Bacteria Inhabiting Wood of Roots and Stumps in Forest and Arable Soils

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Abstract This chapter discusses the effect of sawdust amendment on the bacterial populations in wood and rhizosphere soil in two habitats, afforested post-agricultural sites and forests, and the interactions between bacteria and fungi inhabiting wood. We evaluated and compared the bacterial biota: (i) in two types of soil, before and after the addition of wood (in the form of pine sawdust mixed with soil) under the roots of planted seedlings; (ii) the studies were performed in autumn and spring to evaluate the influence of low temperatures on the bacterial populations, and (iii) in roots of Scots pine at plantations where stumps were previously colonized by the saprotrophic *Phlebiopsis gigantea* or the pathogenic *Heterobasidion annosum* and *Armillaria ostoyae*. The qualitative and quantitative changes in bacterial communities in soil and in wood of roots on both arable and forest soils are discussed.

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Abbreviations

COP Copiotrophs
OLI Oligotrophs
FLU Fluorescent bacteria
SPO Sporulating bacteria
ACT Actinobacteria
CEL Cellulolytic bacteria

Our results underline the following phenomena: Applying sawdust under the roots of planted seedlings increased the number of cellulolytic bacteria in all experimental treatments. On post-arable soil, adding sawdust increased the number of copiotrophic bacteria and reduced the number of Actinomycetes. In forest soils, both types of bacteria, oligotrophic and copiotrophic ones decreased in numbers simultaneously with increasing numbers of Actinobacteria in all treatments. The diversity of microbiota of pine stumps could be weakly inhibited by introduction of *P. gigantea*, The bacteria from Bacillaceae and Pseudomonadaceae were present in *Armillaria* rhizomorphs, as well as some fungal strains belonging to *Umbelopsis* spp., *Mortierella* spp., and *Trichoderma* species. All of them could be considered as potential factors that influence the rhizomorph vitality. Based on our results, seasons with harsh conditions affect the growth of bacteria belonging to genera *Bacillus*, *Paenibacillus*, *Burkholderia, Serratia*, and *Pseudomonas* in forest soils, and the occurrence of bacteria in stumps is several times lower than occurrence in soil.

1 Bacteria—Fungi Relations in the Rhizosphere, Roots and Tree Stumps

Interactions between microbes and plants are complex and act on a number of different levels. The nets of interactions in forests are more densely organized than in other habitats because of trees functioning as nodes interacting with a huge number of microorganisms and invertebrates, as well as other animals (Toju et al. 2015) Steinauer et al. (2016) state that higher plant diversity is associated with higher diversity and biomass of microorganisms in the habitat, and that is partly due to elevated root exudate diversity. Some researchers, using next generation sequencing (NGS) methods, describe these links via network analysis (Agler et al. 2016, van der Heijden and Hartmann 2016).

Bacteria and fungi inhabiting soil are dependent on hosts (roots of plants), nutrients, other microbial populations, and climatic conditions, which stimulate or inhibit their diversity (Bardgett 2011, Lau and Lennon 2011; Eisenhauer et al. 2017). Multi-faceted interactions occurring among microbial antagonists and mutualists (bacteria and fungi) play a special role. This phenomenon is a premise to use microorganisms as natural agents to control root pathogens in afforestation of

e.g. fertilized post-agricultural soils (Duda and Sierota 1987; Kwaśna et al. 2000). A factor influencing the composition of microbial communities is the availability of nutrients, such as nitrogen (N). Celar (2003) has evaluated the presence of different forms of nitrogen within a niche, because symbiotrophs and pathogens differ by nitrogen metabolism. For example, for some fungi, a specific concentration of nitrogen can stimulate sporulation (Watanabe et al. 1987) but ammonia produced by bacteria can strongly inhibit plant growth (Weise et al. 2013). On the other hand, it is largely known that Rhizobiales and other Proteobacteria are responsible for nitrogen accumulation (Hoppe et al. 2014; Lladó et al. 2017). Many rhizospheric bacteria (Vacheron et al. 2013) as well as mycorrhizal fungi (Yang et al. 2015) impact plant productivity by fixation and translocation of nutrients (Behie and Bidochka 2014; van der Heijden et al. 2015). Izumi et al. (2006) showed presence of the *nifH* bacterial nitrogenase gene, responsible for nitrogen fixation in most examined ectomycorrhizal fungi of *Pinus nigra*. The genera *Methylocella* and *Burkholderia* (Alpha- and Betaproteobacteria, respectively) were predominantly detected in these mycorrhizal associations (Izumi et al. 2006). A detailed description of nitrogen distribution in the forest environments with particular emphasis on soil bacteria has been published by Lladó et al. (2017).

In the dead wood, microbial populations also affect the levels of nutrients, besides being affected by other chemical compounds. Hoppe et al. (2014) have indicated that the C/N ratio decreases with time and wood decay intensity; however, changes in the microbial community are dependent on N content, wood density, pH, and water availability. The ratio of bacteria and fungi in the soil is a function of a variety of environmental parameters, such as CO_2 concentration, soil temperature, and precipitation (Blankinship et al. 2011; DeAngelis et al. 2015; Karhu et al. 2014; Hagerty et al. 2014; Kubiak et al. 2017c). In general, metabolism and ratio of Gram-positive and Gram-negative bacteria are predominantly influenced by temperature (Zogg et al. 1997; Bradford Bradford et al. 2008; Frey 2013; Schindlbacher et al. 2011; Giardina et al. 2014; Karhu et al. 2014; Carey et al. 2016), both in the short and in the long term. The temperature affects also beneficial interspecies interactions (Compant et al. 2010). The relationships between quantity and activity of individual components of the rhizosphere communities and microbes inhabiting root tissue, endophytes, depend on the energy needs and are the result of individual life strategies (Blaszczyk 2010). Duffy et al. (2003) state that many fungi produce antibacterial enzymes and antibiotics to counteract antagonism of many bacteria and, in some cases, even to modify their gene expression. The communities are formed spontaneously, but change over time and differ in decayed wood, humus and mineral soil.

