Temperature sensitivity of Antarctic soil biology in response to climate change

Report on the laboratory work carried out in February 2016, supported by the Antarctic Science Bursary

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Project background

Climate change scenarios predict increased temperature and variability including altered precipitation and thawing patterns in the Ross Sea region of Antarctica. The likely result will be changes in soil moisture, substrate availability, and soil biogeochemical processes such as soil microbial respiration (Conant et al. 2011; Davidson and Janssens, 2006). Understanding the response of biochemical processes to changes in temperature is critical for predicting changes in biological cycling of nutrients on various timescales. Biochemical processes are more temperature-sensitive in colder environments (Krischbaum, 1995). Furthermore, there is evidence to suggest that some high latitude regions are warming up to two times faster than the global average (up to 0.4°C decade^{-1}; McBean et al. 2005; IPCC, 2007). Microbial responses to temperature are typically non-linear, and therefore it has been suggested that changes in temperature and climatic variability (including alternations in precipitation and thawing patterns) will lead to more variable soil conditions, and may have disproportionate effects on microbial communities (Scherm and van Bruggen, 1994).

Macro-molecular Rate Theory, MMRT, is a new, more-complete formulation of original theory developed by Arrhenius in 19th century and is particularly important for biological systems at low temperatures (Schipper et al. 2014). One problem with the Arrhenius function is that it predicts a continuous exponential rise in respiration rate with increasing temperature that is not observed in biological systems where there is always a temperature optimum (T_{opt}) observed (Richardson et al. 2012; Schipper et al. 2014). Recent authors have also shown that Arrhenius and Arrhenius-like functions (Lloyd and Taylor, 1994; Kirschbaum, 1995) significantly underestimate the relative temperature sensitivity (Q_{10}) in low temperature environments (Fang and Moncrieff, 2001; Hamdi et al. 2013; Schipper et al. 2014). Unlike Arrhenius, MMRT predicts a temperature inflection point, or T_{inf}, the temperature at which respiration is most sensitive to temperature change, a T_{opt}, the temperate at which respiration is maximal, after which respiration rates decline (without denaturation) and also predicts high temperature sensitivity (Q_{10} values) at low temperatures (Schipper et al. 2014).

It is critical to accurately model the biological temperature dependence of soil respiration and other biological responses. One problem with traditional soil incubation laboratory methods is they only measure biological responses at 3 or 4 temperatures at a time, typically some 5 to 10°C apart

(Robinson, 2016; Robinson et al. 2017). This means that the data is sparse and almost any model of temperature response can be fitted without any real ability to separate different models. In addition, soils are often incubated at set temperatures for quite long periods of time (days to months) over which respiration rates are measured. During this time, available carbon stocks in soil can be consumed leading to declines in respiration during the incubation (Kirschbaum, 2006). When analysing the temperature response curves derived from these longer term incubations it is difficult to differentiate between temperature and carbon availability effects on respiration (Kirschbaum, 2006). Furthermore, microbes can have rapid turnover and response times (Placella et al. 2012) and it is unclear how much adaptation occurs during longer term incubation experiments and whether this adaptation alters temperature response curves (Bradford, 2013).

In response to these uncertainties and limitations, our laboratory developed a new method that allows us to rapidly measure respiration at about 1 °C increments along a temperature gradient block (Robinson et al. in press). This technique has been tested on temperate New Zealand soils and our preliminary incubation studies demonstrate clear T_{inf} and T_{opt} well described by MMRT (Robinson, 2016; Robinson et al. 2017) (Figure 1).

