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Exponential growth of "snow molds" at sub-zero temperatures: an explanation for high beneath-snow respiration rates and Q_{10} values

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Abstract Numerous studies have demonstrated exceptionally high temperature sensitivity of the beneath-snow respiratory flux in cold-winter ecosystems. The most common, but still untested, explanation for this high sensitivity is a physical one based on the observation that water availability in soils increases exponentially as soils warm from −3 to 0°C. Here, we present evidence for a biological hypothesis to explain exponential kinetics and high Q_{10} values as beneath-snow soils warm from −3 to 0°C during the early spring in a high-elevation subalpine forest. First, we show that some of the dominant organisms of the beneath-snow microbial community, "snow molds", exhibit robust exponential growth at temperatures from −3 to −0.3°C. Second, Q_{10} values based on growth rates across the temperature range of −2 to −0.3°C for these snow molds vary from 22 to 330. Third, we derive an analytical equation that combines the relative contributions of microbial growth and microbial metabolism to the temperature sensitivity of respiration. Finally, we use this equation to show that with only moderate snow mold growth (several generations), the combined sensitivities of growth and metabolism to small changes in beneath-snow soil temperature, create a double exponential in the Q_{10} function that may explain the extremely high ($\sim 1 \times 10^6$) Q_{10} values observed in past studies. Our biological explanation for high Q_{10} levels is supported by several independent studies that have demonstrated build up of microbial biomass under the snow as temperatures warm from −2 to 0°C.

Keywords Sub-nivian biogeochemistry · Arrhenius function · Michaelis–Menten kinetics · Soil respiration · Psychrophiles

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Introduction

The under-snow environment in late winter and early spring is surprisingly conducive to the development of microbial communities due to the insulating properties of snow, especially when it is more than 0.3 m deep (Brooks et al. 1997) or more than 1 m deep in especially cold environments (Grogan and Jonasson 2006). These conditions have long been known to facilitate the growth of pathogenic snow molds that parasitize a broad range of plants from grasses (Hsiang et al. 1999) to conifers (Hartig 1888; Simms 1967). In addition, mats of snow mold are commonly observed covering the soil and litter as snow recedes in the spring in both coniferous and tundra ecosystems (Schmidt et al. 2007, 2008a). These fungi have

received almost no attention compared to their pathogenic relatives, perhaps because they are of little direct economic importance. However, recent biogeochemical studies in seasonally snow-covered environments indicate that microbial activity under late winter snows can contribute significantly to fluxes of greenhouse gases and to cycling of nitrogen and carbon (Brooks et al. 1998; Larsen et al. 2007; Lipson et al. 1999; Campbell et al. 2005; Schmidt and Lipson 2004; Monson et al. 2006a). Schmidt et al. (2008a, b) have argued that saprotrophic snow molds are a major component of the sub-nivean environment and play an important and previously overlooked role in nutrient cycling and gas fluxes in seasonally snow-covered environments.

Snow molds are especially prominent in sub-alpine forests of the Colorado Front Range (Rocky Mountains) where they form dense mycelial mats under late season snow packs (Fig. 1). These fungal communities are ephemeral in nature and rapidly disappear once the snow is gone. At these same sites late winter fluxes of beneath-snow, respired CO_2 can be high, amounting to as much as 35–48% the rate of late-winter, whole-ecosystem respiration, and accounting for up to 10% the annual cumulative ecosystem respiratory CO_2 loss (Monson et al. 2006b). Late winter CO_2 fluxes can increase exponentially under the snow (Brooks et al. 1997; Mast et al. 1998; Monson et al. 2006a, b; Sommerfeld et al. 1996), perhaps indicating exponential growth of microbes. In addition, when considered across the seasonal range of sub-nivean soil temperatures, Q_{10} values for sub-nivean CO_2 fluxes are unexpectedly high (Monson et al. 2006a), but it is not known if these high Q_{10} values are due to physical or biological phenomena. Here, we explore the growth kinetics of snow molds from the same sites studied by Monson et al. (2006a, b) in order to determine if they have the potential to account for the extremely high exponential kinetics of beneath-snow CO_2 fluxes observed in the field.