Bacterial endophytes are not only found in green tissue, but also in wood, and their presence and composition significantly affect their host, allowing greater adaptability to environmental changes and stress, e.g., during periods of drought, nutrient deprivation, or in the presence of different fungal groups (Chanway 1997). Rinta-Kanto et al. (2016) have identified a few bacteria (with less than 2x16SDS rRNA copies g^{-1}) involved in the early stages of wood colonization and decomposition. The number of bacteria increased, however, with advanced degradation, showing up to 13×10^9 16S rRNA copies g^{-1}. The taxonomic richness of the

bacterial community in dead wood studied by Hoppe et al. (2014) was equal to approximately 250 operational taxonomic units (OTUs), where Alphaproteobacteria, Acidobacteria, and Actinobacteria strongly dominated. Within the subdominant bacteria, Gammaproteobacteria, Bacterioides, and Betaproteobacteria were present. Bacteria from the order Rhizobiales, especially *Methylovirgula*, influenced the community by nitrogen uptake (Hoppe et al. 2014).

A complex microbiome can be found inside plant tissue, and the microbial community strongly influences the plant's fitness but, in turn, is also influenced by the host (Beckers et al. 2016; Proenca et al. 2017). It is widely known that through symbiosis, organisms gain opportunities and properties that they would not have otherwise (Frey-Klett et al. 2011). However, the term symbiosis includes both negative and positive close interactions (Martin and Schwab 2012) and is rarely a dual phenomenon. The co-operation between bacteria and fungi is described in many papers, e.g. that of mycorrhizal fungi such as *Cantharellus cibarius* (Rangel-Castro et al. 2002), *Laccaria bicolor, Russula exalbicans* (Boersma et al. 2009) *Scleroderma bovista* (Yadav et al. 2015), or *Tuber* species (Deveau et al. 2016; Barbieri et al. 2005, 2007, 2010) with different types of bacteria, e.g. *Pseudomonadaceae* or *Sphingomonadaceae*. Relatively recent studies deal with viruses and bacteria living inside pathogenic and endophytic fungi occurring in plants (Hoffman and Arnold 2010, Deng et al. 2003; Xie et al. 2011). The fungal viruses complicate microbial interactions with the host (Ghabrial et al. 2015). The presence of bacteria inside fungal cells has been shown for endomycorrhizal Glomeromycota inhabiting roots of herbaceous plants (Hoffman and Arnold 2010; Miransari 2011). Endomycotic bacteria influence plant physiology via *Gigaspora margarita*, which forms arbuscular mycorrhizae (Bianciotto et al. 2004); this relation is obligatory both for fungus and the bacterium *Candidatus Glomeribacter gigasporarum* (Kobayashi and Crouch 2009). Similarly, there is a complex relation among the host plant, fungi, and bacteria in rice. *Burkholderia rhizoctonica* and *B. endofungorum* produce the virulence factor rhizoxin inside hyphae, causing rice seedling blight. These bacterial compounds are secreted by the fungus *Rhizopus microspores*, which harbors bacteria and attacks plants. Without bacterial endosymbionts, the fungi live as saprotrophs (Partida-Martinez et al. 2007).

The complexity of various microbial interactions between fungi, bacteria and viruses both in the living and decaying plant tissue as well as in the rhizosphere and soil should be considered, when developing biocontrol agents. Fungal antagonists such as *Trichoderma* are used as biofungicides for crop protection in agronomy, horticulture, and forestry (Butt and Copping 2000). Wrzosek et al. (2017) stated that the ubiquitous *Trichoderma* species with their strong antagonistic abilities demonstrated their opportunistic nature and expansion within an environment. The presence of *Trichoderma* in a community is not exclusively antagonistic; they can also exist as symbionts or endophytes in the wood of living roots and enhance growth, resistance, and nutrient uptake of the host (Chaverri et al. 2011, Harman et al. 2004). In arable soil, *Trichoderma* species and some Mucorales members can suppress *Penicillium* spp. strains and other fungi after enrichment with wood (Kwaśna et al. 2016).

The forest management often is realized by selective cutting. The remaining tree stumps are colonized by microbes that potentially act as saprotrophs, mutualists and antagonists in the new growth of trees. They could become a suitable habitat also for some root pathogens. The monitoring of microcoenoses in stumps and controlling of pathogens occurrence is preventive of forest diseases. In this regard, attention should be paid to the strong competitor *Phlebiopsis gigantea* and its impact on bacterial and fungal communities inhabiting wood tissues (Sierota et al. 2016). This fungus is used throughout Europe and Canada as a biofungicide against the root pathogens *Heterobasidion* and *Armillaria* in coniferous stands (Pratt et al. 2000). The knowledge of inter-species relations among fungi, bacteria, oomycetes, and even mites or nematodes in the wood of forest trees is constantly growing. The influence of bacterial and fungal strains could be important to the forest environment by interactions with other bioceonotic elements, which could directly affect the remaining trees. The research on the impact of *P. gigantea* treatment on bacteria in the stumps of *Picea abies* was performed by Sun et al. (2013). They concluded a negative influence on the bacterial community richness in the first months of wood decay by *P. gigantea*. However, 13 years after the *P. gigantea* treatment, the bacterial community was no longer suppressed in the stumps. Sierota et al. (2016), analyzing biota inhabiting the wood of stumps of two Norway spruce regions one year after *P. gigantea* treatment, found that bacteria represented on average 33.3% of all isolated colony-forming units (OTUs). It was noted that bacteria were often found in the northern spruce range (45.2% of all obtained OTUs from studied stumps), whereas in the south range of spruce (mountain region) the presence of bacteria was much lower in comparison to fungal strains (35.6% of OTUs). There are many possible reasons for this disparity. The observation could be related to differences in wood density, coexisting fungal taxa with antibacterial properties or difference of climatic factors. In both ranges, fungi such as *P. gigantea, Sistotrema brinkmanii, Trichoderma* spp., and *Giberella avenacea* dominated (Sierota et al. 2016).

