Review Article

Arctic Terrestrial Microbial Communities in a Changing Climate, their Roles in, and Responses to, Changing Atmospheric CO$_2$ Concentrations: A Brief Review of Recent Advances

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Abstract

Global warming has brought major changes in arctic terrestrial ecosystems, including significantly increased efflux of terrestrial respiratory CO$_2$ to the atmosphere, thus potentially exacerbating atmospheric concentrations of CO$_2$ and contributing to increase global warming. This brief review focuses especially on some recent advances in our knowledge of how global climate change is affecting high latitude terrestrial microbial communities and their role in respiratory CO$_2$ release to the atmosphere. Although substantial research has been published on changes in arctic ecosystems due to increased warming, including broad scale assessments of soil respiratory CO$_2$ efflux, much less is known about changes that are occurring in eukaryotic and bacterial communities or the contributions of belowground microbial communities to CO$_2$ efflux at high latitudes. Some current advances in understanding the effects of warming on arctic soil microbial communities, and their respiratory responses, are reviewed. Moreover, some remaining challenging research areas are identified.

ABBREVIATIONS

P: percent of active soil amebas; R$_s$: Soil Respiratory CO$_2$; B$_d$: Bacterial Density; C: Carbon; M: percent of soil moisture (g g^{-1}); No.: Number; Wt: Weight; °C: Degrees Celsius

INTRODUCTION

Arctic Terrestrial Communities and Respiratory Co$_2$ Efflux

Global warming, first predicted as early as the nineteenth century by Arrhenius [1] and developed more fully in the mid twentieth century [e.g., 2], has increasingly affected climate and biological ecosystems on a global scale. The Arctic is one of the global regions most affected by climate change, especially recent global warming. Increasing temperatures have produced massive changes in the terrestrial and marine environment of the Arctic. The terrestrial environment is among the most adversely affected. Due to current defrosting rates of the permafrost, substantial amounts of soluble organic matter (previously immobilized and unavailable for microbial uptake for millions of years) are increasingly available for heterotrophic microbial nutrition. Moss-rich arctic soil contains substantial amounts of organic matter up to 80% of soil dry weight. The combination of more favorable growth temperatures and longer periods of moderate temperatures during the arctic summer months has promoted larger amounts of microbial respiratory activity and release of CO$_2$ to the atmosphere. Although considerable research attention has been given to the broad scale affects of climate change on arctic ecosystems [3-7], less attention has been given to the effects on heterotrophic microbial communities and their response as potential sources of additional respiratory CO$_2$ flux to the atmosphere, a topic particularly reviewed here.

Heterotrophic microbial communities are complex associations among bacteria and protists (e.g. small heterotrophic nanoflagellates, naked amebas, and testate amebas). Arctic heterotrophic microbial communities are organized in a classical hierarchical food web, with bacteria at the base as a primary source of nutrition (Figure 1) [8]. Very small flagellates prey almost exclusively on bacteria. Naked amebas, without an enclosing shell or test, prey on bacteria and on flagellates. Larger testate amebas at the top of the hierarchy tend to prey on all biota beneath them. As is typical of a trophic hierarchy, the predators increase in size, but decrease in density (No. g^{-1} soil), at increasing levels higher up the hierarchy. Total C-biomass decreases with increasing level in the hierarchy. Fungi, not included in this trophic hierarchy, are also a significant component of the arctic soil communities. Their biomass (e.g. 5 to 10 mg g^{-1} soil dry wt) is substantially larger than the total combined biomass

of the bacteria and protists, typically in the range of µg g^{-1} soil dry wt, but in some cases exceeding 100 µg g^{-1} dry wt [8]. As with other biota, the metabolic activity and respiratory CO_2 produced by fungi varies depending on the source of nutrition and physiological state – a topic requiring much more research in the Arctic. The densities of the biota in microbial communities increase with increasing sources of organic compounds used as nutrients, driven largely by the higher densities of the prey bacteria at the base of microbial food webs. Soil respiratory CO_2 (R_s) is emitted from biota at each level in a trophic hierarchy, and it increases with increasing metabolic activity, partially in response to increasing favorable growth temperatures.

While it is not always feasible to measure the respiratory activity of each of the biota in a microbial community, laboratory studies with arctic tundra soil indicate that total arctic R_s activity is highly correlated with the density of bacteria [9]. This is likely due to the bacteria serving as proxies for the amount of soluble organic nutrients in the soil that are available to the total community of heterotrophic microbes, fungi and other belowground biota. Regression equations relating R_s to bacterial densities have been derived based on laboratory measurements with soil samples from arctic tundra in northwestern Alaska. Two examples at 10 °C and 20 °C are given.

