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ECOLOGY

Decomposition of Meadow and Forest Plant Roots in the Ash Substrate of Power Plant Dumps: A Laboratory Experiment

A. A. Betekhtina[a], *, O. A. Nekrasova[a], M. I. Dergacheva[b], T. A. Radchenko[a], and V. N. Bolshakov[c]

[a] *Yeltsin Ural Federal University, Yekaterinburg, 620083 Russia*

[b] *Institute of Soil Science and Agrochemistry, Siberian Branch, Russian Academy of Sciences, Novosibirsk, 630090 Russia*

[c] *Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia*

**e-mail: betechtina@mail.ru*

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Abstract—It is noted that plant roots make a significant contribution to the formation of technozems during self-overgrowing of the technogenic substrate. The rate of decomposition of a mixture of fine roots (<0.5 mm thick) of meadow arbuscular mycorrhiza species (AM) in comparison with forest ecto mycorrhiza species (EM) in the ash substrate from the power station was studied in a 150-day experiment in the laboratory. Differences in the rates of decomposition of root mixtures, as well as in carbon (C) and nitrogen (N) content before and after decomposition in different variations of the experiment, have been revealed. AM species have higher losses of biomass, nitrogen, and carbon in contradistinction to EM species.

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INTRODUCTION

Solid fuel fired thermal power stations create large areas of ash dumps. The latter are composed of coal ash, which is characterized by adverse water, thermal, and nutritional conditions, primarily the complete absence of nitrogen (N) (Pasynkova, 1974). Some ash dumps are being reclaimed, while others overgrow on their own. In the latter case, the main role in the emergence of the formed technozems is played by plant litter and the soil organic matter (OM) formed after its decomposition (Makhonina, 2003). In recent decades, it has been shown that the accumulation of OM in soil is affected by the type of mycorrhiza (Averill et al., 2014), which largely determines the carbon (C) cycle in above ground ecosystems (McClaugherty et al., 1984; Gill and Jackson, 2000; Silver and Miya, 2001).

A study of communities with dominance of ecto-mycorrhizal (EM) and arbuscular-mycorrhizal (AM) plants showed that EM fungi characteristic of forest communities contribute to the accumulation of C in the semi-decomposed litter, while AM fungi prevailing in grassy communities contribute to the rapid C cycle and the formation of fertile, humus-rich soils (Averill et al., 2014; Soudzilovskaia et al., 2015). Earlier (Dergacheva et al., 2012), it was noted that C/N in humic acids varies from 17–24 in forest soils with a predominance of EM-associated plants to 12–17 in steppe soils with a predominance of AM species.

The differences in the C cycle in ecosystems with a predominance of AM- and EM-plants are traditionally explained by the following:

EM fungi (unlike AM fungi) have specific enzymes that allow them to get nitrogen from organic sources. Therefore, it is assumed that its absorption by EM plants slows down the rate of decomposition of plant litter and increases C accumulation (Averill et al., 2014; Makarov, 2019);

in ecosystems where EM plants predominate, higher gross and net primary production of plants is observed, which ultimately leads to increased production of litter (Read, 1991; Averill et al., 2014);

EM plants secrete more C to their fungi partners than AM plants (Jones et al., 1998; Orwin et al., 2011);

the litter of EM plants decomposes twice as slowly as the litter of AM plants (Cornelissen et al., 2001; Phillips et al., 2013). The last statement more often refers to land litter. However, it was shown that plant roots make a more significant contribution to the formation of soil OM than the above ground parts of plants (Balesdent and Balabane, 1996; Ghafoor et al., 2017). The rate of decomposition of the root litter and the pathway of nutrient release are controlled by various factors, including the morphological, physiological, symbiotic, and chemical characteristics of the roots (Poirier et al., 2018). Root decomposition correlates positively with the content of N, Ca, P, and hemicellulose and water-soluble compounds and negatively with the content of C, cellulose, and lignin, as well as with the ratios C/N, lignin/N, and lignin/P (Silver and Miya, 2001; Roumet et al., 2016).

The type of mycorrhiza is the leading factor affecting the rate of root decomposition: EM roots are more resistant to decomposition than AM roots, presumably due to the dense and multilayer fungal cover and the relatively high content of hydrophobic proteins in the hyphae (Fernandez et al., 2016; Beidler and Pritchard, 2017). There is information in the literature on the decomposition of tree roots with different types of mycorrhiza and without mycorrhiza in the soil (Langley and Hungate, 2003; Langley et al., 2006). However, it must be borne in mind that the roots of different species grow and decompose together, and isolated data on the behavior of the mixture of plant roots of the community during decomposition indicate that the rate of destruction of the root mixture in the soil cannot be predicted based on the decomposition rate of its components separately (Robinson et al., 1999; Prieto et al., 2017). Interpretation of the results of studying the process of root decomposition in complex objects, such as soil, is difficult due to the interaction of a large complex of factors affecting this process. The use of technogenic substrates, such as ash from power plants, greatly simplifies the analysis of the results of studying the influence of the mycorrhiza type on the processes of destruction and chemical changes in the roots of the community. There is no information in the literature on the CN composition of the mixture of roots of either meadow or forest communities of ash dumps, as well as on the rate of their decomposition in the ash substrate and the direction of changes in the content of C and N in the process of destruction.

