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Selective successional transport of bacterial populations from rooted agricultural topsoil to deeper layers upon extreme precipitation events

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ABSTRACT

Substantial amounts of organic matter are mobilized from upper soil layers during extreme precipitation events. This results in considerable fluxes of carbon from plant-associated topsoil to deeper mineral soil and to groundwater. Microbes constitute an important part of this mobile organic matter (MOM) pool. Previous work has shown that specific bacteria associated with the rhizosphere of decaying maize roots were selectively transported with seepage water upon snowmelt in winter. However, effective mechanisms of mobilization and also possible distinctions to microbial transport for living root systems remain poorly understood. In the present study, bacteria in seepage water were sampled from lysimeters at an experimental maize field after extreme rain events in summer. We show that a distinctive subset of rhizoplane-associated bacterial populations was mobilized after summer rain, especially including abundant members of the *Bacteroidetes*, representing a microbial conduit for fresh plant-derived carbon inputs into deeper soil layers. Marked distinctions of seepage communities were not observed between lysimeters with a different relative contribution of preferential vs. matrix flow. Time-resolved analyses of seepage water during an artificial rain event revealed temporal patterns in the mobilization of certain lineages, with members of the *Chitinophagaceae*, *Sphingomonadaceae*, and *Bradyrhizobiaceae* preferentially mobilized in early and late seepage fractions, and members of the candidate phyla *Parcubacteria* and *Microgenomates* mobilized mostly in intermediate fractions. While average bacterial cell counts were at $\sim 10^7$ ml^{-1} in seepage water, the recovery of amended fluorescently labeled cells of *Arthrobacter globiformis* was low (0.2–0.6%) over seepage events. Still, mobilized bacteria clearly have the potential to influence bacterial activities and communities in subsoils. These findings demonstrate that dynamic hydraulic events must be considered for a better understanding of the connectivities between microbial populations and communities in soil, as well as of the links between distinct carbon pools over depth.

1. Introduction

Soil is the largest terrestrial reservoir of organic carbon, playing an essential role in global carbon sequestration (Lal, 2004). A primary source of soil organic matter (SOM) is provided by plants (Kögel-Knabner, 2002), which largely determine the distribution of OM (Jobbágy and Jackson, 2000). Transport of OM from topsoil to deeper soil layers with seepage water is a main component of carbon fluxes in soil, representing a significant share of fresh inputs of OM to subsoil and even to groundwater (Rumpel and Kögel-Knabner, 2011; Küsel et al., 2016).

Mobile organic matter in soil consists mostly of dissolved and colloidal organic carbon, including biocolloids like bacteria, fungi and their fragments (Totsche et al., 2007; Lehmann et al., 2018). The mechanisms of release and transport of such biocolloids and larger organic particles from the topsoil to subsoil are complex and poorly understood so far. They are highly influenced by dynamic environmental conditions like fluctuations in soil moisture, soil gas and temperature (Or et al., 2007). The soil pore network structure is a main controlling factor as a path for these fluxes, especially with the presence of macro- and biopores favoring the preferential and pronounced transport of OM (Jacobsen et al., 1997; Lægdsmand et al., 1999) and microorganisms (Bundt et al., 2001; Wang et al., 2013; Dibbern et al., 2014). The mobilization of viable microbes from topsoil mediated by preferential flow could also act as an important influx of biodiversity to subsoils, where the translocated microbes may significantly contribute to local microbial activities (Kieft et al., 1998; Jaesche et al., 2006; Küsel et al., 2016).

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The importance of understanding bacterial mobility and transport mechanisms in soil has been increasingly recognized, mostly connected to the input of potential pathogens to groundwater (Bradford et al., 2013). In soil, bacteria either move actively (Sen, 2011), or are mobilized passively by advection after release to the mobile water phase (Wang et al., 2013), via nematodes (Knox et al., 2004), or along growing plant roots (Feeney et al., 2006) and fungal hyphae (Simon et al., 2015). Substantial amounts of suspended materials including bacterial biomass can be transported vertically from topsoil (Totsche et al., 2007; Lehmann et al., 2018), especially triggered by weather events producing large amounts of seepage, such as snowmelt or strong precipitation (Dibbern et al., 2014). Numerous column studies have been conducted to address how the transport of pathogenic bacteria amended to soil is affected by various physical, chemical and biological factors (Bradford et al., 2013). Distinct features, such as cellular shape (Weiss et al., 1995), hydrophobicity (Kim et al., 2009), surface charge (Bolster et al., 2009), and bacterial interactions (Stumpp et al., 2011) were found to influence bacterial detachment and transport behavior. However, while central aspects of the transport of selected bacterial strains in soil have been intensively investigated, our understanding of the release and transport of complex indigenous microbiota in natural soils remains limited.

We have previously addressed this knowledge gap by characterizing natural bacterial communities mobilized with seepage water after snowmelt in late winter on an experimental maize field in Germany (Dibbern et al., 2014). The findings suggested that preferential flow along root channels played an important role in the transport of topsoil bacteria to deeper soil layers, and specific subsets of bacteria associated with decaying roots were selectively mobilized. However, these first insights did not address the potential impacts of more pronounced precipitation events and variability of soil moisture on living root systems in summer. In the present study, we hypothesize that (i) distinct subsets of root-associated bacterial populations will be selectively mobilized and transported to deeper soil layers along living root channels in summer; and (ii) a differential contribution of effective flow paths, i.e. preferential vs. matrix flow, during seepage events should be reflected in dynamics of transported microbiota. To address this, we conducted seepage water sampling after natural and artificial extreme rain events in late summer. Via direct time-resolved sampling, we characterized mobile organic matter (MOM), related physicochemical parameters as well as mobilized complex microbiota throughout the seepage process and compared them to the surrounding soil- and root-associated microbiomes. Furthermore, we used fluorescently labeled viable cells of a bacterial strain characteristic of the site as a tracer, to quantify their mobilization and transport behavior during seepage events.

