Reduction of air- and liquid water-filled soil pore space with freezing explains high temperature sensitivity of soil respiration below 0 °C

Colin Tucker[*]

University of Wyoming, Botany Department and Program in Ecology, 1000 E. University Avenue, Laramie, WY, 82071, United States

ABSTRACT

At temperatures just below 0 °C, the temperature sensitivity of heterotrophic soil respiration (R_H) is orders of magnitude higher than above 0 °C. Two primary mechanisms have been proposed for this high sub-zero temperature sensitivity: changes in soil microbial community composition and physiology, or the physical effects of the transition of water between liquid and ice phases. In this study, the effect of soil freezing on R_H was modeled using a simple modification of the Dual Arrhenius Michaelis–Menten model, to account for both the reduced liquid water content of the soil pore space and the reduced air-filled pore space as water expands during freezing. Using parameters derived from previous studies, R_H was modeled at a range of sites throughout Southeast Wyoming, ranging from prairie to high elevation forest. Across the study region, R_H at sub-zero temperatures was low in the prairie (0.002 mg C m^{-2} h^{-1} at -1 °C and optimal water content) and sagebrush (5·10^{-7} to 0.012 mg C m^{-2} h^{-1} at -1 °C and optimal water content) sites, with lower organic matter and higher sand content, and much higher in the high sub-alpine forest (0.71 mg C m^{-2} h^{-1} at -1 °C and optimal water content) and meadow (3.5 mg C m^{-2} h^{-1} at -1 °C and optimal water content) sites with high soil organic matter content. The modeled Q_{10} (the multiplicative response of R_H to a 10 °C increase in temperature) above freezing was ~3.2, while below freezing the median value ranged from 15 to 255, and the maximum was 1.6·10^{24}. These values capture the range of Q_{10}'s described in the literature, suggesting that the model based on changing liquid water contented presented here can explain much of these observed apparent temperature responses. Hence, this model may prove valuable for predicting soil C fluxes in environments that undergo seasonal freezing.

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1. Introduction

In regions at high elevation and latitude that experience long, cold winters, heterotrophic respiration (R_H) from snow-covered soils may be a quantitatively important part of the annual carbon (C) cycle (Sommerfeld et al., 1993). While R_H is generally low at cold temperatures (Lloyd and Taylor, 1994), over the duration of the snow-covered period the cumulative winter efflux of CO_2 may be as much as 50% of the annual flux (Grogan and Chapin, 1999). This efflux is, however, highly sensitive to soil temperature. A number of studies have found that just below 0 °C, the temperature sensitivity of soil respiration increases sharply (Mikan et al., 2002; Monson et al., 2006; Tilston et al. 2010; Schmidt et al., 2009). The Q_{10} (multiplicative increase in reaction rate to a 10 °C temperature increase) of soil respiration above 0 °C generally ranges from 1.5 to

3.4 (Raich and Schlesinger, 1992), while just below 0 °C, Q_{10} values commonly range from 60 to 200 (e.g., Mikan et al., 2002), and may be high as 6.65·10^5 (Monson et al., 2006). Snow-covered soils in cold regions may remain just above freezing for a significant fraction of the winter (Brooks et al., 2005; Buckeridge and Grogan, 2008; Groffman et al., 2001; Miller et al., 2007), depending on the timing and depth of the snow cover. Thus, changes in snow cover such as those occurring over the last half century in the Intermountain West (Groisman et al., 2004; Pierce et al., 2008) and projected to continue over the coming century (Weare and Blossier, 2012), may result in significant shifts in annual C loss from soils.

