Soil Biology & Biochemistry 43 (2011) 1333–1340

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Soil bacterial growth and nutrient limitation along a chronosequence from a glacier forefield

Hans Göransson [a,b,*], Harry Olde Venterink [a], Erland Bååth [c]

[a] Institute of Integrative Biology, ETH Zurich, Universitätstrasse 16, CHN 8092 Zurich, Switzerland
[b] School of the Environment and Natural Recourses, Bangor University, Bangor LL 57 2UW, UK
[c] Microbial Ecology, Department of Biology, Ecology Building, Lund University, SE-223 62 Lund, Sweden

ARTICLE INFO

Article history:
Received 4 October 2010
Received in revised form
1 February 2011
Accepted 6 March 2011
Available online 21 March 2011

Keywords:
Leucine incorporation
Carbon quality
Microbial activity
Chronosequence
C:N:P stoichiometry
Soil development

ABSTRACT

Resource availability and limiting factors for bacterial growth during early stages of soil development (8–138 years) were studied along a chronosequence from the glacial forefield of the Damma glacier in the Swiss Alps. We determined bacterial growth (leucine incorporation) and we investigated which resource (C, N or P) limited bacterial growth in soils formed by the retreating glacier. The latter was determined by adding labile sources of C (glucose), N and P to soil samples and then measuring the bacterial growth response after a 40 h incubation period. Bacterial growth increased with increasing soil age in parallel with the build up of organic matter. However, lower bacterial growth, when standardized to the amount of organic C, was found with time since the glacier retreat, indicating decreasing availability of soil organic matter with soil age. Bacterial growth in older soils was limited by the lack of C. The bacteria were never found to be limited by only N, only P, or N + P. In the youngest soils, however, neither the addition of C, N nor P singly increased bacterial growth, while a combination of C and N did. Bacterial growth was relatively more limited by lack of N than P when the C limitation was alleviated, suggesting that N was the secondary limiting resource. The availability of N for bacterial growth increased with time, as seen by an increased bacterial growth response after adding only C in older soils. This study demonstrated that bacterial growth measurements can be used not only to indicate direct growth effects, but also as a rapid method to indicate changes in bacterial availability of nutrients during soil development.

1. Introduction

Glaciers in the Alps have been withdrawing since the little ice age ended in 1850. This has resulted in chronosequences, with increasingly older soils with distance from the ice, that can be used to study soil formation, and microbial and vegetation succession (Matthews, 1992). Immediately following the withdrawal of the glacier, the rocky 'soil' is poor in organic material. The concentration of carbon (C) and nitrogen (N) is low, whereas phosphorus (P) can be higher but will be present mainly as apatite (Matthews, 1992). During the first 100 years after deglaciation, the concentration of organic matter, and thus also those of total C and N, increase exponentially in the soil, after which they stabilise and eventually reach plateaus (Jacobson and Birks, 1980; Matthews, 1992; Walker, 1993; Chapin et al., 1994). In contrast, total P usually declines with soil development through weathering processes and leaching (Walker and Syers, 1976). Thus, the limiting nutrient for plant growth may shift from N to P with time, although only after several hundred to thousand of years (Chapin et al., 1994; Wardle et al., 2004).

Even though the changes in total amounts of C, N and P in the soil during the early soil development, and changes in limiting nutrients during plant succession, are rather well known, changes in the available amounts of nutrients for microorganisms have been less studied. However, it is well known that the size of the microbial biomass and activity will be determined by the amount of organic matter in soil (Wardle, 1992). The increasing concentration of organic matter with soil age along a retreating glacier transect will thus likely result in increased microbial activity, e.g. respiration, and increased microbial biomass (Insam and Haselwandter, 1989; Wardle et al., 2004). However, at the same time as the soil

* Corresponding author. School of the Environment and Natural Recourses, Bangor University, Bangor LL 57 2UW, UK. Tel.: +44 1248 383056; fax: +44 1248 354997.
E-mail addresses: h.goransson@bangor.ac.uk (H. Göransson), harry.oldeventerink@env.ethz.ch (H. Olde Venterink), Erland.Baath@mbioekol.lu.se (E. Bååth).

0038-0717/$ – see front matter
doi:10.1016/j.soilbio.2011.03.006

organic matter concentration will increase, a larger proportion of it will become older and more resistant to decomposition, resulting in soil organic matter becoming less available for microbial use. Microbial activity normalized to soil organic matter, that is, measured as respiration per soil organic matter or soil organic C, will therefore likely decrease with soil age along a glacier chronosequence (Schipper et al., 2001; Tscherko et al., 2003).

The amount of available nutrients for soil microbes is difficult to estimate. There are no standardised extraction methods available to determine microbially available C, N and P fractions. Methods using respiration as a proxy for microbial growth to indicate available N or P usually rely on initial additions of large amounts of glucose (Nordgren, 1992), and thus the relation between C availability and availability of other nutrients cannot be studied. An alternative approach is to directly estimate bacterial growth in soil. Aldén et al. (2001) described such a method, which later has been used to study limiting factors for bacterial growth in different soils (Demoling et al., 2007, 2008; Rinnan et al., 2007). The method is based on the addition of single nutrients or of nutrient combinations, followed by the determination of bacterial growth using leucine incorporation. The primary limiting nutrient is identified as the nutrient that increases bacterial growth in comparison to an unamended control soil, at the same time as there are no or only a minor increase in bacterial growth adding any other nutrients. Also, by combining the addition of different nutrients in a factorial design, it may be possible to determine which nutrient is secondary in limiting growth; i.e., the nutrient that further increases growth when limitation by the primary limiting nutrient is alleviated (Demoling et al., 2007; Rinnan et al., 2007). Thus, besides identifying which nutrient has the lowest availability, you also get an indication of the relative availability of other nutrients (Demoling et al., 2008).