The purpose of this work is to analyze the features of decomposition of roots with different types of mycorrhiza in the ash substrate during a 150-day laboratory experiment for a mixture of plant roots in both meadow and forest communities.

MATERIALS AND METHODS

The substrate and root samples were taken from unreclaimed areas of the ash dump of the Verkhnii Tagil State Power Station (VTSPS) (57°20′ N, 59°56′ E) in the vicinity of Verkhnii Tagil (Middle Ural, Russia), confined to the zone with a temperate continental boreal climate.

The physicochemical characteristics of the ash substrate, determined by the generally accepted methods (Vorob'eva, 1998), made it possible to detect the predominance of physical sand in the particle size distribution of ash. The proportion of physical clay is 7–11%, which, in accordance with the soil classification (Kachinskii, 1965), makes it possible to classify it as sand or sandy loam. The predominance of particles with a diameter >0.01 mm and a low bulk density (0.72–0.97 g/cm^3) determine the friability of the ash substrate and the presence of deflation from the surface of the ash dump. Self-growing ash dumps have an alkaline reaction of the environment (pH_{water} ~ 8.3), contain, on average, 2.3% of the total organic carbon (TOC), and are characterized by a low content of mobile potassium (4–9 mg/100 g of soil) and a high phosphorus content (16–24 mg/100 g), as well as the predominance of Ca^{2+} exchange cations (2–8 mmol/100 g) compared to Mg^{2+} (0.6–0.9 mmol/100 g) (Betekhtina et al., 2019).

As a result of self-overgrowth at the VTGES ash dump over the past 50 years, both meadow and forest communities have been formed. In the meadow graminoid–forb community, cereal species such as *Calamagrostis epigeios* (L.) Roth (abundance on the Drude scale: cop1, constancy class IX) and *Poa pratensis* L. (cop1, X) predominate, as well as the following types of forbs: *Pimpinella saxifraga* L. (cop1–cop2, X), *Silene nutans* L. (cop1–cop2, VI), *Achillea millefolium* L. (sp gr, V), *Plantago media* L. (sp gr, IV), *Erigeron acris* L. (sp gr, IV), and others. In the studied areas with forest vegetation (mixed forest with a predominance of *Betula pendula* Roth. and *Populus tremula* L.), *Pinus sylvestris* L. is found singly, and *Pyrola rotundifolia* L. is found in the ground cover.

To study the characteristics of roots with different types of mycorrhiza, three 300 m^2 plots were laid in each community (a total of six plots). Root fibrils with the roots of the last order from the upper 10-centimeter part of the substrate, 4–6 samples per species at each plot (a total of 53 samples), were selected from the plants dominating in these areas. In one part of fine roots with a diameter of <0.5 mm, after fixation in a 70% alcohol solution, the mycorrhiza was analyzed. The other part, after drying at 60°C, was used to conduct an experiment and determine the content of C and N in the roots of each species using a CHNS analyzer. In selecting the roots, we were guided by the modern classification (McCormack et al., 2015), according to which all absorbing roots of the primary structure (in our case, diameter <0.5 mm) are classified as fine roots. Such roots can be considered functionally homogeneous and comparable to each other. When calculating the content of elements in the mixture of the roots of the dominant plant species of each community in the incubation experiment, their weighted average values for individual species were used taking into account the abundance of the species in a particular phytocenosis.

The development of mycorrhiza was evaluated quantitatively by generally accepted methods: for AM species, the abundance of the mycelium, arbuscules, and vesicles was taken into account, for EM species, the share of mycorrhized and degraded root endings in the total number of absorbent roots studied (Selivanov, 1981) was considered.

