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Soil microbial diversity and agro-ecosystem functioning

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Feldfunktion geändert

Soil microbes represent the unseen majority of life on Earth and are essential for the functioning of terrestrial ecosystems as they catalyze unique and indispensable transformations in the biogeochemical cycles of the biosphere (Whitman et al. 1998, van der Heijden et al. 2008). The significance of soil microbial diversity for the functioning of agricultural and natural ecosystems is still poorly understood and soil microbial communities can be considered as a black box (Kennedy & Smith 1995; Cortois & de Deyn 2012). Unraveling what soil microbes are doing in this black box has been identified as one of the major research areas in science.

An increasing number of studies demonstrate that agricultural practices, such as tree based intercropping (Lacombe et al. 2009; Bainard et al. 2012), organic farming (Mäder et al. 2002; Bengtson et al. 2005; Birkhofer et al. 2008; Verbruggen et al. 2010), reduced soil tillage (van Capelle et al. 2012), crop rotation (Altierri et al. 1999; Cavagnaro et al. 2011) and land use extensification (Postma-Blaauw et al. 2010; de Vries et al. 2012) have a positive impact on the abundance and richness of specific groups of soil organisms (e.g. arbuscular mycorrhizal fungi, earthworms) and on soil microbial diversity. Thus, by adapting farm management practices it is possible to favor recruitment of specific groups of soil organisms and enhance microbial diversity. As such, these findings make it possible to provide policy makers with recommendation on enhancing soil biodiversity in agricultural ecosystems. There are a number of mechanisms by which microbial diversity can support agro-ecosystem functioning and particular ecosystem functions such as plant productivity and decomposition. For instance, microbes can form “consortia” that enhance plant productivity (e.g. when different microbes provide different limiting resources to plants) or decomposition (e.g. when plant material is decomposed by specialized microbes with unique physiological properties that succeed each other). As a consequence, microbial diversity can promote ecosystem functioning. However, in other cases, the presence of keystone species (e.g. specific pathogens, nitrogen fixers) rather than diversity "*per se*" may determine agro-ecosystem functioning. Until now, it is still poorly understood whether increased soil (microbial) diversity is beneficial for the functioning and sustainability of agricultural systems.

In this issue (pp. xxx-xxx) an extensive study by Bainard and colleagues showed that things are certainly not simple. They used soil from conventional agricultural fields and from tree-based intercropping systems as inoculum in a glasshouse bioassay and assessed the influence of soil biotic communities conditioned by these two different practices on three agricultural crops. In earlier work it was shown that soils from tree based intercropping systems had higher microbial diversity compared to conventionally managed soils (Lacombe et al. 2009; Bainard et al. 2012b). Hence, it was hypothesized that plants would benefit when inoculated with soils derived from tree based intercropping systems. In contrast to their hypothesis, there were no differences in inocula effects between farming systems. Moreover, two of the three crops (barley and canola) grew best in soil with sterilized inoculum. Thus, the results from this study do not indicate that plants benefit from increased microbial diversity (but see below). Instead, soil pathogens appeared to be a stronger driver of plant productivity than diversity for two of the investigated crop species in this study.

Bottlenecks and advances

The great difficulty in assessing the impact of soil microbes on plant productivity and ecosystem processes arises since microbial diversity and abundance cannot be easily manipulated without simultaneously changing other factors or organisms (Read 2002).

Hence, it is a common approach to perform greenhouse experiments under controlled conditions in sterilized soil and add soil inoculum (Bainard et al. 2012a, Verbruggen et al. 2012; Maheraldi & Klironomosi 2007 ; Wagg et al. 2011). By adding soil inoculum from fields with different microbial diversity it is subsequently possible to mimic differences in microbial communities under controlled conditions and test their impact on plants and ecosystems. When doing this, it is important to verify that differences in soil microbial diversity are responsible for observed effects. Consequently, it is required to demonstrate at the beginning and at the end of the experiment that soil microbial diversity differs among treatments. The experiments by Bainard et al. (2012a) were very large (750 pots) and hence such information was not presented (e.g. it is extremely laborious and financially demanding to determine microbial community composition of 750 pots). Thus, with the results presented it was not possible to draw firm conclusions. Further work is needed to test whether enhanced microbial diversity in tree-based intercropping systems can provide additional ecological services to these systems.

A number of recent developments provide opportunities for understanding how soil microbial communities influence the productivity and sustainability of cropping systems. First, costs for the molecular characterization of microbial communities (e.g. by high throughput sequencing) has declined considerably in recent years, making it now possible to characterize microbial communities for a larger number of samples. Second, fluxes of carbon and nutrients that are mediated by microbes can be measured with (stable) isotopes and related technology such as stable isotope probing (e.g. Vandenkoornhuyse et al. 2007; Kiers et al. 2011). With these techniques it is possible to show which microbes are active, thus providing mechanistic insights into the role of specific soil microbial communities in driving ecosystem functioning. Third, it is difficult to manipulate microbial diversity because many microbes readily disperse via air and water. As a consequence, microbes can easily contaminate pots and cause unwanted changes in experimental treatments. Hence, differences in the effects of microbial diversity at the start of the experiment may eventually disappear, especially if experiments are performed over longer periods of time. Recently, we developed an experimental system in which it is possible to manipulate microbial diversity in experimental ecosystems without contamination from the outside (Figure 1). Such tools provide new avenues for testing whether soil microbial diversity influence ecosystem functioning and whether soils with high microbial diversity are important for sustaining agricultural production.