Yoshitake et al. (2007) found that close to a retreating glacier, additions of both C and N were necessary to increase microbial respiration, whereas further away from the glacier only C addition was necessary. This suggests that microbially available N builds up faster in soil than microbially available C, and agrees with observations that microbial growth is primary limited by C and secondary limited by N in most developed soils (Paul and Clark, 1996; Demoling et al., 2007). P limitation of microbial growth has mainly been found in soils with high P sorption capacity (Aldén et al., 2001; Ilstedt and Singh, 2005; Ehlers et al., 2010), but mostly P was only the third limiting nutrient (Demoling et al., 2007).

We investigated resource availability and limiting nutrients for bacterial growth along a chronosequence of soil development in the forefield of the Damma glacier in Switzerland. To our knowledge, this is the first study of bacterial growth limitation along such a chronosequence. We measured bacterial growth and factors limiting bacterial growth by adding C, N and P to soil samples. We tested five hypotheses:

1) Bacterial growth per gram of soil will increase with soil age in parallel with increased soil organic C concentration.
2) Bacterial growth calculated per organic C will decrease with soil age, due to a smaller proportion of the accumulated organic matter being of an easily available form.
3) Bacterial growth will be primarily limited by C. This will be reflected by increased bacterial growth upon C addition, but no increase upon single additions of N or P.
4) Bacterial growth will be secondarily limited by N. This will be seen as a larger increase in bacterial growth after adding C in combination with N, than after C in combination with P.
5) The 'extent of C-limitation' will increase with soil age, due to an decreasing proportion of the accumulated C being in an available form, and also while N will build up with time. This will be seen as an increasing growth response of adding only C with age of the soils.

2. Methods

2.1. Site description

The Damma glacier (8° E 27′30″, 46°N 38′00″) is situated in the Swiss Alps (Fig. 1). The altitude is 2054 m at the front of the glacier and 1920 m at 1 km from the ice, where the oldest sampling site was situated. From October 2007 to October 2009 the mean annual temperature measured on the forefield was 2.2 °C, and the mean annual precipitation was 1781 mm year (J. Magnusson, unpublished data). The Damma glacier has retreated approximately 1000 m since about 1850 (data from the Swiss Glacier Monitoring Network; http://glaciology.ethz.ch/swiss-glaciers/glaciers/damma.html). During this period the retreat has been interrupted, and the glacier advanced twice, once between 1911 and 1928 and once between 1972 and 1991. Thus, the forefield can be divided into three areas: (1) less than 19 years, (2) 58–81 years, and (3) 109–150 years, each

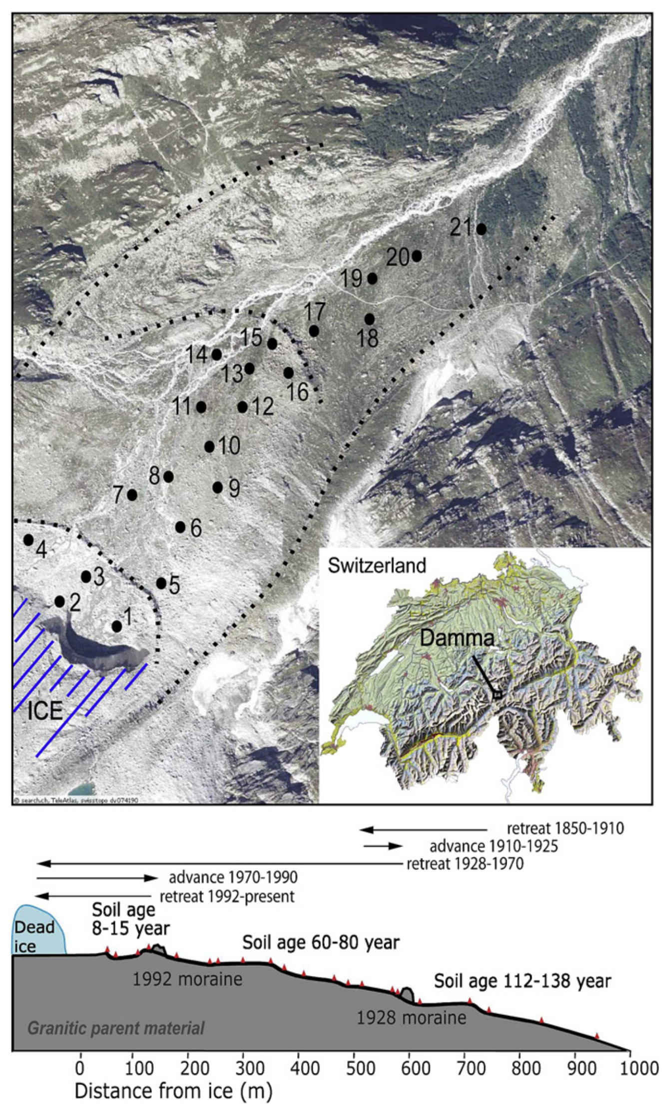

Fig. 1. The Damma glacier forefield with marked sampling sites and glacier advances and retreats.