Soil Biology & Biochemistry 57 (2013) 248–255

Contents lists available at SciVerse ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Warming constrains bacterial community responses to nutrient inputs in a southern, but not northern, maritime Antarctic soil

Paul G. Dennis[a,1], Kevin K. Newsham[b], Steven P. Rushton[c], Victoria J. Ord[c], Anthony G. O'Donnell[c,d], David W. Hopkins[a,e,*]

[a] School of Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, UK
[b] Ecosystems Programme, British Antarctic Survey, Madingley Road, Cambridge CB3 0ET, UK
[c] School of Biology, Newcastle University, Newcastle Upon Tyne NE1 7RU, UK
[d] University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia
[e] School of Life Sciences, Heriot-Watt University, Edinburgh EH14 4AS, UK

A R T I C L E I N F O

Article history:
Received 25 February 2012
Received in revised form
10 July 2012
Accepted 13 July 2012
Available online 1 August 2012

Keywords:
Antarctica
Climate change
Gram negative bacteria
Gram positive bacteria
Nutrient input
Open top chambers (OTCs)
Substrate amendments
Warming
Water application

A B S T R A C T

We investigated the effects of increased soil temperature, water and nutrient availability on soil bacterial communities at Wynn Knolls on Signy Island (60 °S) in the northern maritime Antarctic and at Mars Oasis (71 °S) in the southern maritime Antarctic. After 10–12 months, analyses of the concentrations of ester linked fatty acids (ELFAs) in soil indicated that bacterial communities responded positively to single applications of substrates at both locations, with 20% and 49% increases in total Gram positive and Gram negative bacterial markers, respectively, in response to the application of tryptic soy broth (TSB; a complex substrate containing organic carbon and nitrogen, plus other nutrient elements) at Wynn Knolls, and 120% and 44% increases in Gram positive bacterial markers at Mars Oasis in response to the application of TSB and the amino acid glycine (a relatively simple source of organic carbon and nitrogen), respectively. Responses to the warming treatment were not detected at Wynn Knolls, where open top chambers (OTCs) increased mean monthly soil temperatures by up to 0.7 °C, but at Mars Oasis, where OTCs increased monthly soil temperatures by up to 2.4 °C, warming led to 41% and 46% reductions in the concentrations of Gram positive bacterial markers in soil to which glycine and TSB had been applied, respectively. Warming also led to 55% and 51% reductions in the ratio of Gram positive to Gram negative markers in soils at Mars Oasis to which glycine and TSB had been applied. These data suggest that warming may constrain the responses of bacterial communities to carbon and nitrogen inputs arising from dead plant matter entering maritime Antarctic soils in future decades.

1. Introduction

Mean annual air temperatures in the maritime Antarctic, particularly along the western Antarctic Peninsula, have risen at rates of up to 0.4 °C $decade^{-1}$ over the past 50–100 years (Adams et al., 2009), which is approximately double the rate at which global mean surface temperature has increased over the last 30 years (*c.* 0.2 °C $decade^{-1}$; Hansen et al., 2006). The warming of maritime Antarctic terrestrial ecosystems is having widespread effects on the physical environment: along with the collapse of ice shelves and the retreat of glaciers, changes to precipitation patterns have occurred, with increases in snow accumulation having been recorded in recent decades (Thomas et al., 2008; Adams et al., 2009). In addition to these changes to the physical environment, the warming of maritime Antarctic terrestrial ecosystems is also altering the cover of plant species. For example, the population sizes of *Deschampsia antarctica* and *Colobanthus quitensis*, the two native Antarctic higher plant species, increased by 7–26 fold between the mid 1950s and early 1990s (Fowbert and Smith, 1994; Smith, 1994), and a new southern limit for flowering plants in Antarctica has recently been established (Convey et al., 2011). The expansion of maritime Antarctic plant populations over future decades is likely to enhance and alter nutrient inputs to soils (Hill et al., 2011), with the input of carbon and nitrogen to these soils most probably leading to significant increases in soil microbial biomass (Davey and Rothery, 1992; Malosso et al., 2005). Similar

* Corresponding author. School of Life Sciences, Heriot-Watt University, UK. Tel.: +44 (0) 131 451 3452.
E-mail address: david.hopkins@hw.ac.uk (D.W. Hopkins).
[1] Current address: Australian Centre for Ecogenomics, and Advanced Water Management Centre, The University of Queensland, Brisbane, QLD 4072, Australia.

