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Selective transport of plant root-associated bacterial populations in agricultural soils upon snowmelt

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ABSTRACT

Plants introduce abundant carbon into soils, where it is mineralised and sequestered. Proportions of this fresh organic carbon introduced to top soils can be relocated to deeper soil layers and even to groundwater by event-driven transport upon heavy rainfalls or after snowmelt. It is assumed that a significant fraction of this flux involves biocolloids and possibly microbial biomass itself. However, the nature of such transported microbes, their origin and the mechanisms of their mobilisation are still poorly understood. Here, we provide primary evidence that specific microbial populations are exported from top soils upon seepage events. At an experimental maize field, we have analysed the composition of mobilised bacterial communities collected in seepage water directly after snowmelt in winter at different depths (35 and 65 cm), and compared them to the corresponding bulk soil microbiota. Using T-RFLP fingerprinting and pyrotag sequencing, we reveal that mostly members of the *Betaproteobacteria* (*Methylophilaceae*, *Oxalobacteraceae*, *Comamonadaceae*), the *Alphaproteobacteria* (*Sphingomonadaceae*, *Bradyrhizobiaceae*), the *Gammaproteobacteria* (*Legionellaceae*) and the *Bacteroidetes* (*Sphingobacteriaceae*) were mobilised, all characteristic taxa for the rhizoplane. This highlights the importance of preferential flow along root channels for the vertical mobilisation and transport of microbes. Although the estimated quantitative fluxes of bacterial biomass carbon appeared low, our study allows for an improved understanding of the links between top soil, subsoil, and groundwater microbiota, as well as carbon fluxes between soil compartments.

1. Introduction

Soil organic matter (SOM) is the largest active carbon pool in terrestrial environments (Kindler et al., 2009) and it is known that carbon fluxes in soil can be considerable (Giardina et al., 2005). At the same time, many central mechanisms of carbon fluxes in soils are still poorly understood (Litton and Giardina, 2008). Quantity of SOM and carbon inputs is mostly determined by plants (Kögel-Knabner, 2002), however, SOM properties like stability, aggregation and reactivity are determined by the transforming organisms, most prominently soil microbes (Deckmyn et al., 2011; Kindler et al., 2009). Besides sequestration and mineralisation, transport of SOM by seepage water from top soils to deeper zones is an important factor contributing to carbon fluxes in soils (Kindler et al., 2011). These vertical fluxes represent a significant supply of fresh carbon to deeper soil layers and to the groundwater.

The mobile organic matter pool in soils not only comprises dissolved and colloidal organic carbon, but also biocolloids like bacteria, fungi and their fragments as well as viruses (Totsche et al., 2007). The translocation of colloids and particles, frequently along preferential flow paths including biopores can mediate fast and considerable mass transfer into deeper zones. It has been speculated that translocated microbes from the top soil could be an important source of biomass for subsoils, where they may significantly contribute to microbial activities (Jaesche et al., 2006).

The general understanding of the physical factors controlling vertical carbon transport through soil has improved over the last years (Bolan et al., 2011; Kalbitz and Kaiser, 2008). Already now, there is a basic grasp of bacterial transport mechanisms in soils, mostly focused on the transport of potential pathogens to groundwater (Natsch et al., 1996). Important factors inhibiting bacterial mobilisation are retention at air–water- and soil–water-interfaces, attachment and growth in biofilms, straining and also active adhesion (Sen, 2011). Soil bacteria can move actively in soils guided by chemotaxis (Sen, 2011) or may be mobilised and

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transported passively by water flow (Unc and Goss, 2004), nematodes (Knox et al., 2004), growing roots (Feeney et al., 2006), or along fungal mycelia (Furuno et al., 2012). However, the highest fluxes of bacterial pathogens transported from upper to deeper soil layers occur after weather events producing abundant seepage water, such as long-lasting precipitation, flooding or snowmelt. Especially the detachment of top soil microbes by rain and snowmelt water with low-ionic strength is assumed to contribute to this mobilisation (Aislabie et al., 2011). Once mobilised, transport is assumed to be controlled mainly by the flow of seepage water along macropores, e.g. earth worm burrows, root channels and desiccation cracks (Natsch et al., 1996). Troxler and colleagues observed transport of amended bacteria from top soil down to depths of ~2.5 m only after heavy rainfalls (Troxler et al., 1998). The main route of transport was flow along macropores, which was confirmed also by other more recent studies (Bech et al., 2011; Jiang et al., 2010).