Kubiak et al. (2017b) found that in the roots of Scots pine stumps, treated one year earlier with *P. gigantea*, some *Trichoderma viride* isolates propagated monoclonally and colonized wood more effectively than *P. gigantea*, which was not found in the deeper roots. Furthermore, in healthy roots of stumps from forest soil, the number of bacterial OTUs was twice as high as in the roots infected by pathogens, and 10 times greater in healthy roots of stumps from arable soil than infected by pathogens (Kubiak et al. 2017b). The dominating species were *Paenibacillus pini* in the healthy roots from forest soil, and *Serratia* sp. and *P. chinjuensis* in the healthy roots of arable soil. In the roots from forest soil, *Trichoderma* spp. were much more abundant in the microbial community (Kubiak et al. 2017b) than in roots from arable land. Interestingly, the bacterium *P. pini* was associated with the presence of the root pathogen *Heterobasidion annosum*, which invaded the stumps through the roots (Kubiak et al. 2017b). The relationship between *H, annosum* and *P. pini* should be studied further. If *P. pini* is a stimulator of *H. annosum* growth, treatments reducing bacterial growth may prove to be an effective remedy against this fungal pathogen.

The dieback of trees in temperate climates is also associated with other parasitic fungi, e.g. *Armillaria spp.* (Baumgartner et al. 2011). There is little research made

on the relationship of bacteria with the fungal pathogenesis and rhizomorph development. Studies have shown that in *A. ostoyae* rhizomorphs, the predominant co-existing bacteria belong to the order Bacillales, and, sporadically to Pseudomonadaceae. The microbiota colonizing the interior of the rhizomorphs are known as producers of antibiotic substances, but presumably, they are rather commensal than parasitic ones, because the rhizomorphs were sourced in good condition, vital and producing new hyphae (Kubiak et al. 2017c). However, participation of the bacterial community in the pathogenesis caused by *A. ostoyae* is not yet known. Direct co-operation or competition between fungi and bacteria in rhizomorphs has recently been observed by Przemieniecki et al. (2017) in the roots of Scots pine trees. Many fungal and bacterial components of the microbial community inhabiting the inner part of rhizomorphs were noted. Despite the antibiotic activity of *Trichoderma* spp. in the rhizomorphs, other microorganisms were also found. *Umbelopsis* spp., *Mortierella alpina, Oidiodendron flavum*, *Bacillus* spp., and *Paenibacillus* spp. were the dominant genera co-existing inside the rhizomorphs. These microbes probably can coexist with rhizomorphs and participate both in the decomposition of organic matter and in the uptake of nutrients from its environment (Przemieniecki, pers. comm.). Development within this research field seems to be urgent.

In general, products composed of wood, such as shavings and sawdust are considered to be food niches (stimulants) of microbiological colonization in pits, pastures, or arable soil environments intended for afforestation (Lopez et al. 2006). In many countries, soils from abandoned agricultural farm areas are low in humus and nutrient contents, and therefore unsuitable for effective afforestation (Caravaca et al. 2002; Wei et al. 2012). Therefore, it is interesting, from both a scientific and a practical point of view, to study the influence of different microorganisms on soil quality and seedling growth. In the following sections of this chapter, we present and discuss research on bacteria in arable and forest soils and the changes that occur after introducing sterile fragments of sawdust to soil. We also describe the assessment of the bacterial community present in the roots of stumps originating from arable and forest soils, associated with the previously introduced fungus *P. gigantea.* Both the influence of added sawdust and the winter period were assessed and compared with a control treatment as described by Kwaśna et al. (2016). Fungal communities have been investigated in a similar experimental setup earlier (Kwaśna and Sierota 1999; Kwaśna et al. 2000; Sierota et al. 2016).

2 Influence of Season and Sawdust Addition to the Soil on the Bacterial Population

Our results suggest that addition of wood in the soil generally increases the diversity of bacteria in the microbial community of forest soil, in contrast, in arable soil this results in the decrease of the bacterial diversity during single vegetation

season (Table 1). After winter, amendment of soil with sawdust significantly decreased bacterial diversity in forest soil. The ecological diversity indices showed that before the winter, the forest soil was less diverse than the arable soil, and the winter period changed the structures of the communities both quantitatively and qualitatively. In general, the values of the indices changed, most prominently in arable soil amended with sawdust. The results presented here indicate the influence of disturbances (winter stress, sawdust addition) on the stability of the communities and, therefore, presence of species with a narrow range of tolerance. In general, the number of the bacterial species was quite stable regardless of the season, but decreased after winter in the forest soil amended with sawdust (Table 1).

Some earlier studies have shown that adding sawdust both increases the soil microbiological activity and the numbers of many species (i.e. groups of species) of soil microorganisms (Bekele et al. 2007) and nematodes (Brzeski and Szczech 1999; Kwaśna et al. 2001). Such soil amendments accelerate the transition from agricultural production-supporting soils towards those typical for forested lands, which contain large numbers of fungi such as *Trichoderma* and *Penicillium* (Kwaśna and Sierota 1999; Kwaśna et al. 2000). Kwaśna et al. (2000, 2001) and Kubiak et al. (2017a) used conifer sawdust in post-arable sites under afforestation to amend the soil with an easily compostable form of wood. They confirmed that this procedure had a varying influence on the number of bacteria, depending on the type of soil, as the application of sawdust increased the wood-inhabiting populations of bacteria (Kwaśna et al. 2000, 2001, Kubiak et al. 2017a). A positive influence of

Table 1 Ecological indices for bacterial communities representing the control and sawdust amendment of arable and forest soils before and after winter