2. Materials and methods

2.1. Field site and lysimeters

The agricultural field was located in Holtensen, near the city of Göttingen (Germany). The area has a temperate climate, with a mean annual temperature of 7.9 °C and a mean annual precipitation of 651 mm y^{-1} (1981–2010; Deutscher Wetterdienst, 2017; aggregated). The mean monthly precipitation (1981–2010, Göttingen weather station, 167 MAMSL; source: Deutscher Wetterdienst, 2017, aggregated) ranges between 39 and 66 mm (minima in February, April, October, and maxima in June). Thresholds for extreme precipitation events were determined by rarity (99th percentile; cf. Beniston and Stephenson (2004)) and were at 16.6 mm d^{-1} for summer (April–September) and at 22.0 mm d^{-1} for winter (October–March). The dominant soil types are Cambisols (Braunerden), Luvisols (Parabraunerden) and stagnic Luvisols (Pseudogley) (IUSS Working Group WRB, 2007). The albic horizon typically found for these soils is not detectable, due to the long-term agricultural management with intensive tillage. Two plough layers were found at 20 and 30 cm below surface, with strong compaction below the second plough layer. Further details on chemical and physical soil properties can be found elsewhere (Kramer et al., 2012; Dibbern et al., 2014).

A long-term field experimental for tracing rhizosphere vs. detritusphere-derived carbon into the soil food web was established in May 2012, with 12 experimental plots (5 × 5 m) with three treatments (maize rooted, maize-litter-amended and fallow soil, Loeppmann et al., 2016a, b). All plots with lysimeters used here were planted with maize since 2012. Tension-supported lysimeters (KL2-100, UMS, Munich, Germany) were installed directly below the plough horizon (35 cm depth) and below the main rooted zone (65 cm depth). To do so, a horizontal chute (40 cm width, 40 cm length, 25 cm height) was excavated via a hydraulic pit. The lysimeters were fully connected to the undisturbed soil overburden by a load compensation plate. A specifically designed, small-sized lysimeter setup was chosen to sample naturally low concentrated mobile particles (mineral and organic components, aggregates, biocolloids) up to a size of 10–250 µm (Totsche et al., 2018), which percolate from undisturbed soil. The lysimeters were composed of a stainless-steel ring (diameter: 30 cm; height: 10 cm) filled with inert glass beads (size/diameter: 2.0–2.5 mm) and a porous silicon carbide suction plate (SIC320; pore size of ~20 µm, air entry point of 100 hPa, less resistance to flow, diameter 32 cm, thickness 1 cm; UMS) at the bottom. Suction was applied and regulated via a vacuum controller (VS-twin, UMS) by using the prevailing soil water potential that was constantly measured with a tensiometer (T8, UMS) installed at 35 cm depth. While the porous plate was used to apply the suction to the system, the glass-bead layer served two purposes: It supported the undisturbed soil overburden and it acted as a “retention volume” for larger suspended particles and aggregates that may be released from the soil. Without the glass-bead layer, these materials would have resulted in filter clogging and rapid malfunction of the lysimeter system.

2.2. Sampling after a natural rain event

An extreme rainfall event of 30.2 mm occurred on 11.09.2012, followed by several successive precipitation events (0.2–0.4 mm; Fig. S1a) over the next days. Precipitation was measured with an iMETOS 2 weather station (Pessl Instruments, Weiz, Austria). The volumetric water content and soil temperature were measured with sensors (5TM, Decagon Devices, Pullman, USA) installed at 48 cm (n = 5) and 58 cm (n = 5) below soil surface in the hydraulic pit. Two pairs of co-localized lysimeters (35 cm and 65 cm depth) were investigated in two different plots, coded with A and B (L35A, L65A and L35B, L65B), which were ~15 m apart. On 19.09.2012, a further 2.8 mm rain event occurred before the actual sampling. Directly before sampling, empty sterilized glass bottles were installed to collect seepage water from the four lysimeters. Fresh seepage water was sampled within 24 h. Immediately after retrieval, seepage water was filtered for bacterial analyses (0.2 µm, Corning, New York, USA). Filters with retained microbial biomass were frozen at −20 °C until further processing (~3–6 months). For each 24-h water sample, DNA was extracted in duplicates from two sectioned filter quarters. In addition, subsamples were taken for physicochemical water analysis. On the same day, depth-resolved composite soil samples were taken as described previously (Kramer et al., 2012; Dibbern et al., 2014) from the lysimeter plots. Furthermore, two live root balls were extracted from each plot. All soil and root samples were frozen and stored at −20 °C until further analyses. Rhizosphere (Rh) and rhizoplane (Rp) samples were obtained as previously described (Dibbern et al., 2014). All bulk soil, rhizosphere and rhizoplane samples were obtained and processed in biological triplicates, whereas water samples were processed in biological duplicates due to volume restrictions.