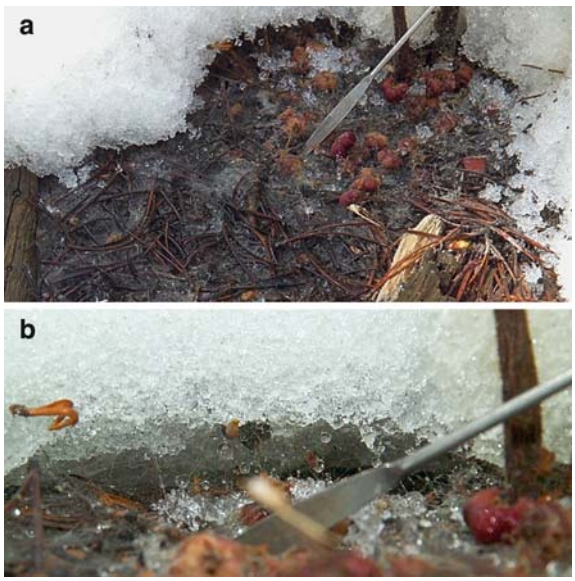

Fig. 1 (**a**) Typical mat of snow mold growing on the litter under snow at our sub-alpine forest research site. The snow was gently removed to reveal the mats as they occur under the late-winter snow pack. (**b**) Close-up of a zygomycetous snow mold under the snow, demonstrating the ability of these fungi to grow vertically up into the snow as well as horizontally on the litter. They also exhibit this vertical growth ability in the laboratory (Schmidt et al. 2008a). Metal weighing spatula is included for scale

Materials and methods

Study site

The study site is at 3050 m above sea level (40°1′ 58″ N; 105°32′ 47″ W) 25 km west of Boulder, Colorado. The forest is dominated by *Pinus contorta* (lodgepole pine), *Picea engelmannii* (Engelmann spruce) and *Abies lasiocarpa* (subalpine fir). The soils are sandy inceptisols derived from granite moraine covered by an organic horizon ranging from ~0 to 6 cm. More detailed descriptions of the site can be found in past publications (Monson et al. 2006a, b; Weintraub et al. 2007).

Growth at different temperatures

The snow molds were isolated from under-snow fungal mats (Fig. 1) and have been characterized phylogenetically and physiologically (Schmidt et al. 2008a, b). To estimate exponential growth rates of these isolates at different temperatures (−3, −2, −0.3, and 3.8°C) we measured rates of increase in the area covered by individual fungal colonies, grown in the dark, as a function of time. Specifically, growth was measured by marking the bottom of the plate in four locations (in order to obtain four measures of radius at right angles to each other) at each time interval (Kerry 1990). The mean radius obtained was used to calculate

the area covered by the colony at each time interval. This approach was used because these fungi grow as concentrically expanding mats at the interface between the snow pack and the litter layer (Fig. 1). All experiments were done in triplicate in low temperature incubators (Sheldon Manufacturing, Cornelius OR) outfitted with data loggers to monitor temperature during the incubations. Temperatures in the incubators remained quite constant with standard deviations less than 0.28°C during the entire incubation period for all incubation temperatures. The media used for growth experiments contained (per liter of water): 5.0 g of inulin, 0.5 g yeast extract, 0.5 g of KCl, 1.0 g of KH_2PO_4, 1.0 g of $(NH_4)_2SO_4$, 2.0 g of $NaNO_3$, 12.3 g of $MgSO_4 \cdot 7H_2O$, 20 g of agar, 50 mg of $CaCl_2$, 10 mg of $FeSO_4$, 10 mg of $CuSO_4$, 5 mg of $MnSO_4$, 1 mg of $ZnSO_4$, and 1 ml of soil extract solution (Schmidt et al. 2008a). After autoclaving, Chlorotetracycline and Streptomycin (50 mg/l for both antibiotics) were added to inhibit bacterial growth.

Inoculum for the experiments was grown at 3.8°C on the above media and uniform plugs for inoculation of experiments were obtained using a sterile 6 mm diameter AcuPunch Biopsy Punch (Acuderm Inc., Ft. Lauderdale FL). All inoculum plugs were taken at the same growth stage from the master plate to insure that the fungi used for all temperature treatments were at same metabolic state at the beginning of the experiment.

Kinetic considerations

One of our goals was to compare rates of snow mold growth at different temperatures to exponential rates of CO_2 production under the snow. It is well established that there is a direct relationship between the rate of primary metabolite production (e.g., ethanol, CH_4, N_2O and CO_2) and the biomass of active microorganisms (Schlegel 1992; Scow et al. 1986). This relationship has been the basis of numerous methods to estimate microbial kinetic parameters (including growth rates and biomass levels) from soil respiration data (Anderson and Domsch 1978; Brunner and Focht 1984; Colores et al. 1996; Hess and Schmidt 1995). Here we apply this principle to analyze and compare growth curves of under-snow microbes to curves of CO_2 flux from snow-covered soils that exhibit exponential kinetics.