		Before winter		After winter	
Index	Soil type	Control	Sawdust	Control	Sawdust
Number of specimens *S*	Arable	14	13	15	14
	Forest	15	18	17	13
Simpson's dominance $\lambda = \sum p_i^2$	Arable	0.08	0.10	0.10	0.10
	Forest	0.11	0.07	0.10	0.13
Simpson's diversity $C = 1-\sum p_i^2$	Arable	0.92	0.90	0.90	0.90
	Forest	0.89	0.93	0.90	0.87
Simpson's diversity $D = 1/(\sum p_i 2)$	Arable	12.00	10.29	10.37	10.25
	Forest	9.00	13.89	10.37	7.74
Simpson's evenness E = D/S	Arable	0.86	0.79	0.69	0.73
	Forest	0.60	0.77	0.61	0.60
Shannon-Wiener's diversity $H' = -\sum p_i \times \ln p_i$	Arable	2.56	2.44	2.54	2.48
	Forest	2.44	2.73	2.58	2.17
Shanonn-wiener's evenness J′ = H′/lnS	Arable	0.97	0.95	0.94	0.94
	Forest	0.90	0.95	0.91	0.85

amending post-arable soil with sawdust and pieces of wood (carbon source) on total numbers (biomass) of bacteria has also been noted by Eschen et al. (2007).

In our study, bacteria described both as copiotrophs (found in environments rich in nutrients) and oligotrophs (usually present in environments with low levels of nutrients) (Koch 2001; Blaszczyk 2010; Kubiak et al. 2017a) dominated in the autumn in both arable and forest soils, but in the spring of the following year (after sawdust application), their community structure changed. The number of copiotrophs decreased in the spring of the following year and increased in the arable soil over time, but decreased in the forest soil, contrary to the number of oligotrophs (Fig. 1). According to Kubiak et al. (2017a) the number of copiotrophic bacteria was two times greater than the number of oligotrophic bacteria in arable soil one year after sawdust application and *Pinus sylvestris s*eedling growth. These results confirmed the findings of Kaczmarek et al. (2008) and Austin and Ballaré (2010), where copiotrophs multiplied intensively after the addition of decomposition-recalcitrant polymeric nutrients, such as lignin from plant remains. Overall, amending arable soils with sawdust intensifies the growth of copiotrophs, previously identified in several studies (Van Veen and Paul 1981; Lavelle et al. 1995; Neher 1999; Blaszczyk 2010; Zhao et al. 2014; Kubiak 2017a). Weyman-Kaczmarkowa and Pędziwilk (1996) showed that amendment of soils with organic matter influences microbial numbers depending on soil type, cultivation method, and environmental conditions.

Apart from the general studies on trophic relationships of micro-organisms, Kubiak et al. (2017a) analyzed the effect of sawdust application on the abundance

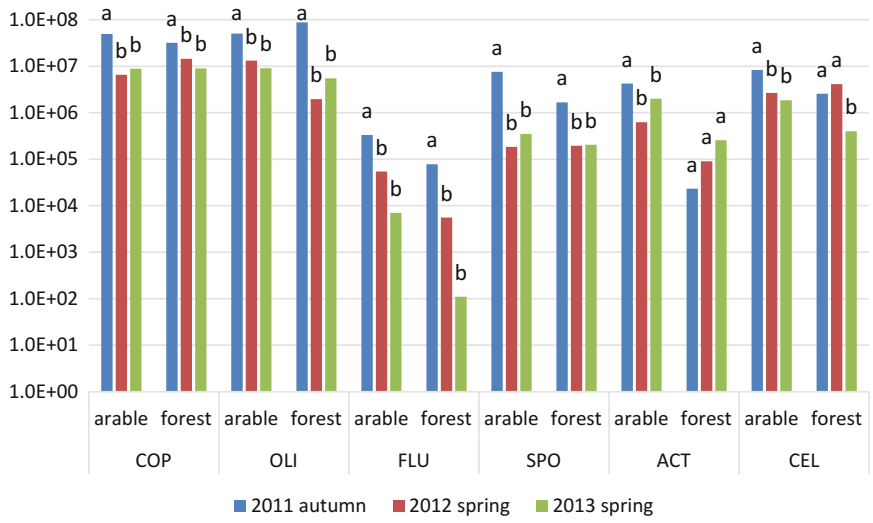

Fig. 1 Changes in number of bacteria groups (OTUs) in arable and forest soil over time (2011–2013): 2011 autumn—control soil, 2012 spring—soil amending with sawdust, 2013 spring—soil amending with sawdust (one year after sawdust treatment)

of other bacterial groups: Actinomycetes, cellulolytic bacteria, fluorescent bacteria (especially *Pseudomonas* spp.), sporulating bacteria (especially *Bacillus* spp.), which were chosen because of their specific roles in the environment. The number of Actinomycetes (*Streptomyces* spp., *Leifsonia* spp., *Streptosporangium* spp.) increased over time in the forest soil (Fig. 1), while their number decreased (*Arthrobacter* spp., *Kitasatospora* spp., *Micrococcus* spp., *Streptomyces* spp.) in the arable soil amended with sawdust in the following year and increased after two years (Kubiak et al. 2017a). This was an interesting result and might correlate with the soil type, because the abundance and diversity of Actinobacteria depend on soil conditions, such as moisture, and on the cultivation method (Nowak et al. 1993). Wyszkowska and Kucharski (2005) have also observed that the amendment of arable soil with sawdust reduced Actinobacteria by about 7%.

Numbers of cellulolytic bacteria decreased over time in the arable soil, which is quite obvious, whereas their numbers in the forest soil varied with time. After the first year of observations in forest soil, the number of cellulolytic bacteria slightly increased, but after two years significantly decreased (Fig. 1). In a study by Kubiak et al. (2017a), the addition of sawdust both to forest and arable soils increased the number of cellulolytic bacteria when the sawdust was added directly under the roots of planted seedlings, likely due to better access of bacteria to the nutrient sources and plant exudates as well thanks to soil mixing. The copiotrophs and cellulytic bacteria are present in croplands (Zvyagintsev 1991; Aira et al. 2006; Alam et al. 2011; Anderson et al. 2012), and the addition of sawdust to the arable soil probably stimulates resting spores (Figs. 1 and 2). Fluorescent bacteria mainly belonging to the genus *Pseudomonas* had higher numbers in the arable soil compared to the forest soil (Fig. 1, FLU column). This result confirms the results by Zvyagintsev (1991) and Błaszczyk (2010), who showed that *Pseudomonas* bacteria generally occur in agricultural soils rather than in the forest ground.

