Heterotrophic microbial communities use ancient carbon following glacial retreat

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When glaciers retreat they expose barren substrates that become colonized by organisms, beginning the process of primary succession. Recent studies reveal that heterotrophic microbial communities occur in newly exposed glacial substrates before autotrophic succession begins. This raises questions about how heterotrophic microbial communities function in the absence of carbon inputs from autotrophs. We measured patterns of soil organic matter development and changes in microbial community composition and carbon use along a 150-year chronosequence of a retreating glacier in the Austrian Alps. We found that microbial communities of recently deglaciated terrain differ markedly from those of later successional stages, being of lower biomass and higher abundance of bacteria relative to fungi. Moreover, we found that these initial microbial communities used ancient and recalcitrant carbon as an energy source, along with modern carbon. Only after more than 50 years of organic matter accumulation did the soil microbial community change to one supported primarily by modern carbon, most likely from recent plant production. Our findings suggest the existence of an initial stage of heterotrophic microbial community development that precedes autotrophic community assembly and is sustained, in part, by ancient carbon.

Keywords: microbial communities; organic matter; carbon; chronosequence

1. INTRODUCTION

The global retreat of glaciers is receiving much attention, especially as a signal of climate change (Oerlemans 2005). When glaciers retreat they expose barren substrates that become colonized by organisms, beginning the process of primary succession. The common view is that primary succession is started by autotrophs, including algae, mosses, lichens and higher plants, owing to a lack of carbon for heterotrophic organisms (Walker & del Moral 2003). Fixation of carbon by autotrophs then leads to the build-up of organic matter providing resources for the development of heterotrophic communities that drive ecosystem processes of decomposition and nutrient cycling (Bardgett & Walker 2004; Bardgett et al. 2005). Recent studies, however, show that diverse heterotrophic microbial communities occur in newly exposed glacial substrates before autotrophic communities have established (Tscherko et al. 2003). This study aimed to examine how heterotrophic microbial communities of recently deglaciated terrain function in the absence of carbon inputs from autotrophs, and how microbial carbon use changes as succession proceeds and autotroph-derived organic matter accumulates in soil. This was tested by measuring patterns of soil organic matter development and changes in microbial community composition and carbon use along a 150-year chronosequence of a retreating glacier in the Austrian Alps.

2. MATERIAL AND METHODS

We sampled soils from the foreland of the Odenwinkelkees glacier (47°06’ N, 12°39’ E), above the treeline (2050–2200 m) in the Austrian Alps. The glacier has been retreating since 1850 at an average rate of 10 m yr\(^{-1}\), creating a chronosequence of soil development over 1.5 km. The glacial moraine is composed of feldspathic rocks, mica schist and gneiss; soils are leptic regosols.

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The proportion of recalcitrant organic matter, measured as weight loss due to thermal decomposition of discrete components of organic matter, was determined by thermal analysis (thermo-gravimetry and differential scanning calorimetry) using a Netzsch thermal analyser STA 449C Jupiter (Lopez Capel et al. 2005).

3. RESULTS

Very little (less than 0.1 mg g$^{-1}$) organic carbon was detected in substrates recently exposed by glacial retreat (table 1), and the carbon that was present was isotopically distinct from that found in older sites (figure 1b). Radiocarbon dating of soil organic matter of older sites (more than 50 years ice free) revealed that it was relatively young, being derived from recent plant inputs (>100% modern) (figure 1a). In contrast, organic matter of the youngest site was significantly enriched in $^{13}$C, relative to that of the older sites, with an average radiocarbon age of more than 7000 years, suggesting that it was derived from ancient carbon (figure 1a,b).

The soil of the recently deglaciated site had a much greater humin concentration than that of older sites, indicating that the ancient carbon was mostly recalcitrant (table 1). Thermal analysis demonstrated that 58.8% of the organic carbon of the youngest site was recalcitrant, declining to 26.9% at the oldest site (table 1). The average $^{13}$C age of carbon respired by heterotrophic microbes was 1282 and 644 years for the 3- and 18-year ice-free sites, respectively, whereas at the older sites (i.e. more than 50 years ice free) respired carbon was derived primarily from modern sources, most likely from recent plant production, but potentially also carbon fixed by cyanobacteria (figure 1c,f). Ordination analysis of PLFA data revealed that microbial communities of the two younger sites were significantly ($F_{4,24}=24.1$, $p<0.0001$) different from those of older (i.e. more than 50 years ice free) sites (figure 2a). The size of the microbial biomass, measured as total PLFA ($F_{4,24}$, $p<0.0001$), and the fungal-to-bacterial PLFA ratio ($F_{4,24}$, $p<0.02$), a measure of the abundance or fungi relative to bacteria, were at their lowest at the youngest site (figure 2b,c).