0038-0717/$ – see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.soilbio.2012.07.009

increases in nutrient inputs from microbial and cryptogam sources (via photosynthesis and nitrogen fixation) have also been postulated for dry valleys soils in continental Antarctica (Novis et al., 2007; Hopkins et al., 2008). These predictions are supported by studies showing larger microbial biomass in vegetated than in non-vegetated maritime Antarctic soils (Yergeau et al., 2007a).

Warming also influences the size and composition of bacterial communities in maritime Antarctic soils. For example, the deployment of screens over soil at Signy Island in the South Orkney Islands increased the abundances of Cyanobacteria in soil by 2–17 fold, with substantial increases in the biomass of *Phormidium* and *Nostoc* spp. in warmed soils (Wynn-Williams, 1996). Recently, it has been shown that bacteria are more frequent in vegetated soils that have been passively warmed with open top chambers (OTCs) at two sites in the maritime Antarctic, and that warming increases the ratio of Alphaproteobacteria to Acidobacteria (Yergeau et al., 2011). At present, however, these are the only data on soil bacterial responses to warming in natural maritime Antarctic environments, and, importantly, nothing is known of the combined effects of warming and nutrient inputs on the bacterial communities of maritime Antarctic soils. Given that soil bacteria are pivotal to ecosystem processes, such as the mineralisation of nutrients from dead organic matter, the current lack of data on the responses of these microbes to warming and nutrient input in the region represents a significant gap in knowledge.

Here we report the results of an experiment designed to test the hypothesis that warming, in combination with either nutrient input or water application, would influence Antarctic soil bacterial communities. The study was undertaken at two sites with different climates, one on Signy Island in the northern maritime Antarctic, and the other on Alexander Island in the southern maritime Antarctic. Both of the locations studied have warmed in recent decades: air temperature at Signy Island increased by 1 °C between 1950 and 1990 (Quayle et al., 2002) and surface temperatures at a site 240 km to the south of Mars Oasis are estimated to have increased by 2.7 °C between the mid 1940s and the late 2000s (Thomas et al., 2009). We used OTCs to warm soil to temperatures that are predicted to be reached during the next two to five decades at either location, given these current rates of warming (Adams et al., 2009).