The winter period induced no changes the abundance of bacteria in soils but influenced the microbiome structures (Kubiak et al. 2017a) (Fig. 2a). Among the taxonomic groups in the arable soil (Fig. 2a), the most common before winter were: *Bacillus pumilus, A. oxydans, P. fluorescens*, and *Burkholderia sediminicola*, and after low-temperature stress *Streptomyces* sp., *B. flexus/B. megaterium*, *Pseusomonas* and *Paenibacillus* species. In the forest soil, before the winter, *S. atratus* and *S. scabrisporus* were the most frequent species, while after winter, the populations of *S. indigoferus, S. prunicola, S. liquefaciens, Pseudomonas* and *Burkholderia* species were most common. Based on our results, seasons with harsh conditions stimulated the growth of *Burkholderia* spp., *Serratia* spp., and *Pseudomonas* species (Kubiak et al. 2017a).

In general, the endophytic bacterial community is subject to seasonal variations in abundance and species compositions. Temperature alters plant physiology as well the metabolism of the microbial community in stumps (Classen et al. 2015). However, the concentration of nutrients has a key role in shaping microbial community inside plant tissue. Hill et al. (2013) indicates soluble sugars, proteins, amino acids, and organic acids as factors influencing bacterial composition inside a host (Fatima and Senthil-Kumar 2015). This would explain why the tree species

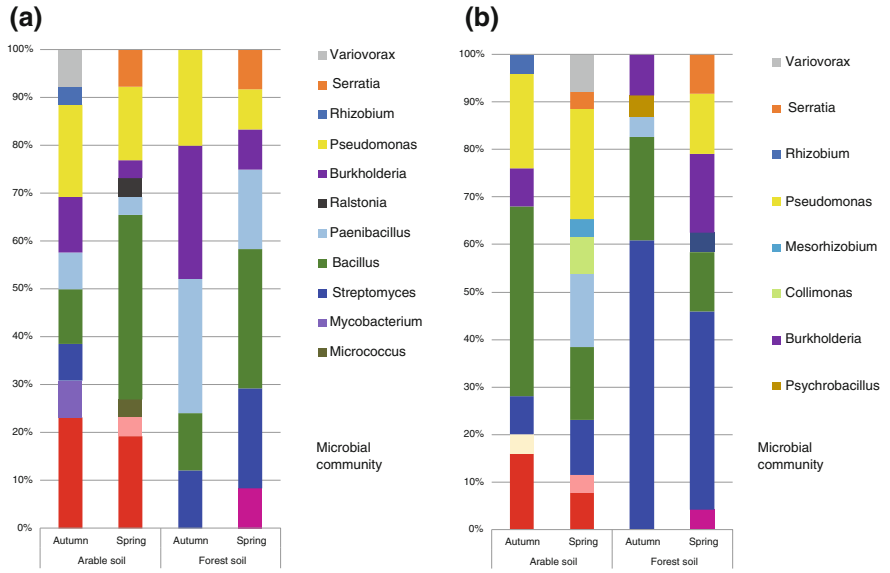

Fig. 2 Changes in the bacterial biota (%) in arable and forest soil before and after winter in control soil (**a**) and after amendment with sawdust before and after winter (**b**)

after winter stress strongly affects the endophytic community. It has also been suggested that the host plant plays an active role in colonization of endophytes by attracting specific bacteria by releasing certain compounds (Mendes et al. 2013; Nihorimbere et al. 2011) or through plant defense reactions and phytohormones (Farrar et al. 2014). Changing environmental conditions (temperature, drought, CO_2 concentration) are likely to lead to changes in the composition, abundance, or activity of plant-associated microbial communities. Consequently, microorganisms known for their beneficial effects on plant might also become impaired in exhibiting their desirable properties and their colonization capacity under certain conditions. However, the mechanism behind the influence of variable environmental conditions on plant-associated microbial communities is still unclear (Compant et al. 2010; Drigo et al. 2009).

Shen and Fulthorpe (2015) have studied endophytic bacterial communities in branches of urban *Acer negundo*, *Ulmus pumila*, and *Ulmus parvifolia* during different seasons (winter, summer, and fall). The authors used both cultivation-based and molecular methods, and their results confirmed that the endophyte communities in these tree species were strongly dependent on the season. Some bacterial genera were isolated from all plant species throughout all three seasons, namely *Bacillus* spp., *Curtobacteriu*m spp., *Frigoribacterium* spp., *Methylobacterium* spp., *Paenibacillus* spp., and *Sphingomonas* species. Also, the authors observed changes in the numbers of culturable endophytes, such as fewer Firmicutes and Gammaproteobacteria in the summer and fall relative to winter samples, and an increase of Bacteroidetes in the fall. Studies of phyllosphere of

Asclepias viridis (Ding et al. 2013), the endophytes inhabiting maple tree sap (Filteau et al. 2010), and the buds of Scots pine trees (Pirttilä et al. 2005) suggest that the main determinant of the endophyte community structure in these tree species are the seasonal fluctuations. The diversity of bacteria in the grape endosphere (Baldan et al. 2014; Bulgari et al. 2014) and the elm endosphere (Mocali et al. 2003) has also been shown to be highly dependent on the season.