The simplest expression for analyzing exponential growth kinetics is the integrated exponential growth equation:

$$N_t = N_o e^{\mu t} \quad (1)$$

where N_t is the microbial biomass (μg C) at time t, μ is exponential growth rate with units of h^{-1} and N_o is the biomass at time 0. To compare growth of a microbial population to the rate of CO_2 flux we can use the relationship derived from basic principles by Colores et al. (1996) to express the rate of CO_2 production in terms of exponential microbial growth:

$$r = \mu(P_o e^{\mu t}) \quad (2)$$

where r is the rate of CO_2 flux (dP/dt) as a function of microbial growth, μ is as defined above, and P_o is the biomass of microbes in terms of CO_2 (μg C) before exponential growth commences. An added utility of Eq. 2 is that it can be used to estimate the biomass of CO_2-producing microbes and related back to Eq. 1, using the relationship (Colores et al. 1996):

$$N_o = P_o Y_c/(1 - Y_c) \quad (3)$$

where N_o and P_o are as defined above and Y_c (μg biomass C/μg substrate C) is the "yield coefficient" or the efficiency of conversion of substrate carbon to microbial biomass.

To obtain estimates of μ Eqs. 1 and 2 were fit to fungal growth curves and curves of CO_2 rate changes over time, respectively, using the non-linear regression package of Kaliedagraph® software (Synergy Software Co., Reading, PA, USA). Estimates of μ can also be obtained using linear regression when the natural log of N_t or r are plotted against time; in which case μ is the slope of the semi-log plot and N_o and P_o are the Y-intercept for the linearized forms of Eqs. 1 and 2, respectively.

The effects of temperature on rates of biological processes, such as CO_2 flux (r), can be evaluated using the Q_{10} relationship, which can be used to estimate the temperature dependence of the rate for Arrhenius-like behavior of enzymes and organisms (Hochachka and Somero 1984):

$$Q_{10} = (r_2/r_1)^{10/(T2-T1)} \quad (4)$$

where r_1 is the measured respiration rate at temperature 1 ($T1$) and r_2 is the rate at temperature 2 ($T2$). Although the Q_{10} relationship is often applied to

broad ranges of temperature with the assumption that it is a conserved property of reaction systems with respect to temperature, the classical derivation of the model as an Arrhenius function requires that Q_{10} decrease as temperature increases (see Davidson and Janssens 2006); this is presumably due to shifts in the Boltzmann distribution of the fraction of molecules that have energy exceeding the required activation energy of a reaction as temperature increases.

One of the assumptions of Eq. 4 is that the quantity of enzyme (or biomass) is constant across all temperatures compared. However, in many field studies of soil respiration, rates are measured across lengthy time scales of weeks or months. For these studies it is therefore likely that the assumption of constant catalyst concentration is violated because microbial populations can vary widely across time at any given site (Schmidt et al. 2007). This is especially true of beneath-snow microbial populations that have been shown to build up with time (concomitantly with temperature increases) under late-lying snow packs (Schmidt and Lipson 2004; Weintraub et al. 2007). Therefore, to compare rates of CO_2 flux across the snow-covered period, we developed a modified Q_{10} equation to take into account both the effects of temperature and increased biomass. It is well established that the rate of CO_2 flux from respiration is a function of both growth rate and the biomass of respiring organisms (reviewed in Simkins and Alexander 1984 and Scow et al. 1986). Thus, r_1 and r_2 from Eq. 4 can be expressed as:

$$r = N\mu \tag{5}$$

where r is the respiration rate at a given temperature and N and μ are as described above.

We can substitute Eq. 5 into Eq. 4 to yield a Q_{10} equation that separates out the effects of growth rate and biomass level:

$$Q_{10} = (N_2\mu_2/N_1\mu_1)^{10/(T2-T1)} \tag{6}$$

where N_2 and N_1 represent the biomass of respiring microbes at temperatures $T2$ and $T1$, respectively, μ_1 is the growth rate at temperature $T1$ and μ_2 is the rate at temperature $T2$. It should be noted that Eq. 6 contains a 'double exponential' function as the increase in biomass between $T1$ and $T2$ can follow exponential growth kinetics. In the present study we used this relationship to determine how the apparent Q_{10} would change as both microbial biomass and temperature increase beneath late winter snow packs.

Several workers have pointed out that substrate availability may limit microbial respiration rate under the snow (Brooks et al. 2005; Lipson et al. 2000) and others have shown that growth-rate limiting enzymes usually show increased substrate affinity as temperatures increase (Davidson and Janssens 2006; Nedwell 1999). The effects of substrate concentration on the growth or reaction rate of a microbial population has been derived elsewhere (Schmidt et al. 1985; Simkins and Alexander 1984). Thus, r_1 and r_2 from Eq. 4 can be expressed as:

$$r = N\,\mu/K_{\mathrm{m}} \tag{7}$$

where μ and N are defined above and K_{m} is the half-saturation constant at the prevailing temperature.

