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Bacterial and fungal growth on different plant litter in Mediterranean soils: Effects of C/N ratio and soil pH

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ABSTRACT

Plant litter represents an important source of nutrients and energy for soil microorganisms, but will also selectively affect which organism group, fungi or bacteria, that will be favoured during decomposition. The balance of fungal to bacterial growth will furthermore be affected by soil chemistry like pH. A laboratory experiment was carried out using two different Mediterranean forest soils differing in pH, adding five types of litter varying in C/N ratio from 15 to 75, including the major litter type from the two soils. Growth of bacteria (using the leucine incorporation technique) and fungi (using the acetate into ergosterol incorporation technique) was then followed during 6 weeks. The balance of fungal to bacterial growth was positively affected by litter with increasing C/N ratio, while the C availability, as judged by evolved CO_2, did not have any influence. Furthermore, low pH in the soil further favoured fungal growth, irrespective of the litter type. Despite differences in fungal to bacterial growth this appeared to have little influence on respiration rates from the added litter, suggesting functional redundancy. Our results highlight how both initial soil conditions (pH) and litter composition (C/N ratio) independently affects fungal and bacterial growth during decomposition.

1. Introduction

In the Mediterranean region, forests cover an area of over 85 million ha (estimated in 2010; FAO, 2010). Trees affect the soil environment in several ways through litter fall, labile C input, rhizodeposition, root turnover and effects on soil microclimate (Eviner and Chapin, 2003). Especially the quality of litter associated with different tree species influences the microbial community (Thoms et al., 2010; Aponte et al., 2014), since leaf litter is the main energy and nutrient source for soil microorganisms. Different microbial communities were also reported in soil under different tree species (Hackl et al., 2005; Thoms et al., 2010; Schweitzer et al., 2011).

Bacteria and fungi are the main decomposer groups involved in the recycle of soil organic matter. The environmental factors determining the importance of these two groups during decomposition processes are not completely understood, although for example the canonical effect of pH has been studied recently (Rousk and Bååth, 2011), with low pH being more conducive for fungal growth. The chemical composition of the substrate (e.g. the C/N ratio) is also predicted to be of importance, with higher C/N ratio of the litter being more conducive for fungal growth due to fungal hyphae having a higher C/N ratio than bacterial cells (Paustian and Schnürer, 1987; Bakken, 1985; Wallander et al., 2003) and the potential to translocate N to overcome limitation (Frey et al., 2003). However, N availability in itself is not always enough to explain differential growth of fungi and bacteria on plant litter, as shown by Rousk and Bååth (2007) after adding extra N to litter with originally different C/N content, suggesting that other chemical and physical conditions of different litter types will be of importance. Growth of fungi and bacteria during decomposition has mostly been studied on fairly easily available substrates, like glucose (Meidute e al., 2008; Reischke et al., 2014), manure (Maienza et al., 2014) or alfalfa and straw (Rousk and Bååth, 2007). Few studies have been focused on comparing different leaf litter (Rousk and Bååth, 2011).

The aim of our study was to investigate the influences of different litter types on fungal and bacterial growth in two forest soils, differing in pH. For this purpose, leaf litters belonging to three different Mediterranean forest systems (beech, holm oak and turkey oak forests) were added to two soils (beech and holm oak) from the same mountain area. Straw and alfalfa were also included as litter treatments having very different C/N ratios. Bacterial and

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fungal growth rate was measured over time using radioactive tracer incorporation techniques (leucine incorporation and acetate into ergosterol incorporation for bacteria and fungi, respectively) and compared with total activity (respiration) and changes in total biomass (SIR). We hypothesized that fungal growth would be relatively more important than bacterial growth in the soil with lower pH, as well on litter types with higher C/N ratio.

2. Material and methods

2.1. Soils

Soil was sampled during summer 2013 from a beech (*Fagus sylvatica* L.) and a holm oak (*Quercus ilex* L.) stand, using the top layer (0–5 cm) after removing litter. Both stands are located in the Matese mountain area (Apennines district, southern Italy). A more detailed description of the two forest stands is reported in Grosso et al. (2014). Soil cores, randomly collected at each stand, were pooled to obtain a representative sample. Soil samples were sieved (<2 mm) and stored at 4 °C until the laboratory analyses. The beech forest soil had a pH of 5.3 and 16.6% of organic C, while the holm oak soil had pH of 7.2 and 16.5% of organic C.