Soil amendment with sawdust introduced additional changes in the structure of the microbial communities (Fig. 2b). After the winter, the numbers of Firmicutes increased in both type of soils, with greater increase in post-arable soil compared to forest soil, whereas the number of Proteobacteria (in OTUs) decreased in both soil types after winter time (Fig. 2a). In spring, the numbers of Proteobacteria increased and Actinobacteria decreased in both type of soils amended with coniferus sawdust (Fig. 2b). Firmicutes were less frequent after winter in the forest soil amended with sawdust, but in the arable soil, their numbers increased in the spring (Fig. 2b). Before and after the winter, the most dominant species of Actinobacteria were *Arthrobacter* spp. in the arable soil and *Streptomyces* spp. in forest soil (Fig. 2a). The numbers of *Bacillus* species in both types of soils increased after winter (Fig. 2a) and decreased after winter in soils amended with sawdust (Fig. 2b). *Pseudomonas*, *Burkholderia* and *Paenibacillus* species decreased after winter time in both type of soils (Fig. 2a). In soils amending with sawdust, decreasing *Arthrobacter* in arable soil and *Streptomyces* species in forest soil was observed in both type of soils after winter time (Fig. 2b). The Fig. 2 presents the major seasonal changes in soil microbiome composition during the cold season in different types of soils, and compares the microbiome of control samples with samples of soil enriched with sawdust. The general remark is the following: with respect to microbiome, the arable soil amended with sawdust is not more similar with forest soil than with arable one without sawdust. Therefore, we need more research to understand the dynamics of soil bacteria and their role in afforestation process.

The species belonging to *Streptomyces* were mostly present in forest soil. This observation is in agreement with results by Błaszczyk (2010), who reported that *Streptomyces* species are widespread in primeval forests and not as frequently observed in second growth forests and farmland soils. *Streptomyces scabies* can penetrate host plants establishing endophytic associations (Qin et al. 2009). It has also been described as an endophyte in *Quercus serrata* (Thongsandee et al. 2013). Sousa and Olivares (2016) underline multifaceted benefits provided by *Streptomyces* to plants. These are, among others, inducement of plant growth and protection against pests. Directed enrichment of arable soil with *Streptomyces* spp. suspension could be tested as an appropriate growth enhancer for tree seedlings as was tested for rice by Gopalakrisnan et al. (2014).

In the arable soil, the most dominant bacteria were *Pseudomonas* spp., but after amending with sawdust, bacteria of the genus *Bacillus* were more abundant. Addition of sawdust to arable soil decreased the amounts of *Pseudomonas* spp. and *Paenibacillus* spp., while *Streptomyces* spp., *Collilomonas* spp., *Mesorhizobium* spp., and *Variovorax* spp. were no longer detected. After amending arable soil with

sawdust, numbers of *Arthrobacter* spp. (*A. globiformis, A. oryzae*), *Bacillus* spp. (especially *B. cereus* and *B. megaterium*), and *Serratia* spp. were increased in the community, and members of *Micrococcus* spp., *Ralstonia* spp., and *Burkholderia* spp. appeared (Kubiak et al. 2017a). Originally, the forest soil was dominated by the genus *Streptomyces* (especially *S. prunicolor*), but after sawdust amendment, the genus *Bacillus* dominated, as in the arable soil with sawdust. Amending the forest soil with sawdust increased also the numbers of Actinobacteria (*Leifsonia* spp.), *Bacillus* spp. (*B. weihenstephanensis*), and *Paenibacillus* spp, whereas the numbers of *Streptomyces* spp., *Burkholderia* spp., and *Pseudomonas* spp. decreased. *Lysisnibacillus* spp., originally present in forest soil, was not detected in it after sawdust amending. The treatment had no impact on *Serratia* species (Fig. 3) (Kubiak et al. 2017a).

In the rhizosphere of pines from both soil types, amended with wood, in both seasons tested, representatives of potential endophytic life-style bacteria were present (Fig. 3). Kubiak et al. (2017a) have shown that pine sawdust stimulates the increase of bacteria belonging to the genus *Bacillus*, which is compatible with previous results described by Wright and Cornelius (2012). In this study,

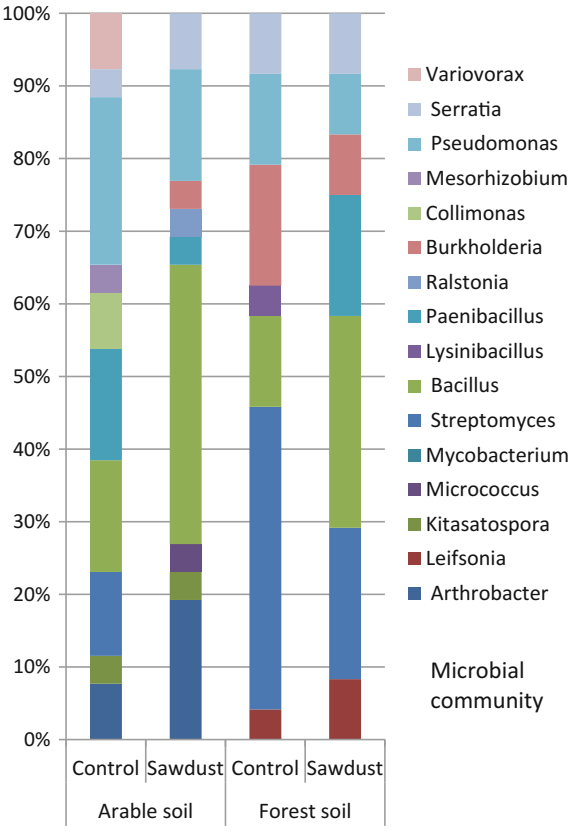

Fig. 3 Changes in the bacterial biota (%) in arable and forest soil before (C) and after (W) sawdust application

amendment of post-arable soil with sawdust increased the quantities of *B. flexus*, *B. megaterium*, *B. cereus,* and *Paenibacillus* species. Many bacteria belonging to these species have been reported with an endophytic life-style (Nongkhlaw and Joshi 2014). In the forest soil treated with sawdust, we observed increasing numbers of *B. muralis* and *B. simplex*, which have been reported previously with cellulosic activity (Trivedi et al. 2011; Shankar et al. 2014; Saha et al. 2013; Venkatachalam et al. 2014). Bacteria belonging to *Pseudomonas, Bacillus*, *Burkholderia*, Actinomycetes, and *Paenibacillus* have also been described by Enebak et al. (1998) and Izumi (2011) as plant growth-promoting rhizobacteria in forest trees such pines. They are known for their disease- and pest suppression, raising the possibility that the rhizospheric microbiome protects the trees against biotic stress (Chebotar et al. 2016; Mendes et al. 1999; Mendes et al. 2013; Raaijmakers and Mazzola 2012). Furthermore, the chelating capabilities of *Bacillus pumilus* promote soil fertilization (Gaiero et al. 2013), which is crucial in post-agricultural soils (Chanway 1997).

