 m^{-3}) for non-irrigated sites were: G, 9.0 ± 6.9 (0.059 ± 0.037) and W, 8.8 ± 6.2 (0.090 ± 0.055). The results for the irrigated sites were: G, 20.8 ± 11.6 (0.138 ± 0.048) and W, 18.1 ± 10.6 (0.168 ± 0.049). Soil respiration (mg CO_2 m^{-2} h^{-1}) during the dry and wet seasons of a tropical forest in Thailand was measured in a 2-ha plot (Adachi et al. 2009). During the dry season, the respiration rate related to moisture (expressed as percent) was 402 ± 206 (3.5 ± 1.8); whereas, in the wet season, the rate was 1,041 ± 542. (31.8 ± 5.0).

Soil Respiration and Pulsed Precipitation Patterns

Sporadic pulsed precipitation events, especially in dry environments, produce a consistent soil respiratory response characterized by a peak in soil microbial biomass and respiration within one or two days followed by several days of decline (at constant moisture), eventually reaching baseline negligible levels when the soil dries. This phenomenon, known as the "Birch effect," first reported by H. F. Birch (1958) and Griffiths and Birch (1961), is particularly pronounced in desert and arid regions, where precipitation is punctuated and the soil is typically dry for relatively long intervening intervals. With increasing interest in global climate change and potential natural sources of CO_2 fluxes to the atmosphere, recent research has focused on the possible contribution of the Birch effect to changing patterns of terrestrial carbon budgets and the contribution of microbial respiration to atmospheric CO_2. In the initial research of Griffiths and Birch (1961), the flux of soil CO_2 and density of bacteria (bacilli and cocci) in a sample of African soil was assessed at 3-hourly intervals for 36 hours after dry soil was moistened to field capacity. Within 18 to 24 hours after wetting, respiratory CO_2 flux reached a peak of ~ 40 µg CO_2 gm^{-1} h^{-1}. The total bacteria count per g soil was ~ 3 x 10^8. The peak was followed by a gradual decline in respiration and bacilli over the next 12 hours. This fundamental pattern has been replicated across geographic locales in a substantial number of research studies, including desert sites (Cable et al. 2008;

Zhang et al. 2010) and arid regions such as Mediterranean environments (Jarvis et al. 2007; Unger et al. 2010). Indeed, the pulsed release of respiratory CO_2 from some Mediterranean forests can reduce significantly the annual net autotrophic carbon sequestration, thus reducing the net sink for CO_2 in these ecosystems (Jarvis et al. 2007). A critical review of relevant research has been published by Wang et al. (2010b).

Soil Respiration, Carbon Budget and Microbial Communities

A substantial amount of research has examined the role of the "microbial community" in the release of soil respiratory CO_2 largely with a focus on the role of bacteria and fungi. Remarkably little attention has been given to the role of protists, even though their role in microbial ecology and soil decomposition has been extensively studied (e.g. Adl 2003). In their comprehensive review of soil respiration and the environment, Luo and Zhou (2006, p. 52) were able to cite only minimal references to the role of protozoa, largely as important predators in the rhizosphere. Adl (2003), however, gives substantial attention to the role of heterotrophic protists in a wide range of soil decomposition processes, but does not address microbial respiration in relation to major environmental issues. A search of the literature (BIOSIS) for the years of 1969 to present using the keywords "soil respiration and protozoa" yielded approximately only a dozen citations, and some considered the protozoa largely as indicator organisms for abiotic soil properties in relation to CO_2 fluxes. In addition to bacteria, heterotrophic protists are likely to contribute directly to soil respiratory CO_2 efflux. Moreover, through their significant role as bacterial predators at the base of soil food webs, they may serve a significant role in the balance between carbon loss from the ecosystem by respiratory CO_2 release and its conservation through sequestration in living biotic particulate fractions. Moreover as a major link in bacterial-based food chains, the bacterial carbon sequestered through protist predation can be transferred up the food chain into higher level consumers. However, there appears to be little published research on this dynamic role of soil protists in soil carbon budgets, and more specifically in relation to climate variables and respiratory CO_2 fluxes. A diagram of the flow of carbon in bacterial-

based, protist food chains (including relationships to respiratory CO_2 loss) pertinent to topics presented here is summarized in Fig. 1.