For 10 °C:

(1) $R_s = 10.25 + 6.26\ B_d$ (n = 14, p < 0.01);

For 20 °C:

(2) $R_s = 12.32 + 14.07\ B_d$ (n = 14, p < 0.01);

Where R_s is soil respiration (n mol min.$^{-1}$ g^{-1} soil dry wt) and B_d is bacterial density (no. x 10^9 g^{-1} soil dry wt).

Soil Respiration Rates and Temperature Effects

Within the limits of temperature tolerance, arctic R_s increases with increasing temperature, largely attributed to greater metabolic activity of the below ground microbial community (e.g. Table 1) [9]. Moreover, the depth of snow cover during winter in high latitudes is directly related to moderation in winter soil temperature, thus increasing terrestrial microbial activity and an increased winter release of respiratory CO_2 [10]. On a global scale, the Q_{10} (relative increase in respiration for every 10 °C rise in temperature) is very close to 2.0 [11]. Current data indicate this is also true for arctic soil (Table 1). This is largely attributed to the well-established physiological principle that microbial metabolism (as well as that of plant roots contributing to soil respiration) tends to double with each ten-degree Celsius increase in environmental temperature within the temperature tolerance range of the organisms. Thus, increasing temperatures due to global warming may promote increased terrestrial emissions of respiratory CO_2, further contributing to atmospheric CO_2 load leading to a feed forward effect and escalating global warming. One of the uncertain variables, however, is the possible compensatory role of plants that consume CO_2 during photosynthesis. There is evidence of increasing densities of plants in the arctic tundra, including small shrubs and trees that may offset the effects of increasing terrestrial emissions of CO_2 [5,7,12] at least in the short term. The balance between terrestrial sources of CO_2 and its uptake by plants is a major question that remains to be
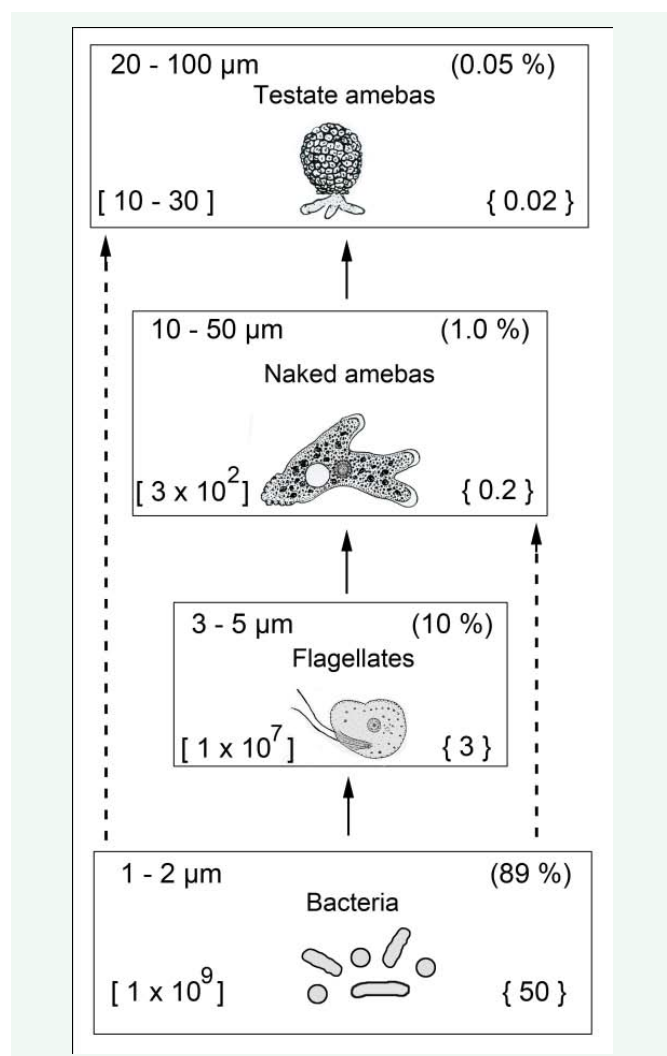
Figure 1 Microbial trophic hierarchy. Carbon and energy flow upward from prey to predator at successive levels (solid arrows) or by direct predation on bacteria at base of the food chain (dashed arrows). Representative data for biota at each level: typical size range in µm, density [no. g-1 soil dry wt], percent of biomass C at each level relative to total C in the hierarchy (%), and C-biomass at each level {µg g-1 soil dry wt}.