Fine roots with a diameter of <0.5 mm were selected for the experiment, taking into account the abundance of the species in a particular phytocenosis. For the first experiment (EM), a mixture of fine roots of two EM species *B. pendula* (0.12 g dry weight) and *P. tremula* (0.12 g) and *P. rotundifolia* (0.01 g) was com-

Table 1. Elemental composition and mycorrhization of roots of species with ectomycorrhiza (EM), and arbuscular mycorrhiza (AM)

Species	Mycorrhization intensity, %	C, %	N, %	C/N
		EM-species		
Betula pendula	86.6 ± 3.9	45.56 ± 0.99	1.41 ± 0.06	33.49 ± 2.45
Populus tremula	71.8 ± 11.5	44.73 ± 1.38	1.21 ± 0.05	37.30 ± 2.42
Pyrola rotundifolia	Low*	42.42 ± 0.63	1.28 ± 0.07	34.43 ± 2.24
		AM-species		
Erigeron acris	98.9 ± 0.6	41.46 ± 0.47	1.51 ± 0.07	27.67 ± 1.02
Pimpinella saxifraga	60.9 ± 11.4	40.76 ± 0.56	1.50 ± 0.06	27.58 ± 1.08
Plantago media	88.6 ± 3.5	42.99 ± 0.35	1.32 ± 0.04	32.90 ± 0.89
Poa pratensis	63.4 ± 8.6	43.60 ± 0.65	1.00 ± 0.07	42.50 ± 1.80
Silene nutans	6.6 ± 1.1	41.05 ± 0.42	1.11 ± 0.06	37.83 ± 1.42

* Glazyrina et al., 2012.

piled; for the second (AM) experiment, we took a mixture of fine roots of AM species *P. pratensis* (0.14 g), *E. acris* (0.01 g), *S. nutans* (0.05 g), *P. media* (0.03 g), and *P. saxifraga* (0.02 g). The root mixtures preliminarily dried at 60°C were incubated for 150 days under laboratory conditions in nylon bags. Each bag contained 0.25 g of roots and was placed in a separate plastic cup filled with 40 g of VTSPS dump ash prepared for the experiment (fivefold repetition). Ash was taken from a depth of 50–60 cm and, before the start of the experiment, was calcined at 850°C for 5 h in order to exclude completely the influence of the previous history of the ash dump functioning. Before the start of the experiment, the presence of trace amounts of C and the complete absence of N were recorded in it. During the experiment, the humidity was maintained at 60% of the total moisture capacity of the substrate with distilled water at 20–23°C. Undecomposed roots after a 150-day experiment were dried at 60°C, then weighed. The fraction of the undecomposed root mass was determined, and the contents of C and N were analyzed. Statistical analysis was performed using one-way ANOVA. The accounting unit for statistical analysis was a vessel with one bag of the root mixture.

RESULTS

Microscopic analysis showed that all selected forb species under the conditions of a self-overgrowing ash dump form mycorrhiza, including *S. nutans*, which had previously been considered non-mycorrhizal (Wang and Qiu, 2006). Mycorrhiza development ranged from 6.6% in *S. nutans* to 98.9% in *E. acris* (Table 1). The analysis also showed that, in the forest EM species *B. pendula* and *P. tremula*, one-third of the roots on the ash substrate have degenerative changes. Most (72–87%) of the nondegraded roots are populated by the fungus and have covers of various structures. In *P. rotundifolia*, mycorrhiza with single loose covers had previously been recorded in this habitat, and in some crustal cells, mycelial tangles, and fungal digestion products, fragments of the Gartig network were found (Glazyrina et al., 2012).

The concentration of C in the roots of EM species ranged from 42% in *P. rotundifolia* to 46% in *B. pendula*, and the N content varied from 1.2% in *P. tremula* to 1.4% in *B. pendula*. Therefore, C/N was naturally higher in the roots of *P. tremula* and equal in the roots of *B. pendula* and *P. rotundifolia* (Table 1). Forb plants did not differ in the C content in the roots ($F_{3, 6} = 3.38$, $P = 0.076$, where F is the Fisher test with the indicated numbers of degrees of freedom for the factor and for the error, P is the significance of differences). The highest values of this indicator were noted in *P. media* and *P. pratensis*; the smallest, in *E. acris*, *P. saxifraga*, and *S. nutans*. Different values of the N content in the roots were noted ($F_{3, 6} = 4.55$, $P = 0.04$): the highest were found in *E. acris*, *P. saxifraga*, and *P. media*; the lowest, in *P. pratensis* and *S. nutans*. The low N content in *P. pratensis* and *S. nutans* caused high C/N values compared to those of the other forb plants studied (Table 1).

Analysis of the C and N content and the C/N ratio between groups of species with different types of mycorrhiza did not yield significant differences ($F_{1, 6} = 5.00$, $P = 0.116$; $F_{1, 6} = 0.01$, $P = 0.947$; $F_{1, 6} = 0.11$, $P = 0.752$) between them.