So, while many factors influencing the transport of carbon and bacteria over depth have been investigated, an understanding of the origin and nature of transported inherent soil bacteria, their contribution to carbon fluxes to deeper zones as well as their fate therein is currently lacking. Practically all studies on bacterial transport in soils and porous media have used only one or a few artificially amended bacterial species, and did not address mobilised natural bacterial communities. Therefore, here we investigated lysimeter samples at an experimental field site recently installed to unravel and quantify organismic and trophic carbon flow originating from maize plants (Kramer et al., 2012; Scharroba et al., 2012). We traced intrinsic bacterial communities mobilised by a snowmelt induced seepage event at different depths underneath the cropped field in late winter. Transported microbes were compared to bulk soil- and root-associated bacterial communities at corresponding depths. We hypothesise that 1) specific subsets of bacteria are selectively mobilised from the top soil and 2) the nature and composition of transported communities is controlled by the mechanisms of water flow. Furthermore, we postulate that 3) the transported bacteria contribute noticeably to net carbon flux. This work extends our current understanding of the event-driven mobilisation of microbes to deeper soils and groundwater, and has the potential to unravel translocation mechanisms of fresh plant-derived carbon inputs to deeper soils, as well as hidden links between depth-resolved microbial communities. Moreover, to the best of our knowledge, this represents the first study to systematically address the nature of a complex soil microbiota naturally mobilised by seepage water.

2. Materials and methods

2.1. The field site

Samples were taken from an experimental agricultural field located on a terrace plain of the river Leine, north–north-west of the City of Göttingen (Niedersachsen, Germany). The local climate, with a mean annual temperature of 8.7 °C and a mean annual precipitation of 645 mm, represents a temperate climate affected by the transgression from the maritime Atlantic climate on the west to the continental climate on the east. The elevation of the plane is 155–160 m a.s.l., striking towards north-west with a mean base slope of approximately 2%. According to IUSS (IUSS, 2007), the dominant soil types are Cambisols (Braunerden, KA5, 2005), Luvisols (Parabraunerden, KA5, 2005) and stagnic Luvisols (Pseudogley, KA5, 2005). Long agricultural use has severely affected the build-up of the soil profiles. The albic horizon typically found for these soils can no longer be detected in the field due to centuries of intensive tillage. In general, two plough layers (0.2 m and 0.3 m below surface) can be detected with particular strong compaction below the second plough layer: Bulk density (1.6 g cm^{-3}) in and below the second plough layer was relatively high (Supplementary Table S1). Most general chemical and physical characteristics of the soil have been previously reported (Kramer et al., 2012), but are listed here again in supplement together with some further relevant characteristics (Tables S1 & S2). In the agricultural year 2010, hybrid maize "Fernandez" (KWS Saat AG, Einbeck, Germany) was grown on the investigated field plot. This and also further relevant information on agricultural practices (fertilisation, pesticide treatments) can be found in Kramer et al. (2012).

To continuously collect seepage water, tension controlled lysimeters (KL2-100, UMS, Munich, Germany) were installed until the end of October 2009 directly below the plough horizon in approximately 35 cm depth and below the main rooted zone in 65 cm depth. The lysimeters were packed with undisturbed soil monoliths that were placed on top of a porous plate (pore size of 10 μm, SIC275, UMS, Munich, Germany). The porous plate served two needs: to allow for a collection of microbes and particles of up to a mean size of ~10 μm, and to enable the application of a matrix controlled suction for seepage water collection. The undisturbed soil monoliths were excavated at the locations of their latter re-installation at the same depth. Soil water potential was measured with a tensiometer (T8, UMS, Munich, Germany) installed at 35 cm depth. The respective suction was applied via a vacuum station (VS-twin, UMS, Munich, Germany).

2.2. Sampling

Before sampling, seepage water was collected at fortnightly intervals in 2 L glass bottles. In 2011, discharge into the subsoil was observed mainly during the fallow season in winter (December through March, 100 L m^{-2} at 35 cm depth and 86.5 L m^{-2} at 65 cm depth). Seepage water quantities below the plough horizon during the vegetation period from April through November 2011 were negligible (<0.1 L m^{-2}). Prior to actual sampling, an intensive snowmelt event in mid-January 2011 was followed by rain. Then, empty lysimeter collection bottles were installed within three successive time spans of 24 h (13, 14 and 17 January 2011), and fresh seepage water was sampled via the tension controlled lysimeters installed at 35 cm (L35) and 65 cm (L65) depth. Details on mean air and soil temperatures in the field as well as precipitation data during the period of investigation are given in the Supplementary Table S3 and Fig. S1. Organic carbon content in lysimeter water was analysed in samples from the first and third 24 h collection period, while bacterial community analysis was done with the second sample. All were successive samples, while the sampling procedure itself prevented true replicate water sampling. To a limited extent, as will be discussed further down, the two lysimeter samples obtained at distinct depth can be cautiously regarded as duplicate seepage water samples.

The sampling of lysimeter water always implies a certain contamination risk, as biofilms from the installation or from tubes can distort the composition of seepage water biota. We minimised this risk by using sterilised sampling bottles, inspecting the tubes for biofilms before the experiment, and mainly by maintaining a minimal retention time of fresh water samples in the lysimeters of only 24 h. Immediately after sampling, the water for the bacterial analyses was filtered (0.2 μm Corning, New York, USA), and filters and retained biomass were frozen at −20 °C until further processing.

At the same day, bulk soil samples were taken as composite samples of ten soil cores taken in a randomised manner via Pürkhauer coring across one 25 m × 25 m field plot as described previously (Kramer et al., 2012). Sampling was done at depths of 0–