Soil Biology and Biochemistry 124 (2018) 227–235

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

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

The legacy of mixed planting and precipitation reduction treatments on soil microbial activity, biomass and community composition in a young tree plantation

Lettice C. Hicks[a,*,1], Md Masudur Rahman[b,1], Monique Carnol[b], Kris Verheyen[c], Johannes Rousk[a]

[a] Section of Microbial Ecology, Department of Biology, Lund University, Ecology Building, 223 62, Lund, Sweden
[b] Laboratory of Plant and Microbial Ecology, InBioS, University of Liège, Botany Bât. 22, Chemin de la Vallée 4, 4000 Liège, Belgium
[c] Forest & Nature Lab, Department of Environment, Ghent University, Geraadsbergseteenweg 267, B-9090 Melle-Gontrode, Belgium

ARTICLE INFO

Keywords:
Plant diversity
Soil carbon mineralisation
Soil decomposer ecology
Bacterial and fungal growth
Precipitation manipulation
Temperate forest ecosystem

ABSTRACT

Drought events are expected to increase as a consequence of climate change, with the potential to influence both plant and soil microbial communities. Mixed planting may be an option to mitigate drought stress to plants, however, the extent to which mixed planting mitigates the indirect effect of drought (reduced plant-derived carbon input) on soil microorganisms remains unknown. Using soils from a young experimental plantation in Central Europe, we investigated whether mixed planting (oak monoculture, and oak admixed with 1–3 other tree species) under simulated drought (50% precipitation reduction for 2 years) influenced soil microbial activity, biomass and community composition. To focus on legacy effects - i.e. indirect effects mediated by plant composition and a history of drought, rather than direct effects of reduced water availability - soils were measured at a standardised moisture content (28 ± 1% water holding capacity). Rates of bacterial growth and respiration were lower in soils with a legacy of drought. In contrast, fungal growth was not affected by a history of drought, suggesting that fungi were less adversely affected by reduced plant-input during drought, compared to bacteria. The effect of drought on the fungal-to-bacterial growth ratio was influenced by mixed planting, leading to a disproportionate decrease in bacterial growth in drought-exposed soils under oak monoculture than when oak was admixed with two or three different tree species. The presence of a particular tree species (with specific functional traits) in the admixture, rather than increased tree richness *per se*, may explain this response. Microbial biomass parameters, reflecting both the direct and indirect effects of past drought conditions, were consistently lower in drought-exposed soils than controls. While bacteria were more sensitive to the indirect effect of drought than fungi, the biomass concentrations suggested that the direct effect of reduced moisture affected both groups similarly. Overall, our findings demonstrate that drought can have lasting effects on microbial communities, with consequences for microbial function. Results also suggest that admixing oak with other tree species may alleviate the drought-legacy effect on bacteria and increase tolerance to future drought.

1. Introduction

Drought events are expected to increase as a consequence of climate change (IPCC, 2013). More frequent and intense periods of drought will influence soil microbial communities directly due to reduced water availability (Borken et al., 2006; Sheik et al., 2011; Manzoni et al., 2012; Canarini et al., 2017), as well as indirectly via drought effects on plants (Fuchslueger et al., 2014). During drought, plant productivity is typically reduced, resulting in lowered carbon (C) input to soil (Ciais et al., 2005; Peñuelas et al., 2007; Ruehr et al., 2009; Wu et al., 2011; Hasibeder et al., 2015) from both aboveground litterfall and belowground roots and root-exudation (Jones et al., 2009). According to the principle of niche complementarity (Tilman, 1999; Hooper et al., 2005), mixed planting may be an option to mitigate drought stress to plants, as the response to environmental change is expected to differ in a mixture of several species with different functional traits and strategies for resource utilisation than the same species in monoculture (Forrester and Bauhus, 2016). Several studies suggest that facilitative processes and niche complementarity, driven by functional dissimilarity, in mixed species stands often lead to higher rates of biomass production, tree growth and C sequestration compared to monoculture, especially under drought stress (Lebourgeois et al., 2013; Pretzsch

* Corresponding author.
E-mail address: lettice.hicks@biol.lu.se (L.C. Hicks).
[1] Equal contribution.

https://doi.org/10.1016/j.soilbio.2018.05.027
Received 16 January 2018; Received in revised form 4 May 2018; Accepted 28 May 2018

et al., 2013; Mina et al., 2017). Differences in plant community composition also affect the composition of soil microbial communities (Thoms et al., 2010; Scheibe et al., 2015; Gunina et al., 2017), demonstrating a clear link between above- and belowground communities. Yet, while mixed planting may mitigate drought stress to plants, the extent to which species mixing can also mitigate the indirect effects of drought (i.e. reduced plant input) on soil microorganisms remains unknown. As effects of mixed planting during drought vary among studies, there is currently insufficient information available to define the expected effect size of mixed planting under drought on microbial communities and microbially-mediated processes.

In addition to the direct effects of reduced water availability during drought (Manzoni et al., 2012; Meisner et al., 2017), a history of drought can also influence microbial mineralisation rates (Evans and Wallenstein, 2012; Allison et al., 2013; Hawkes et al., 2017; Martiny et al., 2017). Historical droughts may affect present-day microbial processes, due to persistent abiotic changes caused by drought, or through drought-related changes in microbial community composition. In one pan-European study, however, no legacy effect of long-term moderate drought (30% precipitation reduction during summer growing season) on microbial activity and composition was observed (Rousk et al., 2013).

