Soil Biology & Biochemistry 115 (2017) 516–525

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Impact of woody debris of different tree species on the microbial activity and community of an underlying organic horizon

Derek Peršoh [a], Werner Borken [b, *]

[a] Geobotanik, Ruhr-Universität Bochum, Universitätsstraße 150, 44801 Bochum, Germany
[b] Soil Ecology, University of Bayreuth, Dr.-Hans-Frisch-Str. 1-3, 95448 Bayreuth, Germany

ARTICLE INFO

Article history:
Received 3 August 2017
Received in revised form
13 September 2017
Accepted 16 September 2017
Available online 28 September 2017

Keywords:
Woody debris
Microbial biomass
CO_2 production
Fungal community
Tree species

ABSTRACT

Woody debris (WD) represents a litter input to forest soils, but its impact on carbon (C) cycling and the fungal community in the underlying forest floor is unclear. Here, we assessed the effect of WD of eight tree species differing in wood quality on CO_2 production, microbial biomass C and fungal community of an Oe horizon from a Norway spruce forest in a combined field-laboratory study. The 78-day incubation at 20 °C comprised three treatments: Oe, WD, and Oe + WD. In the Oe treatment, the Oe horizon was previously covered with WD for 1.5 years in the Norway spruce forest. Oe horizon from control subplots that was not covered with WD in past years served as control (Oe treatment). WD originated from the 1.5-year-old field study and was either separately incubated (WD treatment) or together with Oe horizon from control subplots (Oe + WD treatment). In the Oe treatment, CO_2 production and microbial biomass C were significantly higher in the Oe horizon under fast decomposing WD of *Acer pseudoplatanus, Betula pendula*, and *Fagus sylvatica* than in the Oe control. The effect of WD on the Oe horizon was even stronger in the Oe + WD treatment after separation of both substrates (day 80). CO_2 production and microbial biomass C were 3–6 times or 3–5 times higher, respectively, than the control, either due to ingrowth of wood decomposing fungi or growth of autochthonous microbes in the Oe. Further, WD increased the molar C:N ratio of the Oe horizons by 1.2 units in the Oe + WD treatment. Glucose addition reduced or did not affect the CO_2 production of WD, indicating that wood decomposing microorganisms were not C-limited. The fungal communities in the Oe + WD treatment were altered in both substrates, and differed primarily between angiosperm and gymnosperm WD. Fungi preferably occurring in samples with strong increase in CO_2 production were native Oe fungi, indicating that invasion by wood fungi had little direct effect on C mineralization in the Oe horizon. Our results suggest that WD of common tree species represents a labile C source that can accelerate the C mineralization in the Oe horizon.

1. Introduction

Woody debris (WD) is a component of the carbon (C) and nutrient cycle in forest ecosystems. Its relevance for element cycling strongly varies among forest ecosystems and relies on production, stock and decay of WD (Harmon et al., 1986; Brassard and Chen, 2008). Chemical and physical wood traits associated with tree species as well as the decomposer community have great impact on the initial decay of WD (Kahl et al., 2017; Weedon et al., 2009). Gymnosperms and ring-porous angiosperms like *Fraxinus excelsior* and *Quercus robur/petraea* decay slower than diffuse-porous angiosperms with the fastest decay rates of *Carpinus betulus* and *Fagus sylvatica* among 13 temperate tree species (Kahl et al., 2017). Another important factor of the decay process is the location of WD in the forest. Contact of downed WD to soil accelerates the decay by many years relatively to standing snags (Vanderwel et al., 2006).