2.2. Litter sampling and analyses

Leaf litters were collected in the two forest stands above and in a turkey oak (*Quercus cerris* L.) stand also located in the same area (see Grosso et al., 2014 for a description of this forest stand). Litters were sampled between autumn 2012 and winter 2014 by litter traps (1 m × 1 m) placed randomly in the forest stands. Annual leaf-litter forest productivity was 337, 638 and 171 g/m^2 in holm oak, beech and turkey oak stands. Litters were dried (75 °C) to constant weight, and pH in water suspension (1:50, w/v, litter:water) was determined. Holm oak, beech and turkey oak litters showed pH values in a sub-acid range (5.6, 5.8 and 4.9). Oven-dried leaf litter was ground into a fine powered by an agate mortar and pestle (Fritsch Analysette Pulverisette 0), and analyzed (CHNS-O analyzer, Thermo Flash EA 1112) for total carbon and nitrogen. C/N ratios of the litter types were: holm oak 42, beech 43, turkey oak 34. We also used wheat straw and alfalfa litters as positive controls, since straw, with high C/N (75), has been shown to favour fungal growth and alfalfa, with low C/N ratio (15), bacterial growth (Rousk and Bååth, 2007). pH for straw was 6.8 and for alfalfa 5.9.

2.3. Experimental set-up

Five dry litters (holm oak, beech, turkey oak, straw and alfalfa) were ball-milled and sieved to recover the fraction in the range of 250 μm–1 mm. The five litter types were added both to the beech and holm oak soils. A soil sample without litter addition was used as control for each soil. All the six treatments (5 litter additions and 1 control) were replicated three times per soil. Each soil replicate (25 g moist soil) were mixed with litter (0.5 g) and incubated in plastic containers with lids at room temperature (approx. 21 °C) at darkness for 42 days. The amendment rate is similar as earlier used by Henriksen and Breland (1999) and Kamble and Bååth (2014) for straw. At time intervals, basal respiration (over 27 days), microbial biomass (over 28 days), and bacterial and fungal growth (over 42 days) were analyzed.

2.4. Basal respiration and microbial biomass

Basal respiration was measured on 1 g of soil in 20 ml vials with gas tight rubber seals. The vials were flushed with pressurized air before sealing and incubated overnight at room temperature. CO_2 released was measured by gas chromatography (6500 GC system, YL Instrument).

Microbial biomass was determined by the Substrate Induced Respiration (SIR) method (Anderson and Domsch, 1978). Soil (1 g) was mixed with glucose-talcum (10 mg; 4:1 w/w), flushed with pressurized air and incubated for 2 h at room temperature. CO_2 released by microorganism respiration was then measured by gas chromatography as above.

2.5. Bacterial and fungal growth

Microbial growth rates were measured by incorporation techniques based on the addition of tracer amounts of radioactively labelled precursors, which will be incorporated into macromolecules synthesized during microorganism growth. Bacterial growth was estimated by the ^{3}H-Leucine incorporation method adapted for soil (Bååth et al., 2001). Bacteria were extracted by vortexing soil (1 g) with distilled water (20 ml), and after centrifugation (1000 x g) the supernatant with extracted bacteria was recovered (1.5 ml into microcentrifugation vials). This bacterial suspension was mixed with L-4,5-^{3}H-Leucine (2 μl, 37 MBq ml^{-1}, 1.48–2.22 TBq mmol^{-1}, Perkin Elmer) together with non-radioactive Leu (final Leu concentration 275 nM) and incubated for 2 h at room temperature. Bacterial growth was stopped by adding 75 μl of 100% trichloroacetic acid. Removal of non-incorporated Leu by centrifugation and subsequent measurement of radioactivity on a scintillation counter was as described by Bååth et al. (2001).

