The Microbial Wildcard in Peatland Carbon Storage: Implications for Global Warming

Markus N. Thormann
Department of Biological Sciences, University of Alberta
Edmonton, Alberta, Canada, T6G 2E9
E-mail: mthorman@ualberta.ca

Suzanne E. Bayley
Department of Biological Sciences, University of Alberta
Edmonton, Alberta, Canada, T6G 2E9
E-mail: s.bayley@ualberta.ca

Randolph S. Currah
Department of Biological Sciences, University of Alberta
Edmonton, Alberta, Canada, T6G 2E9
E-mail: rcurrah@ualberta.ca

Introduction

Peat accumulation over the millennia has formed large stores of terrestrial carbon (C) in peatlands. Peat (approximately 50% C) accumulates each year (Gorham 1991; Mäkilä 1997) because of slow rates of decomposition rather than high rates of net primary plant production (Clymo 1965; Vitt 1990). Calculations indicate C accumulation rates of 14.1–28.1 g m^{-2} yr^{-1} and peatland C stores of 180–277 Gt, estimated to represent 10%–16% of total terrestrial C (Gorham 1991). Peatlands are wet environments, with most of the peat stored under anaerobic conditions beneath an aerobic surface layer that is up to 2 m thick. At present, these ecosystems serve as long-term net C sinks by removing carbon dioxide (CO_2) from the atmosphere (Bellisario et al. 1998).

Many global climate models predict significant increases in atmospheric temperatures in northern latitudes covered by peatlands (IPCC 2001), which may have profound effects on peatlands by lowering water levels, drying and aerating the peat, increasing soil temperatures, increasing peat decomposition, and changing plant communities (Gorham 1994), ultimately yielding more C to the atmosphere as CO_2 and thereby providing a positive feedback to global warming (Gorham 1991). Similarly, the effects of global warming are predicted to affect microbial communities (fungi and bacteria) by altering community composition, diversity, competition dynamics, biomass and production, substrate accessibility and colonization dynamics, and ultimately decomposition of organic materials (Zogg et al. 1997; Kandeler et al. 1998). For example, fungi synthesize a diverse suite of enzymes, such as cellulases, polyphenol oxidases (PPO), pectinases, and amylases. These enzymes allow fungi to degrade a variety of organic materials and make them some of the most important decomposer organisms in acidic ecosystems. Many fungi can degrade simple molecules, such as starch; however, the ability to degrade complex structural polymers (lignins, tannins, and their derivatives) is uncommon in fungi (Domsch et al. 1980). The impact of increasing atmospheric temperatures on enzyme synthesis by fungi remains unclear, with some studies showing increased and others decreased activity of enzymes such as cellulases and PPOs (Forbes and Dickinson 1977; Zadražil 1985; Moorhead and Linkins 1997).

Our objective was to determine the effects of elevated temperature on fungal and bacterial decomposition dynamics for the dominant peat-forming plant species of the southern boreal peatlands to elucidate if peatlands might become C sources, because of increased rates of peat decomposition, under a global warming scenario.

Methods

We measured mass losses (an indicator of decomposition) associated with the dominant indigenous fungi and bacteria (three of each) of peat moss (*Sphagnum fuscum* (Schimp.) Klinggr.) and sedge (*Carex aquatilis* Wahlenb.) leaves and rhizomes at 14°C and 20°C in vitro. The fungi and bacteria were isolated from senesced plant materials of these three litters. The three most frequently occurring fungi and the three most frequently occurring bacteria were used to inoculate the litter samples.