4. DISCUSSION

Recently exposed glacial substrates are typically skeletal in nature and have negligible organic matter contents (Bardgett & Walker 2004). Consistent with this, we found little carbon (less than 0.1 mg g$^{-1}$) in recently exposed glacial substrates. The carbon that was present, however, was chemically distinct from that of sites that had been ice free for more than 50 years, being much older, with an average radiocarbon age more than 7000 years, and dominated by recalcitrant organic matter. The organic matter of older sites was more abundant and younger, with a lower proportion of recalcitrant carbon. This build-up of organic matter is typical of primary succession, reflecting the increasing input of litter (root and shoot) from the developing plant community and the fixation of carbon by cyanobacteria (Walker & del Moral 2003). Probable sources of the old carbon in recently exposed sites were organic matter that was previously beneath the glacier (figure 1c,d) and that from the surface of the glacier (cryoconite). While both these sources had approximately the same carbon isotope signature, they are likely to have different origins. Organic matter beneath the glacier most likely contains remnants of preglacial soils and/or geological carbon, whereas that on the glacier surface might include $^{14}$C-dead carbon from fossil fuel burning (black carbon) and modern carbon, such as algal-derived carbon (Kasťovská et al. 2006).

While little carbon was present in recently exposed glacial substrates, it supported a functioning microbial community, as evidenced by the detection of fatty acids from living bacteria and fungi. Moreover, the microbial community composition of recently exposed substrates differed from that of older substrates with a significantly greater abundance of bacteria relative to fungi. This was evidenced by the relatively low fungal-to-bacterial PLFA ratio of the youngest site, which subsequently increased along the chronosequence; this pattern is consistent with the idea that the abundance of fungi relative bacteria within the soil microbial community increases as succession proceeds and resources become more available (Bardgett et al. 2005). The average age of carbon respired by microbes of the two youngest sites was relatively old. In contrast, respired carbon of older sites was derived primarily from modern sources, most likely from recent plant production. These data suggest that ancient and recalcitrant carbon, along with modern carbon (e.g. cyanobacteria fixed carbon), sustains the microbial community of recently exposed glacial substrates, whereas microbial communities of older sites are sustained mainly by modern carbon from recent plant production. Ancient carbon, along with modern sources, has also been shown to sustain heterotrophic microbial communities in low carbon ecosystems of Antarctica (Hopkins et al. 2006). Our findings highlight

Table 1. Changes in soil carbon content and organic matter quality with substrate age. (Values in parentheses are standard errors ($n=0$).)

<table>
<thead>
<tr>
<th>years ice free</th>
<th>total C (% DM)</th>
<th>humin (% OM)</th>
<th>recalcitrant organic matter by thermal analysis (% OM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>0.094 (0.03)</td>
<td>91.0</td>
<td>58.8</td>
</tr>
<tr>
<td>18</td>
<td>0.22 (0.06)</td>
<td>70.0</td>
<td>43.2</td>
</tr>
<tr>
<td>49</td>
<td>0.51 (0.27)</td>
<td>62.7</td>
<td>38.6</td>
</tr>
<tr>
<td>101</td>
<td>0.90 (0.25)</td>
<td>62.2</td>
<td>31.5</td>
</tr>
<tr>
<td>145</td>
<td>1.12 (0.39)</td>
<td>47.9</td>
<td>26.9</td>
</tr>
</tbody>
</table>
the significance of this carbon source for microbial functioning in low carbon alpine environments.

Collectively, our data provide new insights into the functioning of microbial communities during early stages of succession in glacial forelands, highlighting the role of old and recalcitrant carbon as an energy source in these low carbon environments. Our data are also of relevance for understanding primary community assembly, showing that community assembly by autotrophs is preceded by an initial heterotrophic phase (Hodkinson et al. 2002).

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Bardgett, R. D., Hobbs, P. J. & Frostegård, Å. 1996 Changes in fungal: bacterial biomass ratios following...