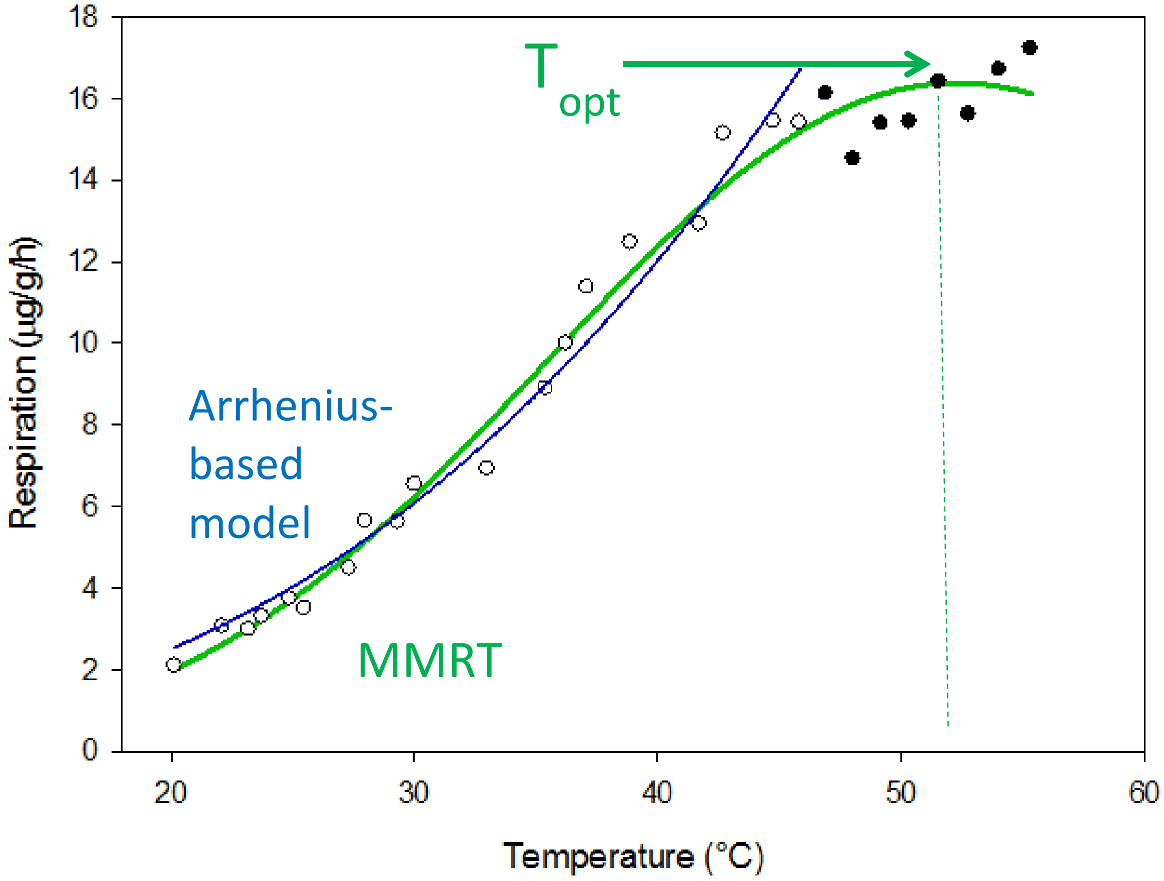

Figure 1: CO_2 respiration data from Horotiu Silt Loam, Waikato region, New Zealand, fit to Lloyd and Taylor (Arrhenius-derived function) (blue) and MMRT (green) functions. Note MMRT clearly fits the temperature optimum and lower temperatures observed over previous models.

The Antarctic Science Bursary grant allowed an extension of this research to a high latitude Antarctic soil ecosystem. The temperature sensitivity of soil microbial respiration was investigated at seven sites across a transect of penguin-influenced soils at Cape Adare (Figure 2). The transect included ultra-eutrophic (nutrient rich/moisture abundant) sites (active penguin colony), abandoned penguin colony sites, and ultra-oligotrophic (nutrient poor/moisture limited) sites never influenced by penguins. The high concentrations of organic matter and nutrients common to penguin-influenced soils are thought to stimulate biology and associated biochemical fluxes compared to surrounding uninfluenced nutrient poor soils (Wall and Virginia, 1999; Ball et al. 2015). The rate of CO_2 evolution during laboratory incubation experiments was used as an index for microbial activity. This research was the first test of MMRT on soils of extremely cold environments and we hypothesized that MMRT will better predict the temperature sensitivity of respiration than existing models and could alter estimates of C cycling in the high latitudes during a warming climate.