2. Materials & methods

2.1. Site descriptions

The experiment was established at Wynn Knolls (60° 41′ 56″ S, 45° 38′ 10″ W) on Signy Island in the South Orkney Islands and at Mars Oasis (71° 52′ 42″ S, 68° 15′ 00″ W) on south-eastern Alexander Island in the southern maritime Antarctic (Fig. 1). Wynn Knolls is situated at *c.* 500 m from the western shoreline of Signy Island at an altitude of 199 m above sea level. The island has an oceanic climate, characterised by dense cloud cover during the austral summer (7.2–7.4 oktas; Collins et al., 1975). Precipitation in the northern maritime Antarctic, where Signy Island is located, varies between 350 mm and 500 mm water equivalents per annum, with much falling as rain in the austral summer (Smith, 1984). Soils on the island are derived from schists, amphibolites and marbles (Collins et al., 1975). The more southerly site, Mars Oasis, is formed from a contact moraine between the George VI ice shelf and the south-eastern coast of Alexander Island. The oasis, consisting of areas of till, fluvial and lacustrine sediments (Sugden and Clapperton, 1981), with streams and ponds forming during the austral summer, is located at an altitude of 20 m above sea level. Soil at the site is derived from the sandstones and mudstones of Two Step Cliffs massif. The western Antarctic Peninsula, and in particular its southern reaches, have a relatively continental climate, with frequent periods of cloudless skies during the summer. Precipitation in the southern maritime Antarctic is *c.* 350 mm water equivalents per annum, most of which falls as snow (Smith, 1984). The soils at Wynn Knolls and Mars Oasis had similar chemical properties, with mean (±SEM) pH values of 7.5 ± 0.15 and 7.3 ± 0.12, electrical conductivities of 29.4 ± 2.9 μS and 31.9 ± 2.7 μS, NO_3^-–N concentrations of 0.033 ± 0.019 mg kg^{-1} and 0.007 ± 0.007 mg kg^{-1}, and NH_4^+–N concentrations of 0.138 ± 0.065 mg kg^{-1} and 0.095 ± 0.015 mg kg^{-1}, respectively (Dennis et al., 2012). The concentrations of both total organic carbon and total nitrogen in the soils were very small, with organic carbon concentrations of 0.140 ± 0.010% and 0.260 ± 0.020%, and nitrogen concentrations of 0.038 ± 0.004% and 0.020 ± 0.002% in the two soils, respectively (Dennis et al., 2012).

2.2. Manipulation experiment and sampling

Three treatments were applied at each site in factorial combination. Soil was warmed using OTCs, water was applied to soil to simulate short-term changes in moisture availability arising from melting snow and ice, and growth substrates were added to alter carbon and nitrogen availability to soil microbes. The addition of the substrates broadly simulated increases in soil nutrients associated with organic inputs from algae and cyanobacteria, in a way directly analogous to a corresponding experiment in the dry valleys region of continental Antarctica (Hopkins et al., 2008). In order to apply these treatments, 64 circular plots of 1 m diameter were established at each site within a 17 m × 17 m area that was devoid of vegetation. Thirty-two of the plots were covered with conical clear polycarbonate OTCs of 1 m diameter (see Fig. 1b in Marion et al., 1997). The moisture content of the soil in 16 of the chambered plots and in 16 of the control plots was adjusted to 100% of water-holding capacity in the surface 5 cm of soil using water purified with ion exchange columns (Fistreem, UK). For each temperature–water combination, four replicate plots were each

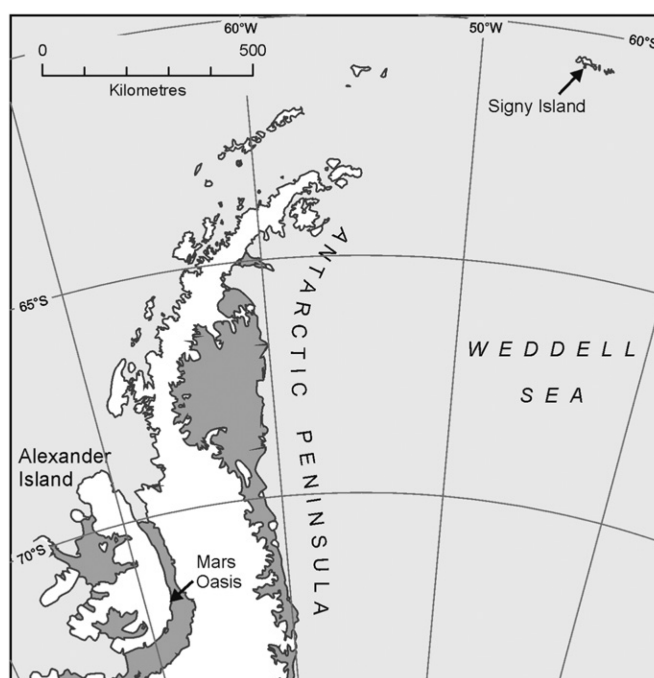

Fig. 1. Map of the maritime Antarctic, indicating the locations of Signy Island, Alexander Island and Mars Oasis.