Fungi and bacteria have been shown to respond differently to drought (Bapiri et al., 2010; Yuste et al., 2011; de Vries et al., 2012). Fungi may be more tolerant to reduced water availability during drought (Harris, 1981; Manzoni et al., 2012; Guhr et al., 2015). Moreover, bacteria are often considered to be more dependent on labile plant-derived C input from roots (Singh et al., 2006; Bird et al., 2011; Andresen et al., 2014). Consequently, a reduction in plant-derived C input during drought is expected to affect bacterial communities more than fungal communities (Fuchslueger et al., 2014).

To investigate whether mixed planting mitigates against the effects of drought on soil microorganisms, we used soils from an experimental plantation with an oak-admixture gradient in Belgium under simulated drought (two years of 50% precipitation reduction). The oak-admixture gradient provided the opportunity to compare soils from under oak monoculture with soils where oak was growing together with one to three other tree species (hereafter referred to as differences in "tree species admixture; TSA"). Rather than assessing the direct influence of reduced soil moisture on microbial processes, here we evaluated the influence of a legacy of drought on soil microbial processes and community composition (Rousk et al., 2013). Hence, microbial activity and community composition in control and historically drought-exposed soils were measured at the same optimal soil moisture content (28 ± 1% water holding capacity). We expected that (1) process rates would be lower in soils with a legacy of drought, as plant input to soil is often reduced during drought (lower availability of labile C). Moreover, we predicted that (2) there would be a greater effect of drought on bacterial compared to fungal communities, as bacteria are often considered to be more dependent on labile C input from plants. According to the theory of niche complementarity, mixed planting should maintain plant productivity, and thus sustain the plant-derived C input to soil, even under drought conditions. We therefore expected that (3) the drought-legacy effect on microbial growth and respiration would be more pronounced in soils under monoculture compared to mixed species stands. Microbial biomass was also measured, integrating the recent history of environmental conditions and thus reflecting both the direct (reduction in soil moisture) and indirect (reduced C input) effects of past drought. Thus, we predicted that (4) microbial biomass would be lower in soils with a history of drought, due to the long-term effect of lower net microbial growth under drought conditions.

2. Materials and methods

2.1. Soils and field treatment

The study site was located at the Zedelgem site of FORBIO plantations in Belgium belonging to the worldwide Tree Diversity Network (http://www.treedivnet.ugent.be/; Verheyen et al., 2016). Zedelgem is one of the three FORBIO experimental plantations (Verheyen et al., 2013). The site is close to the North Sea (51°9′ N 3°7′ E), with a mean annual precipitation of 855 mm and an average air temperature of 10.5 °C (1981–2010). The site was previously agricultural land and was planted with five locally adapted tree species in the winter of 2009–2010. Soils have been classified as relatively dry sandy soil (Podzol) to moderately wet loamy sand (Gleysol) (Verheyen et al., 2013) according to the IUSS Working Group World Reference Base for soils (2006).

The FORBIO plantations follow a synthetic community approach using a fixed species pool of five tree species (Verheyen et al., 2013). Five site-adapted but functionally dissimilar tree species were planted. The species pool includes *Quercus robur* L. (hereafter oak), *Fagus sylvatica* L. (hereafter beech), *Betula pendula* Roth (hereafter birch)., *Tilia cordata* Mill. (hereafter lime), and *Pinus sylvestris* L. (hereafter pine). Monocultures and admixtures of two to four tree species were planted on the environmentally homogeneous site: all five monocultures, all five possible four-species combinations and a random selection of five two- and three-species combinations. Trees were planted in monoculture patches of 3 × 3 trees with a distance of 1.5 m between each tree. Vegetation in the understorey was inventoried after establishment of the plantation in 2011, revealing that most species were typical of a moist, nutrient rich grassland environment (Verheyen et al., 2013). In the first 3 years following planting, the understorey was mown once each year but has since been unmanaged. In the plots used for this study, dense tall grasses form the understorey, with no other woody shrubs present (M. M. Rahman, personal observation). Consequently, vegetation in each plot is determined by the planted tree composition, and the grass-dominated understorey associated with these trees.

A precipitation reduction (hereafter "drought") experiment was started in April 2015, to assess the performance of oak and beech saplings under drought conditions. Three drought and three control subplots of 3 m × 3 m for each tree species admixture level were established around oak and beech trees in the south-east side of the FORBIO plantation (Rahman et al., under review). This experimental set-up created monoculture-admixing gradients, with oak and beech trees surrounded only by oak and beech, respectively, as well as oak and beech trees surrounded by one, two or three other species (Supplementary Fig. S1). Here we use soils from the oak-admixture gradient, and henceforth we refer to 1–4 levels of tree species admixture (TSA) (Table 1). As this design is not fully-factorial, i.e. all combinations of different tree species in mixtures are not considered, TSA effects cannot be directly attributed to differences in species richness, and findings must be interpreted in light of tree species composition within admixtures, and the associated understorey.

The drought experimental treatment has been described in detail elsewhere (Rahman et al., under review). Briefly, precipitation was reduced by installing rain exclusion shelters that consisted of PVC gutters (c. 12 cm wide) placed at intervals of c. 25 cm. To promote drainage, a slope was constructed by placing the gutter at a height of 0.95 m from the ground at the upper side and 0.75 m from the ground at the lower side. A 6 m long gutter was placed at the lower side to channel the intercepted water away from the plot. The gutters covered approximately 50% of the subplot area. The amount of precipitation intercepted by the shelters was assessed over 44 days (mid-August to end September 2016), by placing rainfall collectors under and outside the rain shelter in monoculture, two-species admixture and three-species admixture plots. From this assessment, the total incoming precipitation excluded by the shelters ranged between 45 and 55%.

In addition to the rain exclusion shelters installed in drought plots, three subplots of the same size but with reverse gutters (no precipitation interception) were also installed. Since there was no difference in soil temperature among control, drought and reverse subplots (data not shown), it is reasonable to conclude that rain shelters did not have a