Soil fungal growth was measured by the ^{14}C-acetate incorporation into ergosterol method (Bååth, 2001). Soil (1 g) was mixed with distilled water (1.95 ml), unlabelled acetate (30 μl, 16 mM) and [1^{-14}C] acetic acid (20 μl, sodium salt; 7.4 MBq ml^{-1} and 2.04 GBq mmol^{-1}; Perkin Elmer), resulting in a final acetate concentration of 220 μM. After incubation for 4 h at room temperature, fungal growth was stopped by adding 5% formalin and the samples were centrifuged. The supernatant was removed and 10% KOH in methanol was added to the samples. After sonication (15 min), the samples were incubated for 1 h at 70 °C to extract ergosterol. Ergosterol was purified by phase separation, measured by HPLC (Elite LaChrome, Hitachi) to detect fungal biomass (Grant and West, 1986) and collected using an autosampler. Finally, samples were mixed with scintillation cocktail for scintillation counting analysis.

2.6. Statistical analysis

To compare the effect of litter additions for the different soils, the results are expressed as delta values, i.e. the values in the control soil (without litter addition) were subtracted at each measurement time. Cumulative values were calculated for basal respiration, bacterial and fungal growth for the whole period of soil incubation. Differences between cumulative values were tested by a two-way ANOVA with soil and different litter types as fixed factors, followed by Holm-Sidak test for comparison between groups. To differentiate between soil effects and C/N of the litter types on the cumulative fungal to bacterial growth ratio, ANCOVA on the log transformed ratios were made, with C/N ratio of the litter types as a continues factor and soil type as the fixed one.

3. Results

3.1. Respiration rate and microbial growth

The respiration rate increased after all litter additions in both soils (Fig. 1). The respiration was highest after alfalfa addition and lowest after beech litter amendment in both soils. Respiration

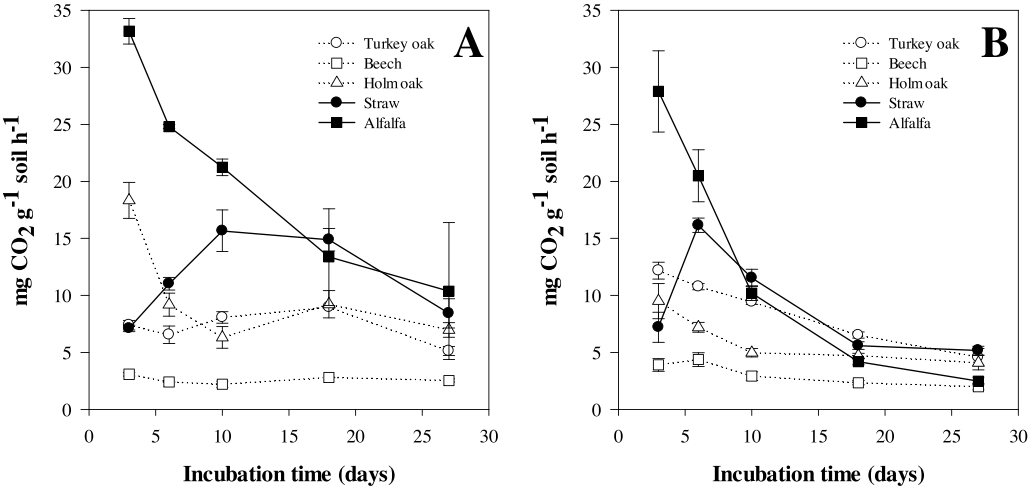

Fig. 1. Basal respiration over time in A) beech soil and in B) holm oak soil after addition of different litter types: turkey oak (open circles), beech (open squares), holm oak (open triangle), straw (black circles) and alfalfa (black squares). Bars indicate s.e. (n = 3). Values are given after subtracting mean values for the non-amended soil at each time point, i.e. only showing effects of the additives.

usually peaked, except for straw additions, after 3 days (the first measurement occasion), and then decreased over time or was similar over the 27 days incubation. Straw additions resulted in highest respiration after 6 days (holm oak soil, Fig. 1B) or between 10 and 18 days (beech soil, Fig. 1A).