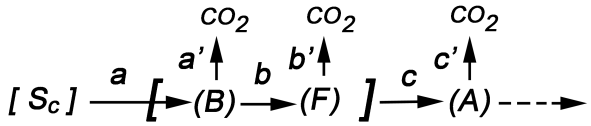

Figure 1. Carbon flow and respiratory CO_2 loss in a bacterial-based, protist food chain. Available soil carbon organic compounds (S_c) utilized by bacteria (B) become incorporated into the biological particulate fractions of the trophic pathway, leading to further incorporation in heterotrophic flagellates (F), and eventually into the amoebae (A) of the food chain through their predation on bacteria (mainly) and possibly flagellates. The proportion of soil nutrient carbon incorporated into bacteria (a), and of bacteria into flagellates, (b) and ultimately into the amoeboid protists (c) can be estimated from analysis of the carbon content of each biological group. Rate of carbon respiratory CO_2 loss from the trophic pathway for each biological group is denoted as bacteria (a'), flagellates (b') and amoeboid protists (c').

Some recent research findings, and a critical analysis of problems and prospects, are presented here with the hope that it may stimulate additional research in this seminal field of the role of terrestrial protists in terrestrial carbon budgets, soil respiratory CO_2 efflux, and global climate change. Given that global climate change may produce marked changes in precipitation, particular attention is given here to the role of bacteria and protists in relation to soil moisture, carbon balance and terrestrial respiratory CO_2 efflux, including some recent data on the role of microbial communities in the carbon budget and CO_2 efflux associated with a pulsed re-wetting of dried soil. A substantial amount of data is available on the effects of repeated wetting of dry soil on the bacterial and fungal communities in soil, including their relationship to soil organic matter, compared to soil protists (e.g. Krivtsov et al. 2004; Schmitt et al. 2010). Among recent studies of a comprehensive analysis of soil microbial communities, Fitter et al. (2005) report some key findings of the UK NERC Soil Biodiversity Programme: 1) an extreme diversity of small organisms - over 100 species of bacteria, 350 protozoa, 140 nematodes and 24 distinct types of arbuscular mycorrhizal fungi were identified, 2) stable isotope (^{13}C) analyses indicated a rapid movement of carbon through the food web, and 3) the combination of taxonomic diversity and rapid carbon flux makes the soil system highly resistant to perturbations. Griffiths et al. (2001) examined the effects of

inoculating sterile agricultural soil with serially diluted suspensions prepared from the parent soil and followed changes over 9 months. They report no consistent effect of biodiversity on a range of soil processes, including respiratory growth response or community level physiological profile and decomposition, leading to a conclusion that the biodiversity and complex interrelationships of the biota were such that the experimental reductions had no direct effects on these soil functions. Fluctuations in soil moisture, however, have consistently shown some major effects. Schnürer et al. (1986) report that oxygen consumption of soil microbial communities was the parameter that responded most rapidly in experimental treatments of either drip irrigation or a single pulse of rainfall. Fungal abundance estimates paralleled oxygen consumption. In the rain plot, bacterial numbers doubled within 3 days and declined during the following period of drought. In the irrigated plot, bacterial numbers increased by 50% and then remained constant. Large numbers of naked amoebae were recorded 2 days after a large natural rainfall. Pulses of precipitation, even in locales that are not moisture-limited, can produce a bacterial biomass peak lasting 1 – 2 days (Clarholm and Rosswall 1980). They suggested that the limited peak, and relatively rapid decline in bacterial abundance after approximately two days, might be due to grazing by microfauna. However, no further evidence for the rapid decline was presented; although the data are consistent with the well-established “Birch Effect.” Additional studies have been published on the effects of moisture pulses on soil responses, especially respiration (e.g. Franzluebbers et al. 2000, Mamilov and Dilly 2002, McCulley et al. 2007, Xiang et al. 2008). The “Effect” has been replicated in varied experimental settings, but further research appears to be needed to fully resolve the cause(s) (e.g. Xiang et al. 2008). Three possible mechanisms for the “Birch Effect” have been published: 1) “microbial stress” resulting from catabolism of osmolytes, accumulated during soil drying, that requires energy expenditure and produces elevated respiration (Harris 1981, Schimel et al. 2007), 2) “substrate supply mechanism” assumes that rewetting of the soil causes fragmentation of soil particles, release of nutrients and their redistribution; thus, providing available nutrients to support a pulse of microbial growth and peak respiration (e.g. Appel 1998, Denef et al. 2001a,b, Miller et al. 2005, Wu and Brookes 2005), and 3) “microbial trophic effects”, a rapid initial bacterial growth upon