We can substitute Eq. 7 into Eq. 4 and rearrange to yield a Q_{10} equation that separates out the effects of substrate concentration, growth rate, and biomass level:

$$Q_{10} = (N_2\mu_2K_{\mathrm{m1}}/N_1\mu_1K_{\mathrm{m2}})^{10/(T2-T1)} \tag{8}$$

where N_2, N_1, μ_1 and μ_2 are as defined above and K_{m1} and K_{m2} are the half-saturation constants at temperatures $T1$ and $T2$, respectively. We present Eq. 8 to show that the net effect of a temperature increase would be to increase the apparent Q_{10}, because K_{m1} would be greater (lower affinity) than K_{m2} in Eq. 8. Likewise a temperature decrease over time would result in a lower apparent Q_{10}.

Results

A series of experiments was conducted to ascertain if snow molds from our research sites (Fig. 1) could grow exponentially at under-snow temperatures commonly observed in the late winter and early spring. These fungi have been phylogenetically identified from our cultures and environmental clone libraries as members of the Mortierellales (Isolate 317) and Mucorales (Isolates 316 and 319) subdivisions of the Zygomycota (Schmidt et al. 2008a, b). Soil temperatures normally range between −2 and 0°C during this period (Monson et al. 2006a, b). All isolates could grow at the lowest temperature tested (−3°C) and full growth curves were obtained at temperatures

of −3, −2, −0.3 and 3.8°C for two of our isolates. The curves for growth at −3 and −2°C for these isolates are shown in Fig. 2. The isolates all showed robust exponential growth for the first 15 days of incubation at −2°C (Fig. 2) and for the entire incubation period at −3°C. At −3°C growth was much slower and isolate 317 seemed to be near its lower temperature limit for growth, whereas isolate 316 was still growing well (Fig. 2). To estimate growth rate (μ) at each temperature, Eq. 1 was fit to the exponential data in Fig. 2 and to the exponentially increasing portions of the curves for each isolate at −0.3 and 3.8°C. Estimates of μ and R^2 values for each fitted curve are shown in Table 1.

Under-snow exponential increases in field CO_2 and N_2O fluxes have been noted in a number of studies at and near our sites (Brooks et al. 1997; Schmidt et al. 2001; Monson et al. 2006a, b). In the present study we analyzed the exponentially increasing portion of the data from Monson et al. (2006b). The curves of CO_2 flux at our sites between February 20 and April 10, 2004 are shown in Fig. 3. During this period soil temperatures were fairly constant at the open (between tree) site ranging from −0.6°C to 0°C, whereas at the near-tree soil temperatures were lower (range −1.9 to about 0°C). To estimate growth rate (μ) at each site, Eq. 2 was fit to the data in Fig. 3.

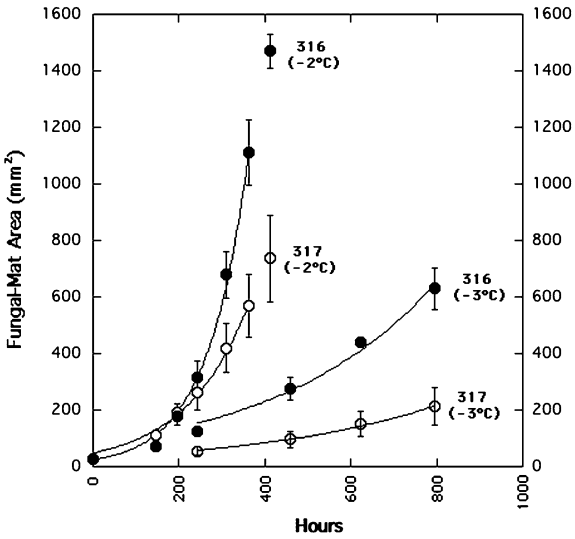

Fig. 2 Exponential growth of isolates 316 and 317 at temperatures of −3 and −2°C. Each curve is the mean of three replicates and error bars are one standard deviation of the mean. Curves are non-linear regression fits of Eq. 1 to the data with R^2-values of greater than 0.98 for all curve fits

Estimates of μ were 0.0013 and 0.0016 h^{-1} for the open and near-tree sites, respectively.

Next we explored the most probable explanations for the marked increase in the rate of CO_2 flux from snow-covered soils (Fig. 3) across a range of relatively small increase in soil temperature. These striking increases in rate versus temperatures resulted in high apparent Q_{10} values for soil respiration as pointed out by Monson et al. (2006a). For example

Table 1 Estimates of exponential growth rate μ (units of h^{-1}) for the three isolates from fits of Eq. 1 to three replicate growth experiments for each isolate at each temperature

	Temperature		
	−2°C	−0.3°C	3.8°C
Isolate 316	0.0106 (0.0007)	0.0180 (0.0007)	0.0338 (0.0017)
Isolate 317	0.0069 (0.0008)	0.0185 (0.0008)	0.0175 (0.0001)
Isolate 319	0.0078 (0.0007)	0.0203 (0.0012)	0.0268 (0.0003)

Standard deviations of the mean of the replicates at each temperature for each isolate are shown in parentheses