Bacterial growth was especially favoured by the addition of alfalfa litter to both soils (Fig. 2). For the other litters, lower growth rates were observed, but always higher than in the unamended control. Bacterial growth rates were initially higher for turkey oak and holm oak litter than for straw and beech litter, especially in the holm oak soil (Fig. 2B). In the beech soil bacterial growth after straw addition started to increase after 10 days of incubation to a maximum rate after 28 days, resulting in even higher bacterial growth than after alfalfa addition at the end of the incubation period (Fig. 2A).

The fastest fungal growth was found with straw litter addition in both soils (Fig. 3), with highest levels after 6 to10 days. Growth was faster in beech (Fig. 3A) than in holm oak soil (Fig. 3B). In both soils fungal growth was initially higher after adding alfalfa or turkey oak compared to beech or holm oak litter.

3.2. Biomass

Adding alfalfa increased microbial biomass most compared to the other litter types in both soils (Fig. 4), with high levels already after 3 days. The other litter types promoted a lower microbial biomass, but always higher than in the control. The lowest increase was observed with beech litter addition in both soils. Generally the increase of the microbial biomass was more rapid for holm oak (Fig. 4B) than for beech soil (Fig. 4A).

3.3. Cumulative microbial activity and growth

Cumulative respiration (Fig. 5A) showed a similar trend in the two soils studied, with maximum and minimum rates after alfalfa and beech litter addition, respectively. There was a significant litter-soil interaction ($P < 0.001$, Table S1), since the cumulative respiration rate was higher following alfalfa, straw and holm oak litter addition in the beech soil compared to the holm oak soil, while there was no significant differences between soils for adding beech and turkey oak litters.

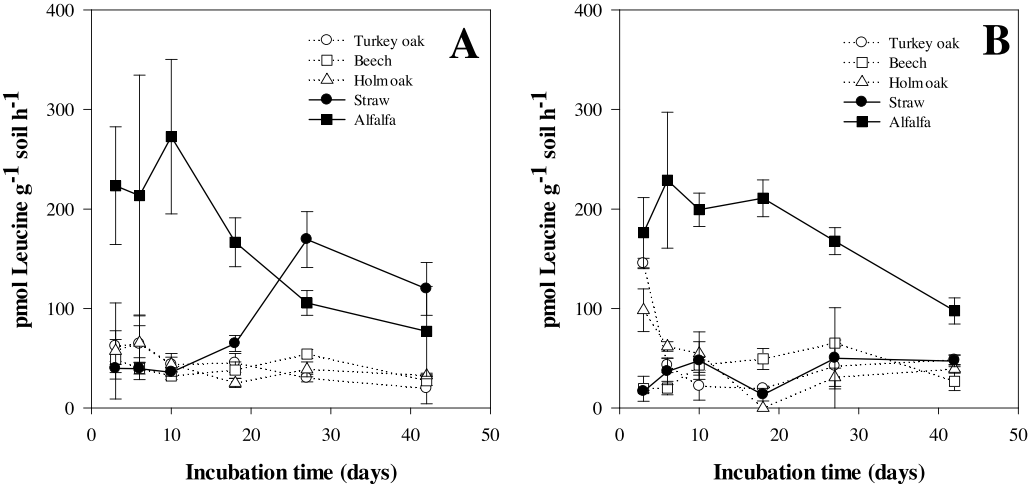

Fig. 2. Bacterial growth (leucine incorporation) over time in A) beech soil and in B) holm oak soil after addition of different litter types: turkey oak (open circles), beech (open squares), holm oak (open triangle), straw (black circles) and alfalfa (black squares). Bars indicate s.e. (n = 3). Values are given after subtracting mean values for the non-amended soil at each time point, i.e. only showing effects of the additives.