Peptone broth agar, a medium used to supply the fungi and bacteria with moisture and some nitrogen, was poured into 10 × 80 mm petri plates. Dried plant litters were weighed to the nearest 0.01 g and sterilized before being placed into the prepared petri dishes. They were then inoculated with the appropriate fungi and bacteria, as follows. Triplicate plates were inoculated with the indigenous fungi of each litter type by themselves and in every possible combination with each other. The plates were inoculated by transferring two mycelial plugs of each fungi onto each appropriate treatment plate. For each bacterium, a suspension was prepared by transferring the bacterial colonies of 1-week-old cultures into sterile phosphate buffer (P buffer) in sterile Pyrex culture tubes. These suspensions were mixed thoroughly before being used to inoculate each plate. Three bacteria indigenous to each litter type were inoculated onto the appropriate plates by themselves and in every possible combination with each other. P buffer was also added to all fungal treatment plates. Triplicate petri plates were inoculated simultaneously with all three indigenous fungi and bacteria of each litter type to investigate possible synergistic relationships among the fungi and bacteria during decomposition. Uninoculated plates served as controls to determine mass losses of the litters due to leaching. A total of 384 petri plates were set up for each litter type ([7 treatments each of fungi and bacteria + 1 fungi plus bacteria treatment + control] × 3 replicates each × 4 decomposition periods × 2 temperature treatments).

Half of the plates were incubated at 14°C (ambient mean annual growing season temperature, May to October, Athabasca 2 weather station) (Environment Canada 1998), and the other half were incubated at 20°C (predicted 6°C increase of the mean annual growing season temperature at northern latitudes under a scenario whereby CO_2 doubles) (Boer et al. 1992; IPCC 2001). After 2, 4, 8, and 12 weeks, the litters were removed from three petri dishes for each litter type, and surficial fungal mycelium was carefully removed. The litters were dried at 48°C to constant mass and weighed to the nearest 0.01 g; mass losses were expressed as percentages of the initial masses. Leaching accounted for mean mass losses of 1.9% for *S. fuscum*, 9.1% for *C. aquatilis* rhizomes, and 15.0% for *C. aquatilis* leaves. These mass losses were subtracted from all data before statistical analyses.

Results and Discussion

We present mean mass losses caused by the three dominant fungi and/or bacteria after 12 weeks' decomposition, rather than mass losses caused by individual fungi and bacteria alone. Mass losses of *Sphagnum* peat by fungi alone, bacteria alone, and fungi and bacteria together were significantly greater at 14°C than at 20°C (Table 1). In contrast, *Carex* leaves had significantly higher mass losses at 20°C than 14°C, whereas mass losses of *Carex* rhizomes were similar at the two temperatures (Table 1). Mass losses of the sedge rhizomes were greater than those of the sedge leaves and peat moss at both temperatures (Table 1).

Decomposition rates vary depending on the plant species, tissue nutrient concentrations, oxygen availability, moisture, and the nutrient status of the ecosystem (Gorham 1991; Szumigalski and Bayley 1996; Thormann et al. 2001). For example, plant materials with higher initial tissue concentrations of nitrogen and phosphorus decompose faster than those with lower tissue nutrient concentrations (Bartsch and Moore 1985; Szumigalski and Bayley 1996). In this study, initial concentrations of phosphorus were significantly higher in the sedge rhizomes (21 mg g^{-1}) and leaves (18 mg g^{-1}) than in the peat moss (5 mg g^{-1}) (Thormann et al. 2001). Sedge leaves and rhizomes lost significantly more mass than the *Sphagnum* peat moss at 20°C (Table 1), which supports the theory that more nutrient-rich plant tissues have higher decomposition rates. This pattern was not observed at 14°C, where mass losses of the *Sphagnum* plants exceeded those of the sedge leaves, despite lower nutrient concentrations. Specific fungi exhibited different

Table 1. Mean mass losses of three litter types from two peatlands in southern boreal Alberta, Canada, after 12 weeks' decomposition in vitro by bacterial, fungal, and bacterial plus fungal populations