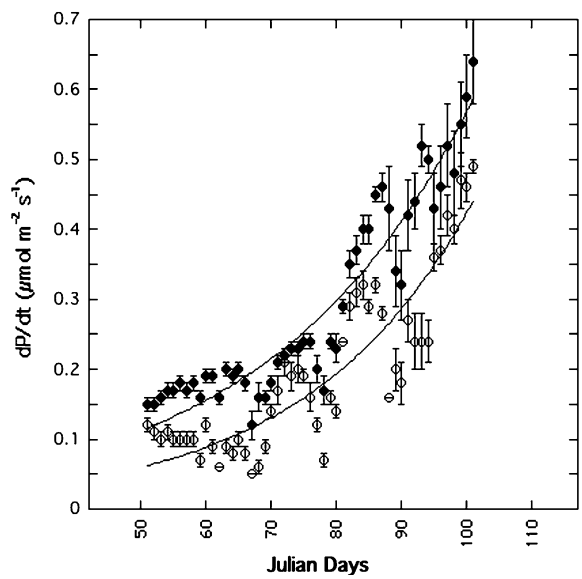

Fig. 3 Rates of CO_2 flux through the snow pack at sites next to trees (*open circles*) or sites in the open (*closed circles*) from 2/20/2004 to 4/10/2004 (Julian day 51 through 101). Curves are non-linear regression fits of Eq. 2 to the data with R^2-values of 0.90 and 0.79 for the open and near-tree data, respectively. Error bars are standard error of the mean ($n = 4$ for near-tree sites and $n = 7$ for open sites)

Monson et al. (2006a) estimated under-snow Q_{10} values of from 105 to 1.3 × 10^6 for the near-tree and open spaces soils, respectively. Various physical explanations have been put forth to explain high apparent Q_{10} values (see discussion in Monson et al. 2006a).

However, our working hypothesis is that these unprecedented increases in respiration rate can be explained biologically. First, we can see that our snow molds show high Q_{10} values (Table 2) when the growth rates (from Table 1) are substituted into Eq. 4 (the standard Q_{10} equation). We only show the Q_{10}-values for the temperature interval of −2 to −0.3°C in Table 2 because this interval best matches the temperatures (−1.9 to 0°C) observed during the period of exponential CO_2 flux in the field (Fig. 3). To evaluate the effects of changes in biomass concentration (simultaneous with a temperature increase in the field) on apparent Q_{10} values, we substituted the rates from Table 1 into Eq. 6 and then assumed that biomass would double once, twice or three times during the period of exponential CO_2 flux i.e. N_2 is 2, 4 or 8 times higher than N_1, respectively in Eq. 6. At least a doubling of biomass during this period has been independently documented for total microbial biomass at and near our sites (Fig. 1a in Schmidt et al. 2007, and Fig. 2 in Weintraub et al. 2007).

Table 2 Q_{10} values for temperature intervals from −2 to −0.3°C calculated using exponential growth rates and Eq. 4 and apparent Q_{10} values calculated using Eq. 6 and assuming either 1, 2 or 3 doublings (generations) of the population size during the incubation period

Temp. interval	Number of generations			
	0 (Eq. 4)	1 (Eq. 6)	2 (Eq. 6)	3 (Eq. 6)
Isolate 316				
−2 to −0.3	22.5	1.3 × 10^3	7.8 × 10^4	4.6 × 10^6
−0.3 to 3.8	4.7			
Isolate 317				
−2 to −0.3	330	1.9 × 10^4	1.1 × 10^6	6.8 × 10^7
−0.3 to 3.8	1.2			
Isolate 319				
−2 to −0.3	277	1.6 × 10^4	9.6 × 10^5	5.7 × 10^7
−0.3 to 3.8	2.0			

These calculations underline the extreme sensitivity of apparent Q_{10} values to changes in microbial biomass levels

Discussion

We know very little about the kinetic behavior of the growth and metabolism of fungi that grow during the final months of snow cover in seasonally snow-covered environments. These fungi may contribute substantially to regional CO_2 fluxes and understanding their physiological attributes could lend important insight into how global CO_2 dynamics will change as global warming affects both the duration and depth of snow packs in high-latitude and high-altitude ecosystems. The fungi used in this study were isolated from hyphal fragments taken from mats of snow mold at the same high-elevation sites as those studied by Monson et al. (2006a, b); related fungi have been isolated from cold Arctic and Antarctic soils (Bergero et al. 1999; Pugh and Allsop 1982; Wynn-Williams 1985) and have also been identified from clone libraries of snow-covered high-elevation tundra (above treeline) soils, but not from libraries of summer soils (Schadt et al. 2003; Schmidt et al. 2008a, b).