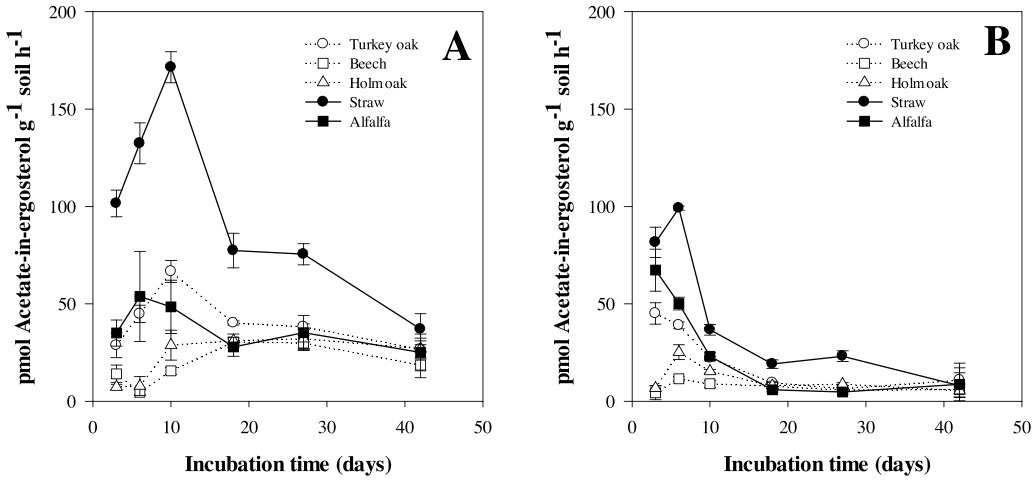

Fig. 3. Fungal growth (acetate incorporation into ergosterol) over time in A) beech soil and in B) holm oak soil after addition of different litter types: turkey oak (open circles), beech (open squares), holm oak (open triangle), straw (black circles) and alfalfa (black squares). Bars indicate s.e. (n = 3). Values are given after subtracting mean values for the non-amended soil at each time point, i.e. only showing effects of the additives.

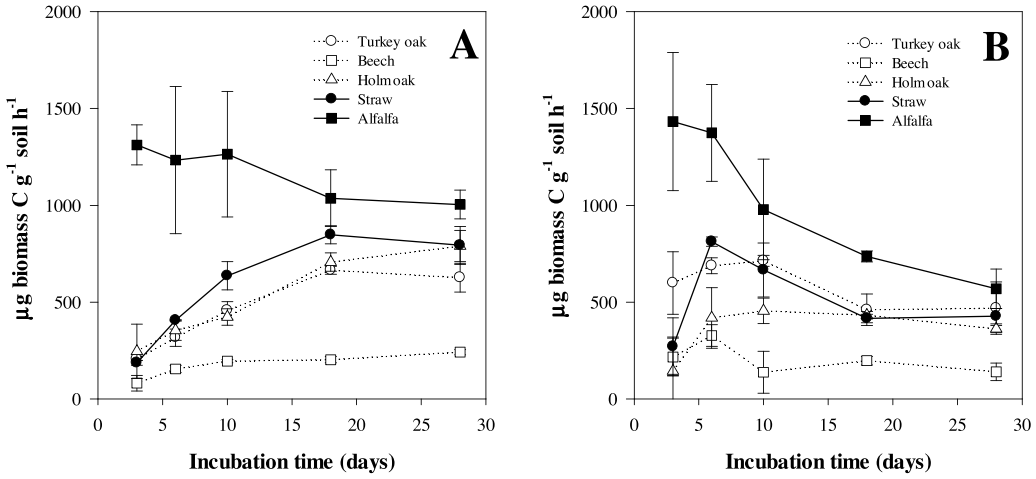

Fig. 4. Microbial biomass (SIR) over time in A) beech soil and in B) holm oak soil after addition of different litter types: turkey oak (open circles), beech (open squares), holm oak (open triangle), straw (black circles) and alfalfa (black squares). Bars indicate s.e. (n = 3). Values are given after subtracting mean values for the non-amended soil at each time point, i.e. only showing effects of the additives.

Cumulative bacteria growth (Fig. 5B) did not significantly differ between soils except for straw litter addition ($P < 0.001$), with higher growth in beech than in holm oak soil. The highest cumulative growth rate was found with alfalfa litter addition in both soils, with little difference between the other litter amendments.

Cumulative fungal growth (Fig. 5C) showed similar results in both soils with highest growth with straw litter addition and lowest after adding beech litter. Significant ($P < 0.001$) higher growth was found in beech compared to holm oak soil irrespective of the litter type. A positive correlation was found between the ergosterol content at the end of the experiment (mean of the two last time values) and the cumulative fungal growth for both the beech ($r = 0.939$; $P < 0.05$) and the holm oak soil ($r = 0.902$; $P < 0.05$).