Table 1: Arctic soil respiration rates (nmol min.$^{-1}$ g^{-1} soil dry wt) at 10 °C and 20 °C, and percent moisture content for samples from the top and base of Alaska tussocks.

	10 °C	20 °C	Q$_{10}$	Moisture
Top	39.4	80.0	2.1	83.6
Base	53.3	107.3	2.0	

Abbreviations: °C = Degrees Celsius. Q$_{10}$ = Respiratory Quotient

resolved, especially for future scenarios in the Arctic. A more perplexing problem includes the possible increased release of organic exudates from plant roots accompanying increased high latitude summer temperatures and greater spread and density of plants, thus further enhancing microbial metabolism and elevated release of soil respiratory CO_2.

Soil Respiration Rates and Amount of Available Organic Compounds

Respiration of soil microbiota increases with increasing sources of soluble organic compounds available for metabolism and growth. One critical factor in predicting the rate of respiration in relation to C-sources of microbial nutrition is how much of it is used for respiration and how much is consumed for growth and production of solid biological matter. Especially, how much C is used for production of non-living organic matter, such as resilient surface coats, cyst walls, surface tests, cuticles, etc. that are resistant to decay? These indurated biological products are less likely to be metabolized and released as respiratory CO_2. In general, there is good evidence that C sequestered in biota at higher levels in a trophic hierarchy is less likely to be lost as respiratory CO_2 compared to C assimilated by biota at the lowest levels [13]. For example, in experimental laboratory studies of soil devoid of plant roots, but containing ambient microbial populations, where the effects of added soluble organic C on arctic R_s were examined; there was a brief spike (minutes to a few hours) in increased respiratory CO_2 ($\sim$ 2 to 3 times basal rate) immediately after addition of the organics into the temperature controlled soil cultures. But the amount of the added C that was lost as microbial respiratory CO_2 during the spike in respiration was less than 1 % of the total organic C added. Concurrently, the amount of C in the microbial biota increased substantially during subsequent growth in the cultures for one week at 20 °C [13].

During one week of experimental culture, the amount of organic C consumed and bound in microbial biomass varied with the season that the soil was sampled. Approximately 5 to 17% of the added organic C in the laboratory experiments was sequestered in micro biota in the spring arctic soil samples, but up to 39% accumulated in summer samples [13]. The remainder of the added C may be bound in soil particles, assimilated by fungi, or accumulated in predatory invertebrates higher up the trophic hierarchy. Furthermore, some of the added organics may not be immediately accessible to the microbes, but gradually become available through diffusion to sites where the microbes are located in pockets of soil.

These data suggest that pulses of organic C secreted into the soil, such as pulsed exudates from plant roots in the rhizosphere where microbial biota are very abundant, may not produce a substantial spike in respiratory CO_2 emission to the atmosphere. However, this may depend on how sustained and substantial the root exudation is. There is good evidence that increased atmospheric CO_2 promotes plant primary production with sufficient secretion of root-derived organics into the soil to enhance microbial densities and increase Rs [14,15]. In the long term, it is critical to assess how much of the C that is fixed by photosynthesis is bound in plant living matter and how much is secreted by roots into the soil. Excessive plant root exudates can contribute to elevated microbial respiration with consequent soil C loss and increased CO_2 emission to the atmosphere [15-18]. This critical balance between CO_2 sink and source is another significant factor that requires much further research before we can make more substantial predictions about the fate of atmospheric CO_2 in arctic terrestrial sites.