In this paper, it is posited that the high sensitivity of soil respiration to small changes in temperature just below 0 °C is primarily a response to the transition of water between the liquid and solid phases (e.g., Tilston et al. 2010). The dynamics of the liquid–ice transition of water in soils may be complex and related to the soil texture, organic matter content and concentration of dissolved solutes (Farouki, 1981; Lovell, 1957; Romanovsky and Osterkamp, 2000; Tilston et al., 2010) (Fig. 1). In general, soils

* Present address: University of Alaska, Fairbanks, Institute of Arctic Biology, 902 N. Koyukuk Drive, P.O. Box 757000, Fairbanks, AK, 99775, United States.
E-mail addresses: cltucker@alaska.edu, colinleetucker@gmail.com.

with a higher clay fraction, or higher soil organic matter, tend to freeze more slowly, while sandy soils tend to freeze abruptly just below the 0 °C boundary. As soils freeze, a number of limitations may be imposed on soil microbes. Liquid water availability is reduced to micro-films, thus inhibiting the diffusion of substrates to microbial cells, and leading to a higher reliance on recycling of microbial biomass and metabolic by-products as the primary source of respired C (Ostroumov and Siegert, 1996; Rivkina et al., 2000; Schimel and Mikan, 2005). Additionally, the reduction in liquid water is accompanied by a decrease in the amount of air-filled pore space, because as water freezes, it expands. This reduction of air-filled pore space, which may be accompanied by the formation of ice lenses (Talamucci, 2003), will result in reduced diffusion of oxygen through the soil and increased limitation of aerobic respiration by anoxic conditions.

In this study, I developed a modification of the recent Dual Arrhenius Michaelis–Menten (DAMM) model (Davidson et al., 2012) of soil respiration to account for changes in soil structure and function driven by freezing water. The DAMM model is a semi-mechanistic model where soil respiration responds to temperature, substrate availability and the amount of liquid water and air-filled pore space in the soil volume. The mean values of soil properties from several field sites were used as the input variables to predict and analyze the temperature and moisture responses of soil heterotrophic respiration (R_H) across the 0 °C boundary. These sites include mixed grass prairie, sagebrush steppe, and high altitude coniferous forest and meadow systems, spanning the range of ecological variability in southeast Wyoming. I hypothesized that the R_H would be more sensitive to changing temperature below 0 °C than above 0 °C, and this response would be different among sites depending on soil density, texture and C content.

This study is largely a thought-experiment, wherein field data on soil physical properties and organic C content are used, along with a modification of the DAMM model, to simulate the effect of changing liquid to frozen water ratios across the phase change temperature range on the apparent temperature sensitivity of

heterotrophic soil respiration. Data are incorporated from several field sites that illustrate some of the potential range in the physical controls on sub-freezing soil respiration, especially related to soil texture and C content. This study should provide a good basis for future field and lab work to explore these mechanisms in detail, and suggestions on appropriate experiments to do so are provided in the discussion.

2. Methods

2.1. The original DAMM model

The Dual Arrhenius Michaelis–Menten model (Davidson et al., 2012) combines simple functions for the effects of temperature, soil moisture and substrate carbon availability on heterotrophic soil respiration (Eqn. (1)). Unlike other, more empirical, soil respiration models commonly used (e.g., Q_{10} model, Lloyd and Taylor (1994) model), the DAMM model explicitly considers the role of substrate and O_2 transport through the liquid and gas phases of the soil. Because a critical feature of freezing in soils is a sharp change in the proportion of liquid, water and air-filled pore space in soils, the structure of the DAMM model facilitates the current analysis.

In the DAMM model heterotrophic respiration (R_H) is modeled as:

$$R_H = V_{max} \cdot \frac{[S_c]}{kM_s + [S_c]} \cdot \frac{[O_2]}{kM_{O_2} + [O_2]} \quad (1)$$

where V_{max} is the maximum reaction velocity when neither oxygen concentration ($[O_2]$) nor substrate C concentration ($[S_c]$) are limiting, and kM_{O_2} and kM_s are the respective Michaelis–Menten constants. V_{max} is modeled as a function of temperature T (°C) via an Arrhenius exponential temperature response function:

$$V_{max} = \alpha_s \cdot \exp\left(\frac{-E_{as}}{RT}\right) \quad (2)$$

where α_s is the pre-exponential factor (set to $5.38 \cdot 10^{10}$ mg C cm^{-3} soil), E_{as} is the activation energy (72.26 kJ mol^{-1}), and R is the universal gas constant ($8.314 \cdot 10^{-3}$ kJ K^{-1} mol^{-1}). Values for α_s and E_{as} were taken directly from Davidson et al. (2012) for the model analysis conducted here. Similarly, representative values for kM_{O_2} (0.121 cm^3 O_2 cm^{-3} air) and kM_s ($9.95 \cdot 10^{-7}$ g C cm^{-3} soil) were derived from that study. More accurate predictions of soil respiration will require deriving these parameters from field data in future studies. The concentration of soluble substrate C (S_c) was derived from total soil C (S_{Tc}) as follows. S_{Tc} values (see Table 1) were derived from literature estimates as well as field measurements described in Tucker et al. (2013) and Tucker et al. (in review) and values for the Chimney Park sites were provided by B. Borkhuu and N. Brown. The amount of soluble C in the soil ($[S_{Sc}]$) was calculated as $[S_{Sc}] = p \cdot [S_{Tc}]$, where p ($= 4.14 \cdot 10^{-4}$ as per Davidson et al. 2012) is a parameter describing the proportion of the total C pool $[S_{Tc}]$ that is soluble. Then, the concentration of C at the reaction site ($[S_c]$) was calculated as $[S_c] = [S_{Sc}] \cdot D_{liq} \cdot \theta$ where θ is the volumetric water content of the soil, and D_{liq} (= 3.17) is a unitless diffusion coefficient. The O_2 concentration at the reaction site $[O_2]$ is calculated as $[O_2] = D_{gas} \cdot 0.209 \cdot a^{4/3}$ where D_{gas} (= 1.67) is a diffusion coefficient of O_2 in air, 0.209 is the fractional abundance of O_2 in air, and a is the volume of air-filled pore space in the soil.

2.2. Modifications to the DAMM model

Here, the DAMM function is modified to account for changes in θ and a as soil water converts from liquid to ice. First, an empirical
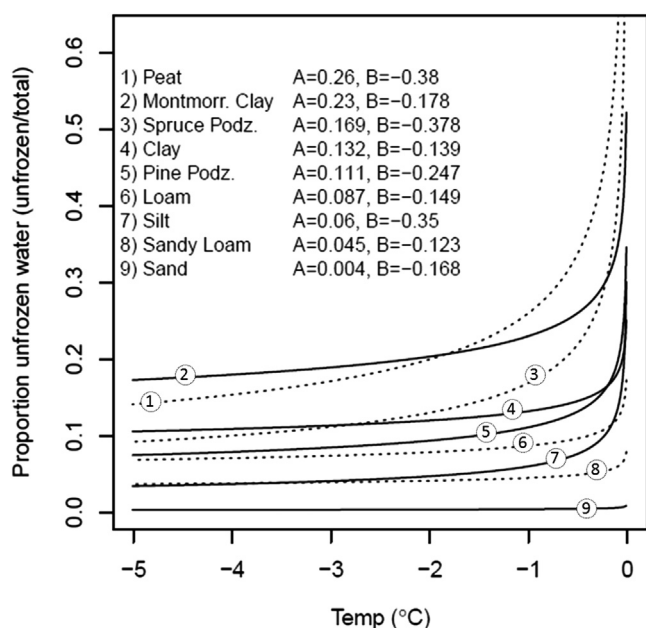

Fig. 1. The fitted proportion unfrozen water (as unfrozen water/total water) plotted against soil temperature from 3 studies: Tilston et al. (2010) (3,5), Farouki (1981) (2,4,6,8,9), Romanovsky and Osterkamp (2000) (1) across a range of soil types. The values of A and B in the legend refer to the parameters of the power function % uf = $A \cdot$ abs(T)^B.