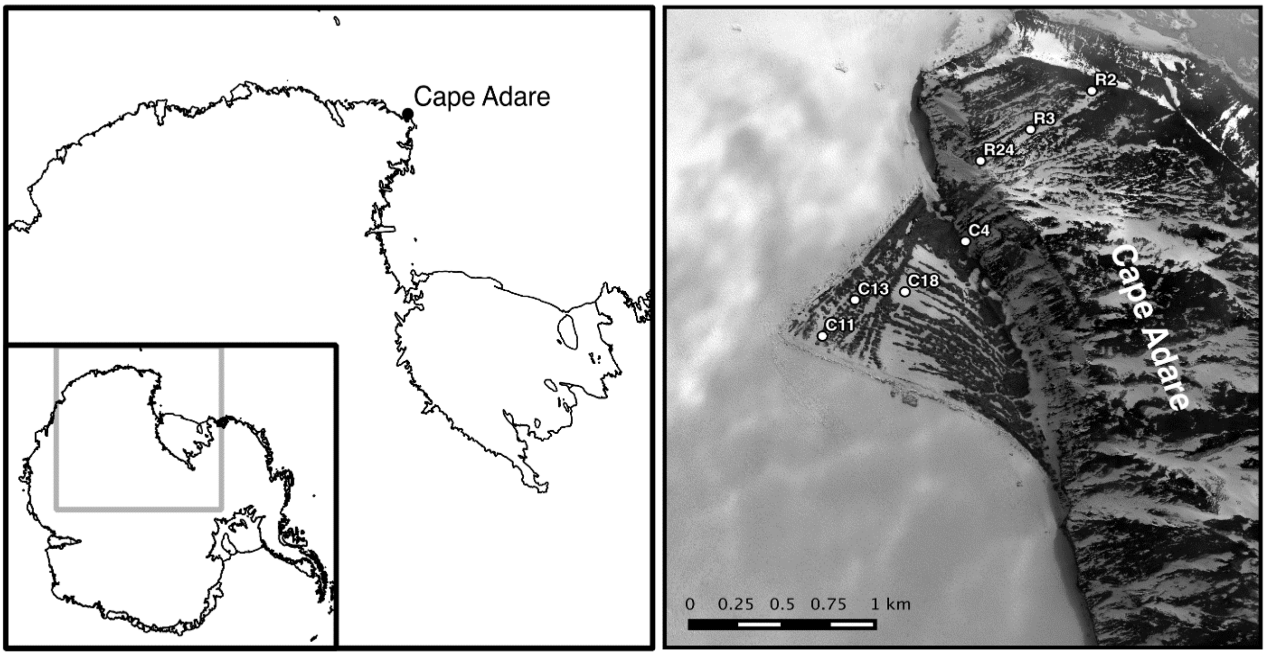

Figure 2: Transect of penguin influenced soils, showing colony "C" and ridge "R" sites, Cape Adare, Northern Victoria-Land, Antarctica (Map courtesy of Mafalda Baptista).

Location and methods

Cape Adare, northern Victoria-Land, comprises one of the largest Adélie penguin colonies in Antarctica, an estimated 250,000 breeding pairs. It is thought that penguins have been active at Cape Adare for over 2000 years (Emslie et al. 2014). Much of the foreland area of Ridley Beach is occupied by nesting Adélie penguins and penguin guano binds to the underlying gravels together (Harrowfield, 2006). Consequently vast deposits of penguin guano form ornithogenic soils. Ridley Beach backs onto a protalus rampart and behind this are steep cliffs of basaltic flows and tuffs, rising to approximately 350 m (Harrowfield, 1992). Soils in the area range from Lithic Anhyorthels on the ridge sites to Ornithogenic Typic Haplorthels and Ornithogenic Typic Aquorthels on the mound and intermound sites respectively.

Transect sites and chemical analyses

To test the temperature sensitivity of sites of different penguin activity seven sites along an 2 km transect were sampled during the summer of 2015 (Figure 2). Sites C13 and C18 were high activity sites within the active nesting areas. C11 and C4 were medium to low activity sites, areas of obvious penguin traffic, but not active nest sites. Sites R24, R3, and R2 were located on the unoccupied ridge where there is no evidence of past penguin activity (Figure 2). Soil was aseptically collected from each site, frozen at -20 °C, and transported back to New Zealand for processing. Soil water content, soil pH, electrical conductivity, Total N and Total C contents were determined on each sample.