Representatives of *Pseudomonas* have been identified in arable and forest soil before and after winter (Kubiak et al. 2017a). *Pseudomonas fluorescens* is common in forest soils and plays an important role in mycorrhizae formation (Frey-Klett et al. 1997; Domínguez-Núñez 2013). Many members in the genus *Pseudomonas* are well known for their growth-promoting effect on forest plants and have been found, for example, in the stem of *Pinus concorta* (Bal et al. 2012) and in roots of *Pinus sylvestris* (Strzelczyk and Li 2000).

3 Bacterial Populations in Roots and Stumps

Roots of Scots pine stumps growing on post-arable and forest soils have been studied for bacteria and fungi after treatment with biological preparations containing *P. gigantea* (Rotstop SC) by Kubiak et al. (2017b). Some of the investigated roots and stumps were healthy, but some were colonized by pathogens (*Armillaria* spp. or *H. annosum)*. The majority of endophytic bacteria inhabiting the wood of pine roots belonged to Firmicutes and Proteobacteria, detected by sequencing. In the healthy stumps that had no symptoms of infection by basidiomycetous pathogens on postagricultural soil, Firmicutes accounted for 54% and Proteobacteria 45% of the community, while in stumps from forest soil comprised 72 and 28%, respectively. In contrast, in roots colonized by *H. annosum*, the incidence of Firmicutes reached up to 100% of the community in both type of soil (Fig. 4).

Within Firmicutes, representatives of *B. cereus, B. pumilus, B. subtilis; Lysinibacillus sphaericus,* and *Paenibacillus pini* were observed and were the most common in roots of healthy stumps in post-agricultural soil. Among Proteobacteria, representatives of *Burkholderia phytofirmans*, *B. sediminicola, Pseudomonas fluorescens,* and *Serratia* sp. were the most frequent species, particularly in healthy roots of stumps in post-agricultural and forest soils (Fig. 4). Among the most frequent species, *P. pini* was dominant in healthy roots of forest soil, while *Serratia* sp., *P. chinjuensis* and *P. fluorescens* were dominant in stump roots from

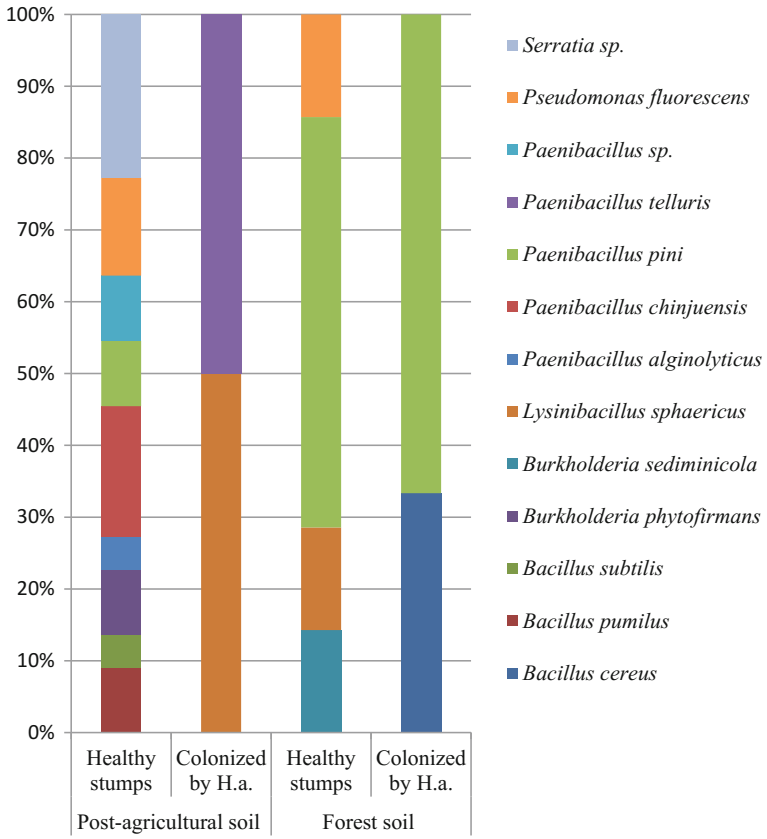

Fig. 4 Bacterial biota (%) in wood of healthy and infected roots on arable and forest soil. H.a. = *Heterobasidion annosum*

post-agricultural soil. In roots of healthy stumps, they were as common compared to stumps colonized by *H. annosum* (Fig. 4).

Several bacterial species belonging to the genera *Pseudomonas* and *Bacillus* are recognized as typically co-occurring with forest trees (Izumi et al. 2011). Izumi et al. (2008) showed that *Bacillus subtilis* and *Paenibacillus* spp. are the predominant bacteria living inside the wood of European trees. Nongkhlaw and Joshi (2014) isolated endophytes belonging to *Bacillus* sp. and *Lysinibacillus* sp. from subtropical forest plants and showed their plant growth-promoting properties. *Bacillus pumilus* is well known as an endophyte and has previously been isolated from the phloem of healthy lodgepole pine (*Pinus contorta*) (Adams et al. 2008). *Bacillus pumilus* was the most frequently isolated species from *Dicksonia sellowiana* hook (Barros et al. 2010). *B. pumilus* and *B. megaterium* have previously been isolated from pine (*Pinus contorta*) needles and stem, respectively, and endophytic *Paenibacillus* spp. were isolated from needles of *P. contorta* (Bal et al. 2012).

Endophytic *Bacillus* spp. (*B. cereus, B. licheniformis, B. pumilus* and *Bacillus* sp.) with strong enzymatic activity were isolated by Tabao and Moasalud (2010) from mangroves in the Philippines and identified as promising cellulase-producing endophytic bacteria.