Litter type	Temperature °C	Mean mass loss (% ± SE)[a] Three dominant bacteria (n = 3)	Three dominant fungi (n = 3)	Three dominant bacteria + fungi (n = 3)
Sphagnum fuscum plants	14	–2.9 (0.03)aA	–2.4 (0.04)bA	–3.5 (0.32) *a1*
	20	0.2 (0.02)aB	–1.3 (0.03)bB	–0.2 (0.01) *a2*
Carex aquatilis leaves	14	0.6 (0.11)aA	9.1 (1.34)bA	–1.7 (0.12) *c1*
	20	–4.5 (0.55)aB	–4.7 (0.98)aB	–8.0 (1.30) *b2*
Carex aquatilis rhizomes	14	–9.4 (0.53)aA	–10.6 (1.09)aA	–24.9 (0.53) *b1*
	20	–6.9 (0.47)aB	–11.4 (1.44)bA	–25.7 (3.01) *c1*

[a] Positive values indicate mass gains by the decomposing litters. Different lower case letters indicate significant differences among the treatments for each litter type; different capital letters indicate significant differences between temperature treatments for each of bacterial, fungal, and bacterial plus fungal mass losses for each litter type.

Note: SE = standard error.

decomposition dynamics at different temperatures. For example, *Mucor hiemalis*, an ubiquitous soil fungus, was sensitive to changes in temperature and tissue type and caused greater mass losses of the peat moss at 14°C than at 20°C, while causing greater mass losses of the sedge leaves at 20°C than at 14°C.

Mass losses of all three plant tissues caused by fungi were generally greater than those caused by bacteria at 20°C (Table 1). Low temperatures impose physiological limits on and control rates of (spore) germination, growth, reproduction, and enzyme synthesis. We propose that these limitations were greater for fungi than bacteria at 14°C in this study, which resulted in generally lower decomposition potentials and subsequently smaller mass losses of the three plant tissues. However, fungi have higher growth rates than bacteria and likely were able to colonize these plant tissues more quickly and effectively at 20°C, thereby causing greater mass losses than bacteria. The moisture regime was constant in the bacterial and fungal decomposition treatments, but a lower water level due to increased droughts in response to global warming in peatlands would favor fungi, which have a filamentous growth habit, over nonfilamentous, colony-forming bacteria, which require external factors, such as moisture or invertebrates, for dispersal.

Fungi, which have the ability to utilize tannic acid, a complex phenolic polymer similar to lignin, caused the greatest mass losses under both temperature regimes (Thormann 2001). These data support the theory that increased activity of PPOs may lead to increased decomposition of phenolic compounds in peatlands (Freeman et al. 2001) and provide a positive feedback to global warming due to increased CO_2 emissions to the atmosphere (Gorham 1991). However, in a related study, we determined that relatively few fungi isolated from living and decomposing peat moss (<24%) were able to degrade tannic acid, a polyphenolic polymer (Thormann et al. n.d.). This finding is likely due to the complex molecular nature of phenolic compounds, which require a suite of enzymes rather than a single enzyme for mineralization. Similarly, few bacteria have the ability to synthesize PPOs (Cerniglia 1992). Furthermore, fungal degradation of substrates is extracellular, whereas bacterial degradation is an intracellular process that requires the bacterium to take up the substrate to be mineralized and to enzymatically degrade it in the cell interior. This makes fungi the principle decomposers of these recalcitrant phenolics, because the molecular complexity and size of phenolic compounds prohibits bacteria from effectively decomposing them in nature. The microbial community of peatlands has a limited ability to decompose phenolic compounds, such as lignin and lignin-like compounds, which constitute 27%–55% of peat and which become more prevalent with increasing peat depths (Turetsky et al. 2000).

Conclusions

These data support the hypothesis that fungal and bacterial communities of different peatlands will respond differently to increasing atmospheric temperatures. Hence, changes in the hydrology and subsequent increased aeration of bog peatlands due to global warming may not lead to the predicted increases in decomposition of phenolic compounds that constitute a significant portion of the peat in peatlands, because PPOs are synthesized by relatively few fungi and even fewer bacteria. Therefore, the scarcity of organisms synthesizing these enzymes in peatlands suggests that not all peatlands will provide positive feedback to global warming, or at least not to the degree currently predicted by global climate models.