Respiration incubations

The temperature-gradient block, an aluminium block (1400 mm long x 130 mm wide x 190 mm high) heated at one end and cooled with recycled anti-freeze through a chilled water bath at the other end (Figure 3), was used to incubate samples between a temperate gradient of -2 °C to +30 °C. Seven

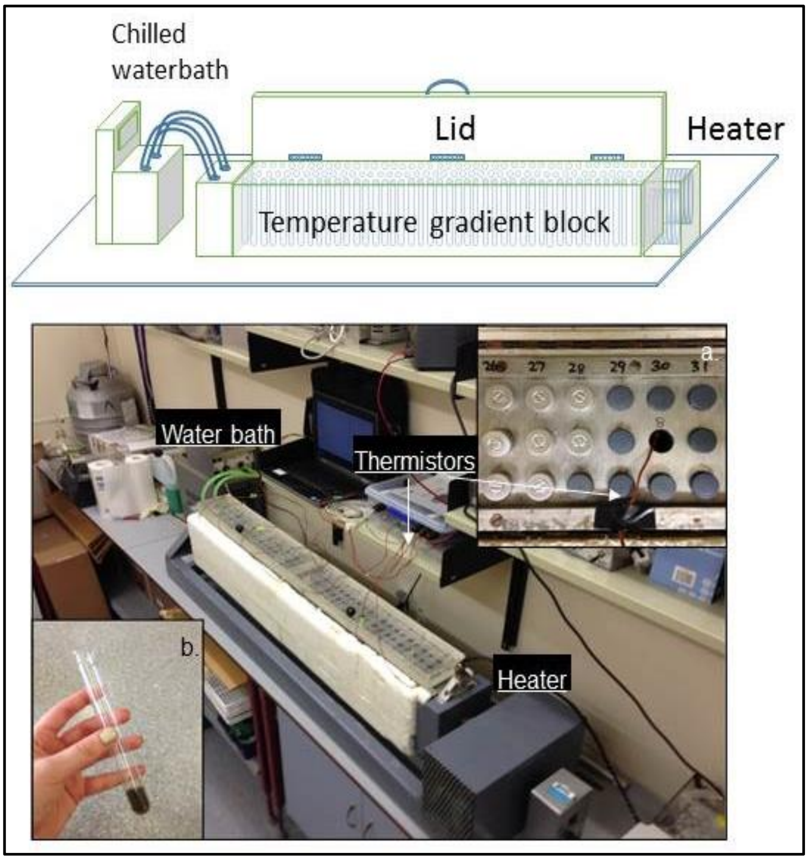

Figure 3: Temperature gradient block used for the incubation of soil samples; aluminium block attached to a refrigerated water bath (containing antifreeze) and an electric element at the other end of the block to create a temperature gradient within the metal. The sides of the aluminium block are wrapped in 2 cm thick polystyrene sheets to increase the efficiency of the temperature control. (a) sealed and crimped Hungate tubes in place. (b) soil in Hungate tube.

temperature thermistors were placed evenly along the block to record temperature at each position and previous studies using this instrument by Robinson (2016) and Robinson et al. (2017) showed that the temperature gradient was strongly linear with distance, very stable and varied by less than 1°C at each position. Respired CO_2 was allowed to accumulate for 24 hours at which point a sample of headspace gas (1 mL) was taken through septa while the tubes were still in the temperature-gradient block. Samples were injected into an infra-red gas analyser for CO_2 analysis. The area under the curve (maximum integration value) was recorded for each sample injection and used to calculate CO_2 concentration by comparison to a standard curve. CO_2 production rates were calculated taking into account oven dry soil weight, incubation time, headspace volume, and adjusting for the blank, and expressed on an oven-dry weight basis. MMRT and the Arrhenius function was applied to the observed temperature response curves to constrain the T_{opt} and predict the temperature sensitivity of respiration. The temperature at which respiration was most sensitive to increasing temperature (T_{inf}) were determined (Table 1, Figure 4)

Results and relevance

Soil respiration varied across the transect with fluxes inside the colony ranging over two orders of magnitude from higher than the unoccupied sites outside the colony (Table 1, Figure 4). Penguin activity influenced all soil properties, with higher %C, %N, EC, and soil moisture content found in the active colony sites and sites with moderate penguin activity (thoroughfare areas). For most of these properties the unoccupied ridge sites had the lowest soil property values (Table 1).