While many studies focus on the decay of downed WD, the impact of WD on forest soils is less well investigated and the few findings are divergent so far. Soils under WD can have higher concentrations of nutrients and organic C (Bade et al., 2015; Goldin and Hutchinson, 2013; Kappes et al., 2007; Stutz et al., 2017) or experience negative to no changes in element concentrations (Spears et al., 2003; Spears and Lajtha, 2004; Kahl et al., 2012; Zalamea et al., 2016). Even large inputs of WD do not inevitably increase the organic C stock of temperate forest soils (Krüger et al.,

* Corresponding author.
E-mail address: werner.borken@uni-bayreuth.de (W. Borken).

https://doi.org/10.1016/j.soilbio.2017.09.017
0038-0717/

2017). Pathways of movement of WD components into the soil are incorporation of WD fragments, leaching of dissolved organic and inorganic matter (Bantle et al., 2014a,b) or transfer by fungal hyphae (Hughes and Boddy, 1994).

Fungi could play an important role in the change of forest soils by overlying WD. Fungal hyphae have the ability to immobilize and translocate nutrients between different compartments including deadwood (Chigineva et al., 2011; Lindahl et al., 2001; Watkinson et al., 2006). The transfer between different compartments may be bidirectional (Lindahl et al., 2001), but is often directed towards the mycelial front (Guhr et al., 2015; Lindahl et al., 2002). Several studies reported N uptake from soil by fungal hyphae to overcome the N deficiency in deadwood or in other N deficient litter (Boberg et al., 2010; Rinne et al., 2017). Nutrient transfer is presumably closely linked to fungal diversity in WD, the underlying soil and particularly to those fungi connecting the two habitats with their hyphae.

Communities of fungal decomposers usually differ among substrates. WD is mostly colonized by fungi specialized on this substrate (Dix and Webster, 1995), though the wood-inhabiting communities often differ among tree species (Hattori, 2005; Yamashita et al., 2010; Stokland et al., 2012; Hoppe et al., 2015). A horizonwise specialization by different fungal communities also occurs along vertical forest soil profiles (Lindahl et al., 2007; Peršoh et al., 2013). WD alters the structure of ectomycorrhizal (EcM) and yeast fungal communities in soil (Walker et al., 2012; Yurkov et al., 2012). The entire community of soil fungi was also shown to be altered by the presence of decaying spruce logs in a spruce forest (Mäkipää et al., 2017). However, it remains unclear if WD of other tree species has different effects on the fungal communities in underlying forest soil.

Here, we addressed the hypotheses that (1) presence and (2) origin of WD alters microbial CO_2 production, microbial biomass and fungal community structure in the underlying organic soil horizon. We tested the hypotheses in a laboratory experiment and assumed that the effect of fast decomposing tree species (*Acer pseudoplatanus, Betula pendula, Fagus sylvatica*) is greater on soil microbial parameters than of slow decomposing tree species (*Fraxinus excelsior, Quercus robur, Larix decidua, Picea abies, Pinus sylvestris*). Oe horizon and WD were derived from a Norway spruce forest where WD of the eight tree species was subjected to initial decay on the forest floor for 1.5 years.

2. Material and methods

2.1. Experimental design, wood and soil characteristics

Woody debris (WD) and Oe horizon were taken from a field experiment in a 63-year-old Norway spruce forest at the Waldstein, Fichtelgebirge, Germany, in April 2016. The field experiment was initiated in November 2014 where WD of eight different tree species was exposed to the forest floor in three WD plots to study the decay process under the climate conditions at the Fichtelgebirge (MAT 5.3 °C, MAP 1160 mm). WD comprised five angiosperms: *Acer pseudoplatanus*, *Betula pendula*, *Fagus sylvatica*, *Fraxinus excelsior, Quercus robur*, and three gymnosperms: *Larix decidua, Picea abies* and *Pinus sylvestris*. Hereafter, the tree species are denoted as *Acer*, *Betula*, *Fagus*, *Faxinus*, *Quercus*, *Larix*, *Picea*, and *Pinus.* We used crown wood (30–45 cm long, 5–11 cm in diameter) because this fraction often remains in managed forests after harvest. Initial amounts of WD ranged between 25.1 and 26.1 kg d.w. m^{-2}, yielding 12.3–13.2 kg C m^{-2} and 0.02–0.06 kg N m^{-2}. Table 1 lists the initial densities (wood + bark) and element concentrations (wood without bark) of each tree species. Bark contributed between 8% (*Pinus*) and 17% (*Picea*) to the initial mass of WD and was characterized by higher element concentrations (not shown) than wood.