Applicability of soil biodiversity research in Agro-Ecosystems

The experiments by Bainard et al. also show that growth responses of crops in response to soil inoculation are variable. Barley and canola performed best in sterilized soil and these crops also did not benefit from the presence of arbuscular mycorrhizal (AM) fungi, soil fungi that facilitate plant growth by providing plant inaccessible nutrients. This is perhaps to be expected since canola does not form AM fungal associations and a number of studies showed that barley does not necessarily benefit from AM fungi (e.g. Grace et al. 2009). Thus, it appears that the impact of plant antagonists of these crops on productivity was larger than those of beneficial soil organisms. In contrast, soybean grew equally well in sterilized and non-sterilized soil and in a second experiment, Bainard et al. demonstrate soybean performed better in pots inoculated with AM fungi, which is typical of most legumes. Thus, the effects of soil organisms on crops is driven by the species identity and plant functional group of the crop, making it difficult to make general recommendations about the benefits of soil microbial diversity in agro-ecosystems. Moreover, microbes not only influence plant productivity, but a wide range of ecosystem functions are affected by soil microbes that indirectly affect plant productivity, not only within a growing season but also over time. (nutrient losses, nutrient cycling, soil structure stabilization etc. – see van der Heijden et al. 2008). Such indirect effects should not be overlooked when assessing the importance of soil microbial diversity.

In conclusion, there are now a wide range of studies describing how soil organisms and soil microbes respond to different agricultural practices. However, current understanding as to whether such changes in soil (microbial) diversity are beneficial for the functioning of agro-ecosystems is only in its infancy. Only a few studies, often theoretical or performed under highly controlled conditions with a particular group of micro-organisms indicate that enhanced microbial diversity can indeed be beneficial by providing a number of ecosystem services (Brussaard et al. 2007; van der Heijden et al. 2008; Berendsen et al. 2012). The work by Bainard et al. provide new insights into the role of soil microbes in agro-ecosystem demonstrating negative soil feedback to be a strong mechanism. At the same time these authors also illustrate there remain many important questions to be addressed about the role of soil biodiversity in agro-ecosystems and its applicability.

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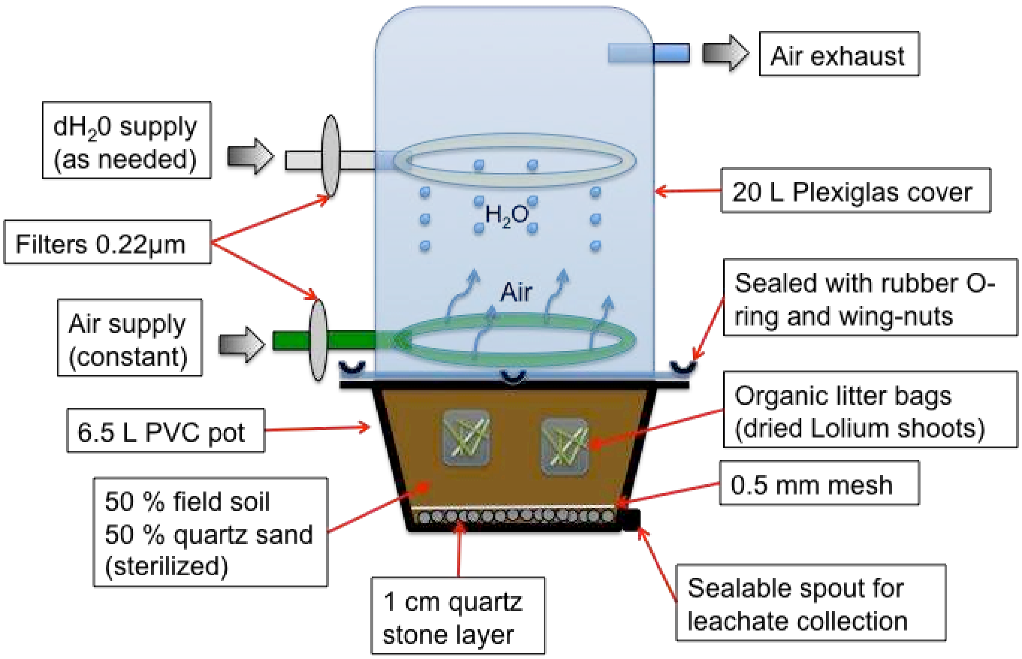
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dH$_2$0 supply
(as needed)
20 L Plexiglas cover
H_2O
Filters 0.22µm
Air
Sealed with rubber O-ring and wing-nuts
Air supply
(constant)
6.5 L PVC pot
Organic litter bags
(dried Lolium shoots)
0.5 mm mesh
50 % field soil
50 % quartz sand
(sterilized)
Sealable spout for leachate collection
1 cm quartz stone layer

Figure 1: *Schematic draw (a) and photograph (b) of an experimental microcosm in which plants can be grown under controlled conditions without microbial contamination from the outside. In order to prevent microbial contamination, filling and planting of the microcosms*

needs to be performed in a laminar flow hood and all material needs to be sterilized or autoclaved before use. Moreover, during the growth period, incoming pressured air is filtered through a hydrophobic filter (0.22 µm), while water/nutrient solution is filtered through a hydrophilic filter (0.22 µm) to prevent contamination from the outside. Replicated microcosms can be inoculated with soil inoculum from different agricultural fields or microcosms can be inoculated with different (numbers of) microbes. Litter bags or hyphal compartments with labelled material (^{13}*C and or *^{15}*N) can be added to the microcosms in order to test whether decomposition and/or nutrient uptake varies between microcosms with different microbial diversity treatments.* ^{13}*CO2 can be added to the microcosms (instead of pressured air) to trace the fate of assimilated C (to facilitate stable isotope probing). Microcosm Design: Marcel van der Heijden & Susanne de Bruin.*