The fungal to bacterial growth ratios (Fig. 5D) were usually higher in beech than in holm oak soil. In beech soil the highest fungal-to-bacterial growth ratio was found for turkey oak litter, being more than 5 times higher than for alfalfa litter; straw, holm oak and beech litter showed a growth ratio in between those of turkey oak and alfalfa litter. In holm oak soil the highest fungal to bacterial growth ratio was found for straw litter, more than 8 times higher than for alfalfa litter. The ratios for turkey oak, holm oak and beech litter were in between those of straw and alfalfa litter.

By plotting the C/N ratio of the litter types versus the fungal to bacterial growth ratio in the two soils, the influence of litter and soil could be separated (Fig. 6). There were no significant interactions between C/N ratio of litter types and soils (ANCOVA). This suggests that irrespective of the litter type, the soil influence was similar, with around 2 times higher fungal to bacterial growth ratio in the low pH beech compared to the holm oak soil ($F_{(1,7)} = 6.5$, $P = 0.038$). The effect of the C/N ratio of the litter ($F_{(1,7)} = 8.8$, $P = 0.021$), resulted in around 5 times higher fungal to bacterial growth ratio in litter with a C/N ratio of 75 compared with 15, irrespective of soil type.

4. Discussion

4.1. Effect of litter types

Our main finding is the importance of the C/N ratio of the different litter types in determining the balance of fungal to bacterial growth during early decomposition, with fungal growth being more important in litter low in N (high C/N ratios). This was