Table 1. Soil chemical data, respiration rate (Rs) at 10 and 20 °C, and T_{opt} and T_{inf} values from MMRT model

Site	**Landscape position and penguin activity**	**pH**	**EC**	**Total OC**	**H_2O**	**Rs @10°C**	**Rs @20°C**	**T_{opt}**	**T_{inf}**
			µS cm^{-1}	**%**	**%**	**µg C g^{-1} hr^{-1}**		**(°C)**	
C11	High energy beach, mod. penguin activity	7.84	3110	0.30	4.75	1.40	1.77	40.11	21.06
C13	Beach ridge, occupied colony	7.53	18950	16.42	38.04	2.66	4.93	52.99	28.06
C18	Beach ridge, occupied colony	6.94	4470	1.00	15.46	6.19	9.21	49.01	23.52
C4	Edge of scree slope, low penguin activity	6.85	517	0.26	5.17	3.73	5.63	43.30	20.22
R24	Ridge site, no penguin influence	6.89	596	0.10	1.64	0.06	0.13	53.46	28.76
R3	Ridge site, no penguin influence	6.90	258	0.10	3.58	0.07	0.10	48.71	27.23
R2	Ridge site, no penguin influence	6.85	589	0.10	4.67	0.02	0.09	56.50	33.35

Average respiration rates for both the colony and ridge sites were fitted with the MMRT model (Figure 4). The average T_{inf} for colony sites was 23 °C compared with ridge sites at 30 °C. There was a marginally significant difference in temperature sensitivity (T_{inf}) between colony and ridge sites (*p-value* = 0.052) (Figure 4).

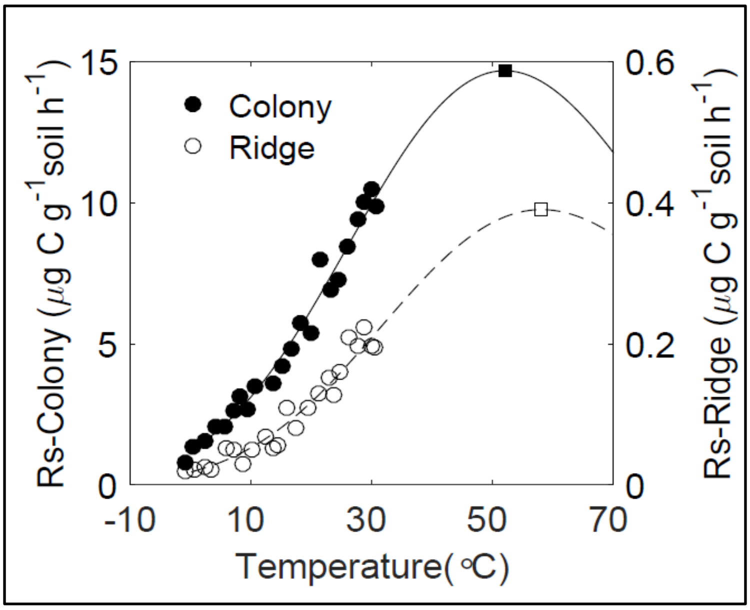

Figure 4: Respiration rate averaged for both the colony and ridge sites fitted with the MMRT model. Note different scales. Black square is the average T_{opt} for the colony sites, open square, the average for the ridge sites

Results suggest colony sites appear more temperature sensitive and may be more responsive to temperature increases than ridge sites (Table 1, Figures 3 and 4). This may have implications for nutrient cycling as some high latitude regions are warming up to two times faster than the global average. Further research is required to determine the factors controlling T_{inf} and why the colony and ridge sites have different temperature sensitivities. Past studies have indicated penguin colonies are significant sources for atmospheric N_2O, CO_2, and CH_4 and have shown increased greenhouse gas emissions during freeze-thaw cycles (Zhu et al. 2008, 2009, 2012). In coastal Antarctica freeze-thaw cycle frequency is considerably higher during the summer and unstable weather conditions and it remains unclear whether climate change will amplify effects (Yeageau and Kowalchuk, 2008). Furthermore, the number of animal colonies is potentially large and therefore any climate-induced changes to the annual fluxes of greenhouse gas from these hotspots is critical to identify.

This research is the first step in understanding the temperature sensitivity of Antarctic soil ecosystems and I would like to thank the Antarctic Science Bursary for the opportunity to carry out this work. This work has been presented at the SCAR Open Science Conference in Malaysia 2016, and it is my intent that the results of this research be submitted to the Antarctic Science journal.

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