This study represents the first analysis to conclude that the exponential increases in CO_2 flux through the snow pack at both our alpine and subalpine sites (Brooks et al. 1997; Schmidt et al. 2001; Monson et al. 2006a, b) could be attributable to the *combined* effects of exponential growth of snow molds and the exponential response of their respiration rate to small changes in temperature beneath the snow. In this case, the modeled temperature response would reflect a double-exponential function; such a function is capable of pushing temperature sensitivity coefficients, such as the Q_{10}, to extremely high values. Our isolates exhibited exponential growth at −3, −2 and −0.3°C, with μ values that were much higher than observed CO_2 fluxes during the final months of snow cover (Monson et al. 2006a, b; Schmidt et al. 2001). Schmidt et al. (2001) estimated an exponential rate of increase in CO_2 flux through the snow pack of 0.0017 h^{-1}, which is similar to the exponential rates of 0.0013 and 0.0016 h^{-1} extrapolated from field observations at our subalpine site in the present study (Fig. 3). In comparison, our fungal isolates from these same subalpine soils exhibited exponential growth rates (μ) ranging from a low of 0.0024 at −3°C to 0.011 h^{-1} at −2°C. The fact that our isolates have potential (lab-based) growth rates that are higher than field-measured exponential rates of gas flux is to be expected because microbes rarely grow

at their maximal potential rates in nature (Lipson and Schmidt 2002).

Using observed exponential growth rates for snow molds, combined with the traditional exponential model (Eq. 4) to explain the temperature dependence of metabolism, we can explain the extremely high Q_{10} values for beneath-snow soil respiration that we previously observed (Monson et al. 2006a). Our isolates demonstrated very high growth-rate sensitivity to temperatures between −2 and −0.3°C, exhibiting Q_{10} values between 23 and 330 (Table 2) across this temperature range. These values bracket the field observed apparent Q_{10} value of 105 observed for beneath-snow CO_2 flux for near-tree sites by Monson et al. (2006b). If we assume that net growth of snow molds is occurring under the snowpack as temperature is increasing through the late-winter and spring, then beneath-snow CO_2 flux rates would be proportional to both temperature and to the biomass of respiring organisms as modeled in Eq. 6. Using Eq. 6 we obtained apparent Q_{10} values of between 1.3×10^3 and 6.8×10^7 (Table 2), depending on assumptions about the number of snow-mold generations per season. These values bracket the field observed apparent Q_{10} value of 1.25×10^6 observed for CO_2 fluxes from the open (between tree) sites by Monson et al. (2006). Furthermore, we can estimate the number of doublings that it would take to produce the field curves in Fig. 3 by converting μ to doubling time (G) using the relationship $G = \ln 2/\mu$. Using this approach, we obtained a G value of 516 hours for the open (between tree) soil resulting in 2.3 doublings in biomass during the 1200 hours of data depicted in Fig. 3. Using this estimated biomass increase in Eq. 6 results in apparent Q_{10} values of 3.7×10^5, 5.4×10^6 and 4.5×10^6 for isolates 316, 317 and 319, respectively. Thus, all of the isolates could produce apparent Q_{10} values for combined growth and metabolism in the range of the apparent Q_{10} value for beneath-snow CO_2 flux of 1.25×10^6 (Monson et al. 2006a), even if they only went through 2.3 generations.

In contrast to our work, the most often stated explanation for exponential changes in rates as temperatures increase between −2 and 0°C is that water availability (and therefore nutrient availability) increases exponentially as soils thaw (Ley et al. 2004; Mikan et al. 2002; Romanovsky and Osterkamp 2000). This physical phenomenon could explain exponential rate changes in soils in which thaw rate changes slowly enough to be reflected in respiration rate measurements. However, in the work of Monson et al. (2006b) the exponential increase in soil moisture occurs over a period of days, whereas the respiration data increase exponentially over almost two months time (Fig. 3), with most of that increase occurring after the increase in soil water content. Indeed the data in Fig. 3 were collected from 2/20/2004 to 4/10/2004, whereas the exponential increase in soil water occurred between 3/18/2004 and 3/23/2004 (Monson et al. 2006b). Thus it is fairly clear that, at least in the present study, the long-term exponential increase in respiration rate and Q_{10} values are more likely due to exponential increases in microbial biomass levels than to physical phenomena. Obviously, more work is needed to parse out the relative contributions of biological and physical controls of exponential kinetics under the snow, but our data and modeling approach present a compelling argument for strong links between microbial population dynamics and under-snow CO_2 fluxes.