rewetting leading to a CO_2 pulse, followed by decline due to top down predation by microfauna, especially protists at the base of the foodweb (e.g. Clarholm and Rosswall 1980). Based on the current evidence, each of these mechanisms may have a contributory effect. However, among these contributing factors, the role of protists as top-down predators has not received as much attention in accounting for the changes in the carbon budget, especially on the subsequent decline in soil respiratory CO_2 flux following rewetting of dry soil.

To more fully document the dynamic role of soil microbial communities in the soil carbon budget and their relationship to changes in respiratory CO_2 efflux during a pulsed re-wetting of dry soil, some recent experimental studies are reported here based on prior published techniques (Anderson 2002, 2006, 2008, 2010a,b). Bacteria, heterotrophic nanoflagellates, and naked amoebae densities were monitored in relation to respiratory CO_2 efflux in laboratory cultures of soil obtained temperate, Northeastern USA forest sites at Torrey Cliff, NY. Illustrative data for three sites are presented. Dried soil samples were moistened to field capacity with micropore filtered water and analyzed at 24 and 72 hours post wetting to monitor effects consistent with the "Birch effect." Organic content of the three soil samples expressed as percent of dry weight was as follows: subalpine elevated berm (130 m elevation) containing mountain laurel and red cedar (15), broad leaf forest (13), and white pine stand (6). The means ± s.e. for soil respiratory flux and estimated carbon content of bacteria, heterotrophic nanoflagellates, and naked amoebae (at 24 h and 72 h post rehydration) for the five sampling sites are presented in Table 1. The densities (N g^{-1}) of the bacteria, nanoflagellates and naked amoebae mirrored the pattern of carbon content. Respiratory CO_2 flux and bacterial densities decreased for all sampling sites after 72 h compared to 24 h; while densities of naked amoebae consistently increased at 72 h for each of the five sampling sites. The heterotrophic nanoflagellates densities varied, sometimes increasing marginally (e.g. berm and forest soil samples) or decreasing (marsh, pine crest and pine slope). Naked amoebae are known to prey on flagellates (Anderson 1994, Bovee 1985) and some of the decline in heterotrophic nanoflagellates densities may be attributed to predation by amoebae or other microfauna. In general, the

decrease in bacterial respiratory CO_2 emissions at 72 hours was commensurate with increasing sequestration of carbon into the biological particulate fractions.