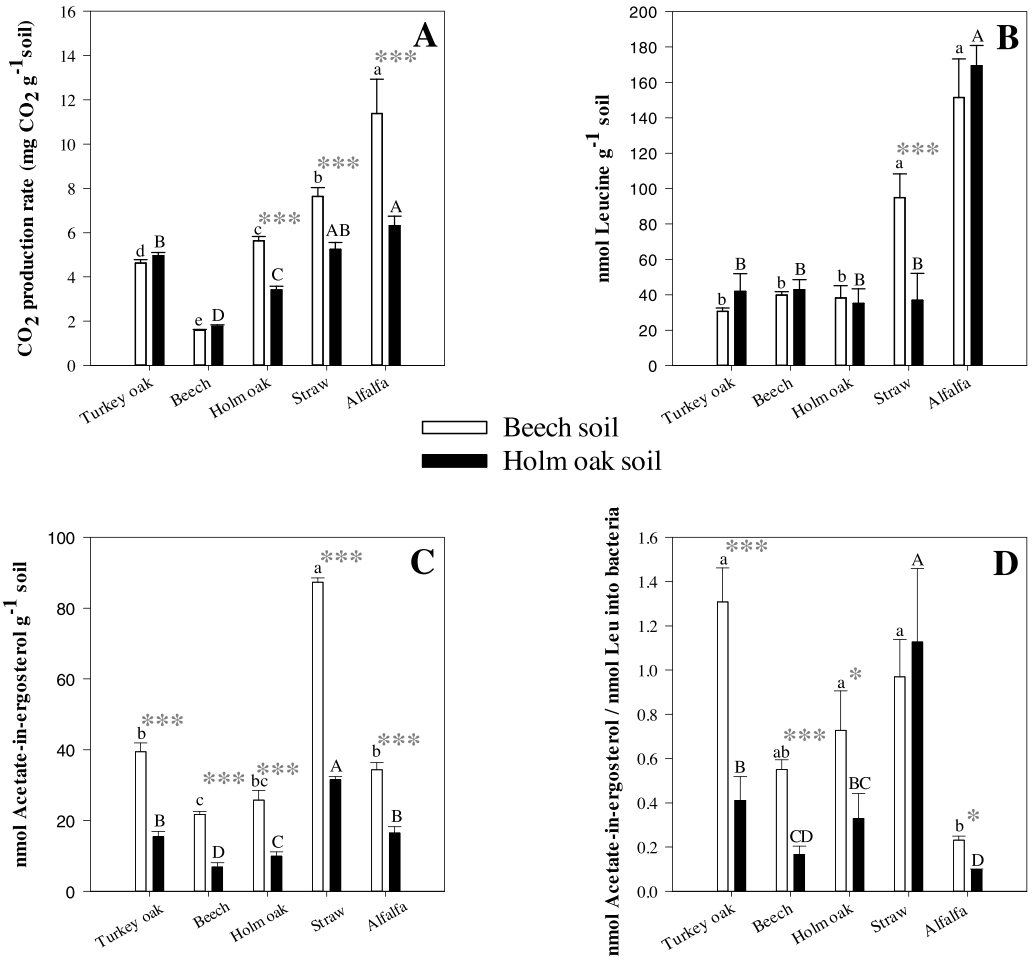

Fig. 5. Cumulative (over the total incubation period) basal respiration (A), bacterial growth as leucine incorporation (B), fungal growth as acetate in ergosterol incorporation (C) in beech (white bars) and holm oak (black bars) soils after addition of different litter types. Panel (D) shows relative fungal-to-bacterial growth ratios due to the different litter types. Bars indicate s.e. (n = 3). Values are given after subtracting mean values for the non-amended soil at each time point, i.e. only showing effects of the additives. Different letters (small for beech soil, capital for holm oak soil) indicate significant differences ($P < 0.05$) among forest systems. Asterisks indicate significant differences between soils (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

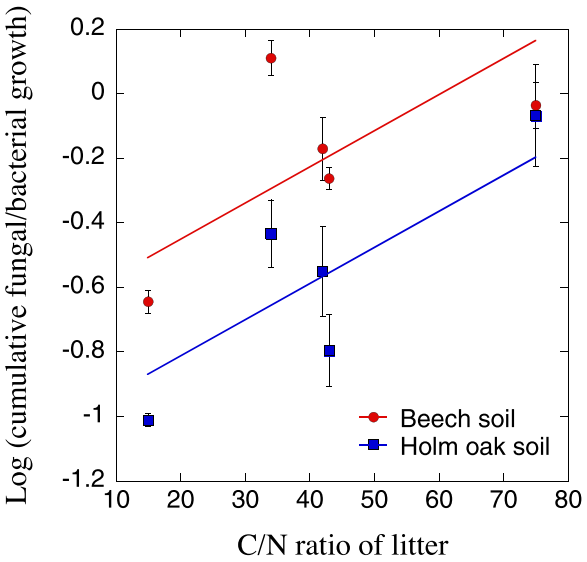

Fig. 6. The effect of C/N ratio of different types of litter on the fungal to bacterial growth ratio during 42 days decomposition in two soils with different pH (Holm oak soil pH 7.2, Beech soil pH 5.3). Lines are from ANCOVA (C/N covariate effect P = 0.021, soil type effect P = 0.038).

earlier reported for litter with C/N of 19.7 and 108 (Bossuyt et al., 2001) and when comparing alfalfa (C/N 15) and straw (C/N 75) addition (Rousk and Bååth, 2007). We got the same results for the latter two litter types, with the leaf litter with intermediate C/N values (34–43) falling in between these two extremes. Barreiro et al. (2016) studied fungal and bacterial growth after adding mulching materials with very high C/N ratios to burnt soil. In their case lowest fungal to bacterial growth ratio was found after straw addition, but since the other plant materials had C/N > 180, this is also in accordance with high C/N ratios of plant material being more conducive for fungal than for bacterial growth (Bossuyt et al., 2001). The low values of fungal to bacterial growth after adding different types of manure and animal waste in mine soils (C/N around 10 or lower; Zornoza et al., 2016) are further evidence in this direction.

Respiration rates of the added litter, indicating the availability or quality of the substrate (Fierer et al., 2006), did not correlate with the C/N ratio of the litter types, being highest for alfalfa and straw, the two litter types differing most in C/N ratio. Thus, chemical composition other than C/N ratio probably determined degradability of the litter types to a large degree. NIR spectra, characterizing the chemical composition of organic material, have earlier been shown to correlate to respiration rates during decomposition (Bruun et al., 2005). Physical structure of litter is also of importance, e.g. leaf traits like specific leaf area and leaf dry

matter content (Garnier and Navas, 2012), but due to milling and only using small particles, we most likely minimized differences in physical structure.