Many *Bacillus* species (*B. cereus, B. subtilis, B. pumilus*) are not only growth promoters, increasing the supply of some nutrients, but also act against forest tree pathogens (Barros et al. 2010; Huang et al. 2011; Nongkhlaw and Joshi 2014). *B. subtilis* has previously been isolated from the tissue of subtropical Indian forest plants, showing a great antagonistic effect on *F. oxysporum* (Nongkhlaw and Joshi 2014). *Serratia* sp., *Pseudomonas* sp., and *Pantoea* sp. have also been isolated as endophytes and epiphytes from subtropical forests, showing plant growth promotion and antagonistic activities (Nongkhlaw and Joshi 2014). *Burkholderia* spp., present in all soil types, have previously been isolated as *Pinus taeda* endophytes and were used as biocontrol agent against *Fusarium circinatum* (Soria et al. 2012). Also, strains of *Paenibacillus macerans, Pseudomonas fluorescens*, and *Serratia marcescens* have been used in the biological control against damping-off (Enebak et al. 1998) or fusiform rust (Enebak and Carey 2000).

The highest biological diversity of endophytic bacteria was found in the roots of healthy stumps from post-agricultural soil (Fig. 4). Kubiak et al. (2017b) stated that Simpson's diversity index (D) was 2.7-fold greater in stump roots from agricultural soil than in stump roots from forest soil, while Shannon–Wiener's diversity index (H') reached values 1.8 times greater, respectively. In roots of stumps colonized by *H. annosum* both in arable and forest soil, the number of bacterial species was the lowest (Table 2).

Overall, the diversity of bacterial communities, estimated by Simpson and Shannon-Wiener indices, decreased after winter in the sawdust treatments in rhizospheric soils of both arable and forest land (slightly in arable soil and significantly in forest soil). However, our results indicate some methodological aspects in the community assessment—the winter period being a factor slightly decreasing the

Table 2 Ecological indices for endophytic bacterial communities in healthy and infected roots of stumps on arable and forest soils (*H. a.* - *Heterobasidion annosum*) (Kubiak et al. 2017b)

Species richness S	Forest soil		Agricultural soil	
	Healthy stumps	Colonized by *H. a.*	Healthy stumps	Colonized by *H. a.*
Simpson's dominance index λ	0.39	0.56	0.14	0.5
Simpson's diversity index C	0.61	0.44	0.86	0.5
Simpson's diversity index D	2.58	1.8	7.12	2
Simpson's evenness index E	0.64	0.9	0.79	1
Shannon-wiener's diversity index H′	1.15	0.64	2.07	1.39
Shannon-wiener's evenness index J′	0.83	0.92	0.94	2

numbers and diversity of bacterial communities in arable soil with and without sawdust treatment (Simpson's diversity). Forest soil amendment with sawdust significantly decreased the richness and diversity of the community after winter, whereas in control, the increased of diversity after winter was noticed (Table 1). In the wood of roots, bacterial richness was higher, in healthy roots on both soils. Likely, the bacterial biota was affected by the presence of a number of fungal taxa, as described by Kwaśna et al. (2000). The active co-existence of many bacteria and fungi in roots has also been described by Sierota et al. (2016) and Kubiak et al. (2017a, b).

4 Conclusions

Addition of organic matter to the soil changed the bacterial community structure, which can have significant effects on plant health. Moreover, bacteria can serve as food for many organisms, being both advantageous and disadvantageous for the plants. Some species of *Pseudomonas* and *Bacillus* (Bending et al. 2002), for example *Pseudomonas fluorescens* (Domínguez-Núñez et al. 2013), *B. subtilis* (Tizzard et al. 2006), and *B. pumilus* (Becker et al. 1997) stimulate plant growth, while a *Paenibacillus* sp. (Garcia-Gonzalez et al. 2014) can act as a biological control agent against diseases and pest insects. Some bacterial species can have several roles, therefore the knowledge on bacterial genus or even species level is too robust to lead to any conclusions. We need the data not only about species but even a specific strain or genotype, because bacterial metabolism can be shaped by the presence or absence of specific plasmids (Smalla et al. 2015).

The influence of bacteria on their host plants is complex and context dependent. The winter period seems to be an important factor influencing bacterial communities, as it strongly reorganizes the microbiota. In general, winter time affect the increase of *Firmicutes* and decrese in *Actinobacteria* community. In arable soil, after winter time, we observed a decrease in the overall diversity of the bacterial community, but it was less significant in soil amended with sawdust than in the soil without sawdust. In arable soil, after winter, decrease of *Actinobacteria* and increase of *Firmicutes* were noticed with or without sawdust, while amended soil with sawdust increased the number of *Proteobacteria* after winter. The addition of coniferus sawdust to forest soil, significant changed the proportion of bacterial group after the winter time.

Our results show that the diversity of endophytic bacteria is significantly higher in roots of uninfected trees than in roots infected by pathogens. The possible explanation for this phenomenon is competition between organisms of the same guild.

We propose that datamining will be used to determine the influence of dominating bacteria on plants. For example, some *Arthrobacter* species are known as bioremediators and can stabilize toxic compounds in soils, while some bacteria belonging to *Streptomyces* have antibacterial properties and could reduce the

harmful effects of pathogenic bacteria on plants (Camargo et al. 2003; Westerberg et al. 2000; O'Loughlin et al. 1999). *Burkholderia* spp. are known as a growth promoting endophytes in forest plants (Proença et al. 2017; Carrell and Frank 2015; Pandey et al. 2005) but on the other hand are able to produce compounds that are toxic for many plants (Eberl and Vandamme 2016) and can also inhibit ectomycorrhizal formation (Bending et al. 2002). Many species within this genus have antagonistic activity towards other bacteria and fungi present in the wood and rhizosphere, and can influence plant fitness. Therefore, in order to establish efficient afforestation programs, the interactions between plants and microbes and between bacteria and fungi should be understood.

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Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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