Table 1. Summary statistics (means ± s.e.) for respiration flux and carbon content of bacteria, microflagellates and naked amoebae

Sample	Respiration nmol min^{-1} g^{-1}	Bacteria µg g^{-1}	Flagellates µg g^{-1}	Amoebae ng g^{-1}
		Berm		
24 h	9.0 ± 0.7	96.8 ± 2.9	6.4 ± 0.3	40.0 ± 0.9
72 h	3.8 ± 0.6	80.1 ± 7.9	10.6 ± 1.6	310 ± 7.2
		Forest		
24 h	10.7 ± 0.06	7.8 ± 0.6	5.7 ± 0.6	60.0 ± 1.4
72 h	5.5 ± 0.7	4.5 ± 0.4	6.8 ± 0.9	300 ± 6.9
		Pine		
24 h	3.0 ± 0.1	45.8 ± 5.6	3.6 ± 0.5	5.0 ± 0.1
72 h	1.2 ± 0.05	27.5 ± 5.1	3.1 ± 0.6	25.0 ± 0.6

Although additional research is needed, especially at other geographic locales, it appears, based on this laboratory research, that some of the decline in bacterial densities, and hence their contribution as a major source of soil respiration, may be due to increased densities of predatory heterotrophic nanoflagellates and naked amoebae. However, further research is required to account for how much of the possible top-down effect can be explained by other predators, such as nematodes and other microfauna, in the bacterial food chain. Bacteria are likely the major source of soil respiration within protist communities in most terrestrial regimes. Prior research has indicated that terrestrial bacteria may account for a larger amount of estimated respiratory CO_2 flux compared to that of heterotrophic nanoflagellates and amoeboid protists, at least in higher latitudes (e.g. Anderson 2008, 2010a). This is attributed to the higher densities of bacteria (at the base of the food web) and possibly their greater capacity to assimilate and respire available soluble carbon sources (e.g. Boddy et al. 2007). In some soil

systems, fungi are a substantial source of respiratory CO_2 exceeding that of bacteria in some upland locations, whereas bacterial respiratory activity may exceed fungal activity in wetter sites. Hence, fungi also must be considered in addition to the contribution from bacteria, especially if mycorrhiza are abundant and nutrient status is low (Sulzman et al. 2005).

With respect to partitioning of carbon resources, the results reported here indicate that, commensurate with pulsed precipitation events, there is a shift in the carbon fractions from a large respiratory loss associated with the initial peak in the CO_2 flux, toward a more distributed component in eukaryotic microbial particulate fractions, including major increases (five-fold or more) within the naked amoebae (Fig. 2).

Although the naked amoeba densities increased substantially, they were not the highest typically observed in soils at these sites based on prior research. The naked amoeba fraction would be expected to increase with time beyond the 72 h assessed here, typically reaching peak densities in c. 10 to 14 days (e.g. Anderson 2010c, Page 1988). Given the importance of accounting for the partitioning of carbon in soil microbial communities, especially estimates of the balance between particle sequestration within biota versus loss as CO_2 to the atmosphere, the current results point toward a significant effect of protistan predation on bacteria as a mechanism to increase the biotic particle-bound carbon resources, and simultaneously to diminish loss through net respiratory CO_2 efflux, especially during early phases after a pulsed rewetting of soil. With respect to Fig. 1, the major shifts are a decreased loss of bacterial CO_2 flux (a') and greater contribution to the carbon sequestration factors (b and c); most consistently in this research, the amoeba fraction contribution (c). Further research is needed to more fully quantify the role of terrestrial heterotrophic protists in sequestration of soil carbon under varying climatic conditions in relation to changing temperature and precipitation patterns.