Soil Respiration and Moisture Content

The moisture content of moss rich soils, in addition to the positive effects of temperature, is directly related to bacterial densities, and in some cases moderately so for fungi [e.g. 19], thus partially accounting for increased terrestrial respiratory loss of CO_2 with increasing soil moisture. Likewise, the biologically available soil moisture also is directly correlated with the ratio of active to encysted soil amebas. There are increasing proportions of active amoeba trophonts with increasing available soil moisture [20]. Regression analysis of data from a temperate soil location [20] yielded the following prediction of percent active amebas (P) in relation to percent soil moisture (M): P = 2.843 M – 5.594 (r^2 = 0.95). However, this was largely for relatively dry, grass-dominant locales with mineral rich soil. In general, on a global scale across varied ecosystems, soil respiration rates tend to increase with soil moisture up to a point where the soil is overly saturated causing excess water logging and lack of sufficient oxygen to maintain microbial aerobic respiration, leading to its subsequent decline [21,22]. Respiration in arctic tundra soil also increases with moderate increases in water moisture content. For example, samples from the water-rich base of tundra tussocks have a higher mean respiratory rate compared to samples from the top of the tussocks (Table 1), consistent with their moisture content of 88.6% and 83.8%, respectively [9]. The substantial amount of water absorbed by the large amounts of moss and peat in most arctic soils accounts for the unusually high percent of moisture observed in many samples from the tundra. As may be expected, the respiration rates in the tussock samples were positively related to soil bacterial densities and C-content. The mean densities of bacteria (no. x 10^9 g^{-1} soil dry wt) in the base and top of the tussock (greater to lesser moisture content) were 6.9 and 4.6, respectively. Likewise, the C-content (μg g^{-1} soil dry wt) was 899 in the base sample and 604 for the top sample. A similar pattern of densities (no. x 10^7 g^{-1} soil dry wt) was observed for heterotrophic nanoflagellates, but less marked (base 1.1 and top 1.0). In some cases, although spring soil samples contain more moisture than summer samples, the favorable growth temperatures in summer can produce higher R_s values compared to spring samples. For example, in a study of soil taken from sampling sites at Toolik Lake, AK, the moisture content of an early spring sample was 83% and the summer sample taken at a different site with different soil composition was 33%, yet the respiratory rate for the spring sample was in the range of 5.0 n mol min.$^{-1}$ g^{-1} compared to a higher rate of 7.0

for the summer sample. The organic content of the spring sample, however, was higher than that of the summer sample, i.e. 80% and 20%, respectively [13].

CONCLUSIONS

Current estimates of arctic CO_2 emissions during each productive season are in the range of 100 to 200 g CO_2-C m^{-2} ($\sim$ 1 – 2 x 10^5 kg km^{-2}), much of it from microbial respiration. Among the biological sources of terrestrial CO_2, bacteria and their predators, including protists, are a diverse and highly productive part of the heterotrophic microbes inhabiting soils, and their role in global warming deserves more attention. The densities of bacteria at the base of microbial food webs, and their efficiency in rapid assimilation of available organic nutrients, appear to make them good proxies for estimating total release of soil respiratory CO_2 to the atmosphere. Recent research has indicated a significant positive correlation of arctic soil bacterial densities with total soil respiratory CO_2 production, and some linear regression equations have been derived to predict respiratory rates in relation to bacterial densities at different soil temperatures. However, more detailed information is needed on the relative contributions of fungi and bacteria to R_s in arctic soils. Some data are available for soil emissions at other regions, such as low latitude montane forests. These studies are based on the differential inhibitory effects of bacterial vs. eukaryotic antibiotics on the amount of recoverable CO_2 emitted from the treated soil [e.g., 23, 24]. In those studies, the fungi and bacteria were reported to contribute equally to the magnitude of the soil Rs. However, current critical analyses of the antibiotic selective inhibition technique suggest that the antibiotics used may not be sufficiently selective to provide a clear delineation of results, but a better combination of antibiotics or other inhibitors may prove to be adequate [25]. There appears to be no current evidence of the effectiveness of these methods for high latitude moss-rich soils. In addition to release of CO_2, there is growing evidence that Archaea (an evolutionary ancient microbe domain, distinct from bacteria) can be a major source of metabolically derived methane, a much more powerful greenhouse gas than CO_2. Archaea are highly productive in low oxygen environments, especially waterlogged terrestrial environments. With increasing defrosting of the permafrost, and increased water saturation of the moss-rich soils in the Arctic, the role of Archaea in global warming is a field of increasing research interest.

Overall, the research reviewed here on bacterial and protist communities in the Arctic indicates that there are increasing amounts of soluble organic compounds released by warming of arctic soil, coupled with longer growing seasons in the summer and possibly increased root exudates from invading vascular plants. These factors may substantially increase microbial metabolism and additional respiratory release of CO_2 from high latitude soils, thus potentially adding to the atmospheric load of CO_2 and exacerbating global warming and climate change. The magnitude of this threat, and the possible ameliorative role of invading photosynthetic vascular plants as sinks for the CO_2, is an arena of current active research.

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