In summary, our snow-mold isolates have the potential to produce the exponential kinetics of CO_2 flux that we have observed in past studies at our alpine and subalpine research sites. The biomass of these fungi increases to such an extent under the late-winter snow pack, that they are visible to the naked eye (Fig. 1) and exhibit remarkably robust exponential growth kinetics at sub-zero temperatures (Fig. 2). In addition, their intrinsically high metabolic Q_{10} values combined with their exponential growth at low temperatures provides the best biological explanation to date for the high temperature-sensitivity of beneath-snow respiration rate that we have observed in our past studies. Further work is under-way to characterize the growth of our isolates in microcosms that more closely resemble the beneath-snow environment and to obtain critical estimates of yield coefficients and other kinetic parameters (Lipson et al. 2008) to allow us to better link fungal growth kinetics to beneath-snow trace gas fluxes.

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References

Anderson JPE, Domsch KH (1978) A physiological method for the quantitative measurement of microbial biomass in soil. Soil Biol Biochem 10:215–221. doi:10.1016/0038-0717(78)90099-8

Bergero R, Ghirlanda M, Varese GC, Intili D, Luppi AM (1999) Psychro-oligotrophic fungi from Arctic soils of Franz Joseph Land. Polar Biol 21:361–368. doi:10.1007/s003000050374

Brooks PD, Schmidt SK, Williams MW (1997) Winter production of CO_2 and N_2O from alpine tundra: environmental controls and relationship to inter-system C and N fluxes. Oecologia 110:403–413

Brooks PD, Williams MW, Schmidt SK (1998) Inorganic N and microbial biomass dynamics before and during spring snowmelt. Biogeochemistry 43:1–15. doi:10.1023/A:1005947511910

Brooks PD, McKnight D, Elder K (2005) Carbon limitation of soil respiration under winter snowpacks: potential feedbacks between growing season and winter carbon fluxes. Glob Change Biol 11:231–238. doi:10.1111/j.1365-2486.2004.00877.x

Brunner W, Focht DD (1984) Deterministic three-half-order kinetic model for microbial degradation of carbon substrates in soil. Appl Environ Microbiol 47:167–172

Campbell JL, Mitchell MJ, Groffman PM, Christenson LM, Hardy JP (2005) Winter in northeastern North America: a critical period for ecological processes. Front Ecol Environ 3:314–322

Colores GM, Schmidt SK, Fisk MC (1996) Estimating the biomass of microbial functional groups using rates of growth-related soil respiration. Soil Biol Biochem 28:1569–1577. doi:10.1016/S0038-0717(96)00253-2

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165–173. doi:10.1038/nature04514

Grogan P, Jonasson S (2006) Ecosystem CO_2 production during winter in a Swedish subarctic region: the relative importance of climate and vegetation type. Glob Change Biol 12:1479–1495. doi:10.1111/j.1365-2486.2006.01184.x

Hartig R (1888) *Herpotrichia nigra* n. sp. Allgem Forst Jagdzeit 64:15–17

Hess TF, Schmidt SK (1995) Improved procedure for obtaining statistically valid parameter estimates from soil respiration data. Soil Biol Biochem 27:1–7. doi:10.1016/0038-0717(94)00166-X

Hochachka PW, Somero GN (1984) Biochemical adaptation. Princeton University Press, Princeton, NJ

Hsiang T, Matsumoto N, Millett SM (1999) Biology and management of *Typhula* snow molds of turfgrass. Plant Dis 83:788–798. doi:10.1094/PDIS.1999.83.9.788

Kerry E (1990) Effects of temperature on growth rates of fungi from sub-Antarctic Macquarie Island and Casey, Antarctica. Polar Biol 10:293–299

Larsen KS, Grogan P, Jonasson S, Michelsen A (2007) Respiration and microbial dynamics in two subarctic ecosystems during winter and spring thaw: effects of increased snow depth. Arct Antarct Alp Res 39:268–276. doi:10.1657/1523-0430(2007)39[268:RAMDIT]2.0.CO;2

Ley RE, Williams MW, Schmidt SK (2004) Microbial population dynamics in an extreme environment: Controlling factors in talus soils at 3750 m in the Colorado Rocky Mountains. Biogeochemistry 68:313–335. doi:10.1023/B:BIOG.0000031032.58611.d0

Lipson DA, Schmidt SK (2002) Kinetics of microbial processes and population growth in soil. In: Bitton G (ed) Encyclopedia of environmental microbiology. Wiley, New York, pp 1748–1757

Lipson DA, Schmidt SK, Monson RK (1999) Links between microbial population dynamics and nitrogen availability in an alpine ecosystem. Ecology 80:1623–1631

Lipson DA, Schmidt SK, Monson RK (2000) Carbon availability and temperature control the post-snowmelt decline in alpine soil microbial biomass. Soil Biol Biochem 32:441–448. doi:10.1016/S0038-0717(99)00068-1

Lipson DA, Monson RK, Schmidt SK, Weintraub MN (2008) The trade-off between growth rate and yield in microbial communities and the consequences for soil respiration in a high elevation coniferous forest. Biogeochemistry (in press, this issue)