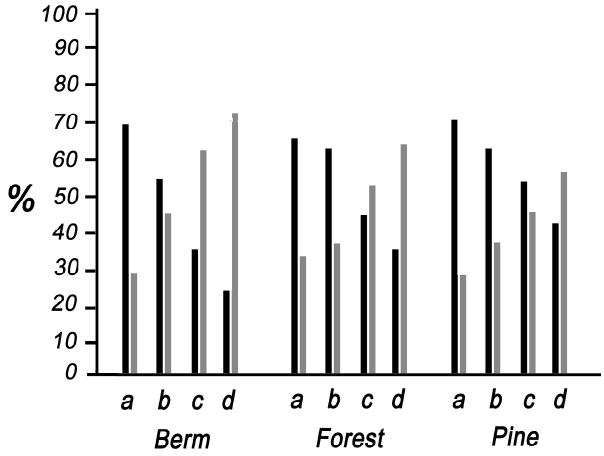

Figure 2. Percent (%) of total carbon content (displaying the 24 and 72 hour results) for each data source (a = respiratory flux, b, c and d = carbon biomass for bacteria, nanoflagellates and naked amoebae, respectively) related to sampling sites (abscissa). Opaque bar = 24 h and grey bar = 72 h measurements. The contribution of respiration declines at 72 h compared to 24 h , and bacterial biomass also declines concurrently for each of the sampling sites. Naked amoeba biomass increases substantially, while the flagellate biomass is variable depending on the sampling site, increasing only moderately in the berm and broad leaf forest samples. See Table 1 for respiratory and carbon mass numerical data.

The balance between respiratory carbon loss and sequestration within biological particulates is likely to be of increasing importance in polar environments. In these biomes, increasing temperatures leading to thawing of the organic-rich permafrost, and changing patterns of precipitation, threaten to increase microbial respiratory CO_2 flux to the atmosphere, thus exacerbating the greenhouse effect and global warming (e.g. Oechel et al. 1993; Chapin et al. 1995; Oberbauer et al. 2007; Anderson 2008, 2010a). Current estimates indicate that bacteria among the microbial community (bacteria and protists) are a major source of respiratory CO_2 in the Alaskan tundra, as elsewhere, comprising as much as 60% during spring and summer (e.g. Anderson 2008). Hence, top-down controls on their abundance may be a significant factor in soil carbon dynamics. Soil fungi are typically abundant (e.g. Griffiths et al. 2001), they are subject to predation by naked amoebae (Old and Darbyshire 1978; Old et al. 1985), and should be included more completely in analyses of microbial standing stock, carbon budgets and respiratory CO_2 fluxes (Nakas and Klein 1980; Stamatiadis et al. 1990; Langley et al. 2005), especially in relation to pulsed precipitation (e.g. Gordon et al. 2008; Bapiri et al. 2010). Clearly, additional research is needed to more fully document the relative

contributions of the various biotic fractions to carbon sequestration versus respiratory loss in high latitudes and other major global biomes.

Future Research: Prospects and Challenges

While the need for expanded research on the diversity and role of microbial communities in climate change and soil respiratory CO_2 fluxes is evident, there are some challenges. Field-based studies of terrestrial CO_2 fluxes using modern techniques (e.g. eddy covariance and portable field-based IRGA monitoring equipment) provide an in-stu assessment of total soil CO_2 exchange including plant and soil biota. To assess the soil microbial contribution, the substantial yield from root respiration, as much as 40 to 60% especially in forests and woodlands (e.g. Olsson et al. 2005), must be subtracted from the total. One solution is girdling of the trees in woodland stands, thus eventually leading to root death and removing the living root contribution (e.g. Olsson et al. 2005) or in combination with methods of root trenching to cut the roots at a place antecedent to the soil sample site and immediately eliminate root contributions (e.g. Schaefer et al. 2009). All of these techniques, however, are intrusive and alter the soil environment. More recently, stable isotopes (e.g.^{13}C-labeled CO_2) as tracers have been used to separate the sources and sinks of carbon in vegetative sites where autotrophic sources of soluble organic matter are of importance (e.g. Andrews et al. 2000; Burke et al. 2003; Leake et al. 2006; Paterson et al. 2009). However, these methods do not provide evidence of the diversity and contribution of different taxonomic groups of microbes (e.g. bacteria, protists and fungi) to the respiratory CO_2 loss. The use of biochemical markers such as analyses of phospholipid fatty acid esters and sterols that are specific to certain microbial taxa, as well as molecular genetic DNA analyses, have provided improved estimates of the diversity of soil microbes, especially for bacteria and some fungal groups (Tunlid and White 1990; zelles 1999; Agnelli et al. 2004; Cleveland et al. 2007; Bartling et al. 2009), but increasingly explored for protists (e.g. Caron et al. 1999; Lara et al. 2011). However, these techniques have not been refined sufficiently to apply to the broad diversity of soil heterotrophic protist at the species level, especially naked amoebae whose molecular genetics remain insufficiently documented . Thus, various methods of microscopic counting and size determinations