The soil, a Haplic Podsol, includes an acidic pH_{CaCl2} (3.3) and 4–8 cm thick, moder-like organic layer, consisting of Oi, Oe and Oa horizons, that is sparsely covered by ground vegetation. The Oe horizon had following element concentrations: 421 g C kg^{-1}, 18 g N kg^{-1}, 1.1 g P kg^{-1}, 2.1 g S kg^{-1}, 0.4 g K kg^{-1}, 0.5 g Mg kg^{-1}, 6.8 g Ca kg^{-1} and 0.3 g Mn kg^{-1}. Further information on soil properties are given by Schulze et al. (2009).

For the laboratory experiment, four 2.5 cm thick slices were cut from WD pieces of the eight tree species per plot. The Oe horizon was sampled under WD of each tree species or from control subplots without visible influence of WD in the past years. Roots, twigs and cones were removed from the Oe horizon by handpicking.

Three treatments were established using 900 ml airtight glass jars, equipped with a septum in the lid for gas sampling. The first treatment (hereafter Oe) consisted of 20 g field-moist Oe horizon sampled under WD (n = 3) and from the respective control subplots (n = 6). The second treatment (hereafter WD) consisted of two slices of 70 g field-moist WD of each tree species (n = 3). In the third treatment (hereafter Oe + WD), the jars contained 20 g field-moist Oe horizon exclusively from the control subplots and two slices of 70 g field-moist WD of each tree species (n = 3). WD slices were placed on the Oe horizon, allowing growth of fungal hyphae between the two substrates. Overall, 78 jars (3 treatments x 3 replicates x 8 tree species + 6 controls (Oe horizon)) were incubated in the dark at 20 °C for 78 days. Afterwards, the Oe horizon and WD of the Oe + WD treatment were separately incubated in glass jars for two days to test for mutual interactions of decomposers on CO_2 production and microbial biomass C. Dry mass and gravimetric water contents of Oe and WD were determined from all jars after drying at 60 °C. Average water contents including all treatments were 2.24 ± 0.20 g g^{-1} in the Oe and 1.15 ± 0.23 g g^{-1} in WD of all tree species.

2.2. CO_2 production, microbial biomass C, C and N concentrations

CO_2 production of the substrates was measured at 10 occasions during 78 days by gas chromatography (GC 8610C, SRI Instruments, Torrance, USA). For this purpose, the jars were opened and flushed with synthetic air for about 2 min. Then, the jars were closed and gas samples (100 μL) were taken immediately after closure and after 2 h for the measurements of the initial and final CO_2 concentrations, respectively. CO_2 production rate was calculated by the linear increase in CO_2 concentration during the 2 h incubation, corrected for actual air pressure and air temperature.

Microbial biomass C of the Oe horizon and WD was determined by substrate induced respiration (SIR) (Anderson and Domsch, 1978) after 80 incubation days. For this purpose, 0.1 mg glucose was applied to 10 g subsamples (fresh weight) of the Oe horizon or WD and then incubated in air-tight jars (900 ml) at 22 °C for 4 h. CO_2 concentrations were measured by gas chromatography (see above) at 0, 2 and 4 h after glucose addition to ascertain the optimum incubation time. Since the CO_2 productions rates were almost identical after 2 and 4 h, we present only data of the first 2 h. The microbial biomass C (MBC in mg C g^{-1} d.w.) was calculated as follows (Anderson and Domsch, 1978):

$$MBC = 40.04 \times \frac{ml\ CO_2}{m\ x\ t} + 0.37$$

where ml CO_2 is the produced amount of CO_2, m is the dry mass (g) of the Oe horizon or WD and t the incubation time (h), 40.04 and 0.37 are empirical constants. Afterwards the subsamples were dried at 60 °C to assess the water content and total dry mass.