Mast MA, Wickland KP, Striegl RT, Clow DW (1998) Winter fluxes of CO_2 and CH_4 from subalpine soils in Rocky Mountain National Park, Colorado. Global Biogeochem Cycles 12:607–620. doi:10.1029/98GB02313

Mikan CJ, Schimel JP, Doyle AP (2002) Temperature controls of microbial respiration in arctic tundra soils above and below freezing. Soil Biol Biochem 34:1785–1795. doi:10.1016/S0038-0717(02)00168-2

Monson RK, Lipson DA, Burns SP, Turnipseed AA, Delany AC, Williams MW et al (2006a) Winter forest soil respiration controlled by climate and microbial community composition. Nature 439:711–714. doi:10.1038/nature04555

Monson RK, Burns SP, Williams MW, Delany AC, Weintraub MN, Lipson DA (2006b) The contribution of beneath-snow respiration to total ecosystem respiration in a high-elevation, subalpine forest. Global Biogeochem Cycles 20. doi:10.1029/2005GB002684

Nedwell DB (1999) Effect of low temperature on microbial growth: lowered affinity for substrates limits growth at low temperature. FEMS Microbiol Ecol 30:101–111. doi:10.1111/j.1574-6941.1999.tb00639.x

Pugh GJF, Allsop D (1982) Microfungi on Signy Island, South Orkney Islands. Br Antarct Surv Bull 57:55–67

Romanovsky VE, Osterkamp TE (2000) Effects of unfrozen water on heat and mass transport processes in the active layer of permafrost. Permafrost Periglac Proc 11:219–239. doi:10.1002/1099-1530(200007/09)11:3<219::AID-PPP352>3.0.CO;2-7

Schadt CW, Martin AP, Lipson DA, Schmidt SK (2003) Seasonal dynamics of previously unknown fungal lineages in tundra soils. Science 301:1359–1361. doi:10.1126/science.1086940

Schlegel HG (1992) General microbiology, 7th edn. Cambridge University Press, Cambridge

Schmidt SK, Lipson DA (2004) Microbial growth under the snow: implications for nutrient and alleochemical availability in temperate soils. Plant Soil 259:1–7. doi:10.1023/B:PLSO.0000020933.32473.7e

Schmidt SK, Alexander M, Shuler ML (1985) Predicting threshold concentrations of organic substrates for bacterial growth. J Theor Biol 114:1–8. doi:10.1016/S0022-5193(85)80250-2

Schmidt SK, West AE, Brooks PD, Jaeger CH, Fisk MC, Holland E (2001) Soil-atmosphere gas exchange. In: Bowman W, Seastedt T (eds) The structure and function of an alpine ecosystem. Oxford University Press, Oxford, pp 254–265

Schmidt SK, Costello EK, Nemergut DR, Cleveland CC, Reed SC, Weintraub MN et al (2007) Biogeochemical consequences of rapid microbial turnover and seasonal succession in soil. Ecology 88:1379–1385. doi:10.1890/06-0164

Schmidt SK, Wilson KL, Gebauer MM, Meyer AF, King AJ (2008a) Phylogeny and ecophysiology of opportunistic "snow molds" from a sub-alpine forest ecosystem. Microb Ecol . doi:10.1007/s00248-008-9387-6

Schmidt SK, Wilson KL, Meyer AF, Porter TM, Schadt CW, Moncalvo JM (2008b) The missing fungi—new insights from culture-independent molecular studies of soil. In: Zengler K (ed) Accessing uncultivated microorganisms: from the environment to organisms and genomes and back. American Society for Microbiology, Washington, pp 55–66

Scow KM, Simkins S, Alexander M (1986) Kinetics of mineralization of organic compounds at low concentrations in soil. Appl Environ Microbiol 51:1028–1035

Simkins S, Alexander M (1984) Models for mineralization kinetics with the variables of substrate concentration and population density. Appl Environ Microbiol 47:1299–1306

Simms HR (1967) On the ecology of *Herpotrichia nigra*. Mycologia 59:902–909. doi:10.2307/3757200

Sommerfeld RA, Massman WJ, Musselman RC, Mosier AR (1996) Diffusional flux of CO_2 through snow: spatial and temporal variability among alpine-subalpine sites. Global Biogeochem Cycles 10:473–482. doi:10.1029/96GB01610

Weintraub MN, Scott-Denton LE, Schmidt SK, Monson RK (2007) The effects of tree rhizodeposition on soil exoenzyme activity, dissolved organic carbon, and nutrient availability in a sub-alpine forest ecosystem. Oecologia 154:327–338. doi:10.1007/s00442-007-0804-1

Wynn-Williams DD (1985) Comparative microbiology of moss-peat decomposition on the Scotia Arc and Antarctic Peninsula. In: Siefried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer-Verlag, Berlin, pp 204–210