are required to augment these approaches and more fully account for protist abundance, diversity, carbon content, and estimated respiratory CO_2 loss (e.g. Baldock et al, 1982; Fenchel and Finlay 1983; Li et al. 2004; Anderson 2002, 2006, 2008). Due to their fragility, naked amoebae cannot be preserved for subsequent microscopic analyses. At present, live amoebae must be observed and sized by light microscopic techniques, each with its particular strengths and limitations (e.g. Darbyshire 1994; Smirnov and Brown 2004; Adl et al. 2008; Anderson 2010c). Nonetheless, a wide variety of amoeba taxa are recoverable by these techniques and good estimates of their contribution to carbon budgets of aquatic and soil environments can be made if care is taken to make observations at appropriate intervals during laboratory preparation (e.g. Anderson 2006, 2007, 2010a,b,c). Microflagellates can be enumerated using fluorescent stains and UV microscopy. However, difficulty in discriminating them from larger bacteria may lead to an overestimation of abundance and biomass, unless careful attention is applied during microscopic visualization and enumeration. A comprehensive review of methodological issues of estimating soil microbial biomass parameters spanning research during the last century has been compiled by stockdale and Brookes (2006).

Laboratory methods of assessing soil respiratory activity, though limited due to disturbance of the in-situ structure of the soil composition during sampling, provide greater control of the soil properties and sources of respiratory CO_2. The soil can be examined to remove fragments of roots and to eliminate detectable soil fauna such as microarthropods, worms, etc. Hence, it is possible to infer the role of the remaining soil microbial community in carbon budgets and how much of the respiratory loss is attributable to various microbial taxa (e.g. Andrews et al. 2000; Anderson 2007, 2008, 2010a,b,c; Bartling et al. 2009; Bapiri et al. 2010). However, current detailed analyses of the role of protists in major aquatic and soil environments are clearly limited by present methods of analysis. In the future, if more substantial methods of molecular genetic analyses are developed, perhaps including microarrays (e.g. Metfies et al. 2007) and/or barcoding (e.g. Nassonova et al. 2010; Chandni et al. 2011; Thierry et al. 2011), we may gain much greater precision and validity for our estimates of the contribution of protists to the dynamics of soil microbial communities and their role in the carbon cycle.

Although these modern techniques may improve our detection of protistan abundance and diversity, challenges remain in defining algorithms that link these data to estimates of carbon biomass and respiratory rate of the individual taxa of protists.

Moreover, additional simultaneous field-based and laboratory experimental studies, using soil from the same sampling site, may enhance inter-calibration of data from these two sources of evidence and improve predictions from laboratory results to the field. This may be increasingly important at geographical locales where global warming and climate change are expected to have major effects, including polar, arid, and tropical environments. Some terrestrial processes that have taken millennia in geological history have become increasingly compressed to decades and centuries in recent years as anthropogenic effects have accelerated climate change. Furthermore, soil sources are currently the second most important source of atmospheric CO_2 (Luo and Zhou 2006). Consequently, we need to examine natural phenomena such as terrestrial CO_2 exchange with the atmosphere much more critically in light of global warming and associated changes in climate within a shorter historical time frame than has been considered previously. With increasing evidence of global climate change, and the corresponding importance of microbial communities as sources of greenhouse gases, we have much to gain by an earnest effort to improve the precision of our taxonomic identification techniques and methods of analyzing the role of heterotrophic protists in the carbon cycle at regional and global scales.

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