References

Bartsch, I.; Moore, T.R. 1985. A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Québec. Can. J. Bot. 63:1241–1248.

Bellisario, L.M.; Moore, T.R.; Bubier, J.L. 1998. Net ecosystem CO_2 exchange in a boreal peatland, northern Manitoba. Écoscience 5:534–541.

Boer, G.J.; McFarlane, N.A.; Lazare, M. 1992. Greenhouse gas induced climate change simulations with the CCC second generation GCM. J. Clim. 5:1045–1077.

Cerniglia, C.E. 1992. Biodegradation of polycyclic aromatic hydrocarbons. Biodegradation 3:351–368.

Clymo, R.S. 1965. Experiments on breakdown of *Sphagnum* in two bogs. J. Ecol. 53:747–757.

Domsch, K.H.; Gams, W.; Anderson, T.-H. 1980. Compendium of soil fungi. Academic Press, London, U.K.

Environment Canada. 1998. Canadian climate normals, 1961–1990. Canadian Climate Program, Ottawa, ON.

Forbes, R.S.; Dickinson, C.H. 1977. Effects of temperature, pH and nitrogen on cellulolytic activity of *Fusarium avanaceum*. Trans. Br. Mycol. Soc. 68:229–235.

Freeman, C.; Ostle, N.; Kang, H. 2001. An enzymatic 'latch' on a global carbon store. Nature 409:149.

Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol. Appl. 1:182–195.

Gorham, E. 1994. The future of research in Canadian peatlands: a brief survey with particular reference to global warming. Wetlands 14:206–215.

(IPCC) Intergovernmental Panel on Climate Change. 2001. Climate change 2001. Cambridge University Press, Cambridge, UK.

Kandeler, E.; Tscherko, D.; Bardgett, R.D.; Hobbs, P.J.; Kampichler, C.; Jones, T.H. 1998. The response of soil microorganisms and roots to elevated CO_2 and temperature in a terrestrial model ecosystem. Plant Soil 202:251–262.

Mäkilä, M. 1997. Holocene lateral expansion, peat growth and carbon accumulation on Haukkasuo, a raised bog in southeastern Finland. Boreas 26:1–14.

Moorhead, D.L.; Linkins, A.E. 1997. Elevated CO_2 alters belowground exoenzyme activities in tussock tundra. Plant Soil 189:321–329.

Szumigalski, A.R.; Bayley, S.E. 1996. Decomposition along a bog to rich fen gradient in central Alberta, Canada. Can. J. Bot. 74:573–581.

Thormann, M.N.; Currah, R.S.; Bayley, S.E. n.d. Microfungi isolated from *Sphagnum fuscum* from a southern boreal bog in Alberta, Canada. Bryologist. Forthcoming.

Thormann, M.N. 2001. The fungal communities of decomposing plants in southern boreal peatlands of Alberta, Canada. Ph.D. Thesis, Univ. Alberta, Edmonton, AB.

Thormann, M.N.; Bayley, S.E.; Currah, R.S. 2001. Comparison of decomposition of belowground and aboveground plant litters in peatlands of boreal Alberta, Canada. Can. J. Bot. 79:9–22.

Turetsky, M.R.; Wieder, R.K.; Williams, C.J.; Vitt, D.H. 2000. Organic matter accumulation, peat chemistry, and permafrost melting in peatlands of boreal Alberta. Écoscience 7:379–392.

Vitt, D.H. 1990. Growth and production dynamics of boreal mosses over climatic, chemical, and topographical gradients. Bot. J. Linn. Soc. 104:35–59.

Zadražil, F. 1985. Screening of fungi for lignin decomposition and conversion of straw into feed. Angew. Bot. 59:433–452.

Zogg, G.P.; Zak, D.R.; Ringelberg, D.B.; MacDonald, N.W.; Pregitzer, K.S.; White, D.C. 1997. Compositional and functional shifts in microbial communities due to soil warming. Soil Sci. Soc. Am. J. 61:475–481.