Straw addition eventually resulted in high respiration, although during the first days low values compared to the other litter types were found (Fig. 1). This was also the case with microbial growth (Figs. 2 and 3). One explanation is that the fresher litter types had larger amount of constituents that were easily available compared with straw. However, straw to a large part consists of cellulose, and once cellulolytic organisms started to grow, degradation, that is respiration, and growth increased rapidly.

In the beech soil growth of bacteria on straw only started to increase after around 10 days to levels even higher than the litter type most conducive for bacterial growth, alfalfa (Fig. 2A). This time point coincided with peak fungal growth (Fig. 3B). A possible explanation is facilitation, earlier described for fungal and bacterial growth on pure cellulose (Meidute et al., 2008) and on decomposing *Phragmites* leaves (Romaní et al., 2006). Fungal growth is mainly on cellulose in straw, resulting in cellulase production, which in turn results in smaller molecules like cellobiose and glucose, which can be used by non-cellulolytic bacteria. Thus, bacteria could be characterized as scavengers in this case, only starting to grow extensively once fungal cellulose decomposition has started.

4.2. Effect of soil

pH has been shown to be of utmost importance in determining the balance of fungal to bacterial growth in soil (Rousk et al., 2009; Rousk and Bååth, 2011; Zornoza et al., 2016), with low pH being more conducive for fungal than for bacterial growth. A similar soil pH influence could be inferred here, even if the microbial activity in soil was subtracted and thus only growth on the added litter was compared. Higher fungal to bacterial growth ratios were found in the low pH (beech forest) than in the high pH soil (holm oak) irrespective of litter type (Fig. 6). Thus, the pH of the soil does not only influence the balance of fungal and bacterial growth in the soil proper, but also in new organic material arriving, like fresh litter in the soil. This was earlier shown to be the case for alfalfa and straw additions (Rousk et al., 2010), but this finding is now extended to include other types of leaf litters. However, there seemed to be no consistent relation between the fungal to bacterial growth ratio and the resulting cumulative respiration among litter types, confirming a certain redundancy in this function between these two microorganisms groups, that is, whether fungal or bacteria was the main responsible group for respiration (decomposition) resulted in similar rates. This was earlier found by Rousk et al. (2009).

Soil microbial communities may adapt to decompose leaf litter from the above canopies, commonly expressed as home-field advantage (Gholz et al., 2000). Thus, the same litter type may be decomposed by different communities at different rates in different soils. However, home-field advantages appear not to be ubiquitous (Prescott et al., 2000; Chapman and Koch, 2007; St. John et al., 2011), as also shown by our results with no better decomposition of beech litter in the beech soil or holm oak litter in the holm oak soil (Fig. 5A). Ayres et al. (2009) predicted that increasing home-field advantage effects would be found the larger the difference in litter quality. Therefore, beech and holm oak litter may have been too similar to induce a home-field advantage in our study.

4.3. Concluding remarks

Our research used tracer based techniques to study soil microbial growth during microbial utilization of forest litters added to soil. By combining different litters and different soils it was possible to entangle the effect of soil pH and the effect of C/N ratio on the balance of fungal to bacterial growth, suggesting that the variation in carbon availability between litter types appeared negligible in this respect. The approach has earlier also shown the importance of the concentration of substrate added to soil on the balance of fungal to bacterial growth, both easily available (glucose; Reischke et al., 2014) and more difficult to decompose (high C/N rich plant material; Barreiro et al., 2016). It can easily be adapted to include other factors of presumed importance for litter decomposition in soil, like mineral nutrients and redox state, as well as litter effects, like degree of fragmentation. For example, the especially high fungal to bacterial growth ratio for turkey oak litter in the beech forest could not be explained by C/N ratio of litter and soil pH, but this may be due to the low pH of turkey oak litter that additionally disfavouring bacterial growth, especially in a low pH soil. Thus, the specific effect of pH of litter types, and its interaction with soil pH, on the balance of fungal to bacterial growth could be worth pursuing.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2016.07.020.

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