The chemical composition of the mixture of AM and EM roots was calculated by the fraction of the root biomass in the mixture and the average values of C, N, and C/N for each species. *P. pratensis* dominated in the mixture of AM species, which was characterized by a relatively high C content and low N content in the roots; therefore, the initial mixture of AM species contained, on average, less N (1.16%) and C (42.64%) than the EM root mixture (N, 1.33% and C, 44.86%), in which aspen and birch roots with a relatively high C content and a significant variation in the N content were

Table 2. Biomass and nitrogen and carbon content in the mixture of fine roots of EM and AM species before and after a 150-day incubation

Experiment versions	Biomass, g		N, %		C, %		C/N	
	initial	after incubation*	initial	after incubation	initial	after incubation	initial	after incubation
EM	0.25	0.21(0.00)	1.33	1.47(0.02)	44.86	41.55(1.42)	33.7	28.3(0.69)
AM	0.25	0.17(0.00)	1.16	1.04(0.04)	42.64	42.36(0.58)	36.8	41.0(1.60)
P		0.000		0.000		0.616		0.000

* Mean values are given ($n = 5$), and the standard in errors are in parentheses; *P* is the significance of differences.

equally represented. The ratio of C and N was naturally higher in the AM variant (C/N = 36.8) compared to the EM type (C/N = 33.7) (Table 2).

In the EM version, during a 150-day incubation, the roots decomposed more slowly and lost 15.9% of the initial mass, in contrast to the AM variant, where the losses amounted to 34.4% (Fig. 1). In this case, the loss of C in the mixture of AM roots was 35.2 versus 21.5% in another variant, and the loss of N was 41.7 and 6.2%, respectively. As a result, in the mixture of roots in the EM variant, which were initially characterized by a higher N content, there was a relative increase in its content by 10%, while in the AM roots, there was a relative decrease by 10% of the initial amount.

DISCUSSION

As the above results showed, among AM species, a high content of C and a low content of N were characteristic of *P. pratensis*. The roots of dicotyledonous plants were characterized by a higher N content and a lower C content (with the exception of *S. nutans*, which was characterized by a low N content). Similar patterns in the content of C and N have been shown for the fine roots of grassy alpine plants in the northwestern part of the Caucasus (Salpagarova et al., 2013). In the EM species, the content of C and N and C/N in fine roots varied to a lesser extent. Plants of different types of communities did not differ significantly in the content of C, N, and C/N; however, the weighted average elemental composition of the mixture of meadow plant roots was characterized by a lower content of C and N and a high C/N value due to the dominance of *P. pratensis* roots in its composition.

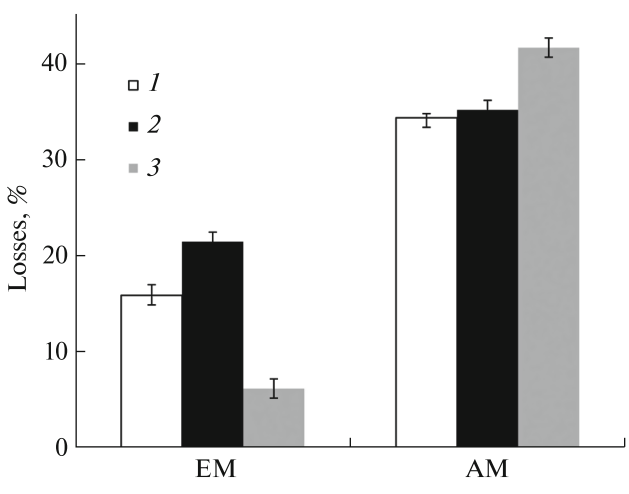

Fig. 1. Losses of biomass and carbon and nitrogen in a mixture of the roots of ectomycorrhizal (EM) and arbuscular-mycorrhizal (AM) species after 150-day incubation in an ash substrate. The mean values and standard errors are given ($n = 5$). (*1–3*) Biomass, C, and N, respectively.

Despite the higher N content, the root mixture in the ash substrate of the EM variant decomposed much more slowly than in the AM variant, which is not consistent with previously published data indicating that fine roots of plants with a high N content and low C/N in laboratory and environmental conditions decompose faster (Melillo et al., 1982; Roumet et al., 2016). A low rate of root decomposition along with a relatively high N content was observed only in *P. sylvestris* when comparing ectomycorrhiza and non-mycorrhizal roots (Langley et al., 2006). There were no close relationships between the content of C and N, as well as the C/N ratio of the root mixture and the loss of biomass during incubation in the ash substrate.

Thus, the main differences between the root mixtures did not consist in the initial content of elements in them, but in the biomass loss and different ways of changing in the C and N content and the C/N ratio during decomposition: in the case of a mixture of EM plants, the biomass loss was ~16%, and that of carbon ~22%. The N fraction in the mass of undecomposed plants with this type of mycorrhiza increased, whereas in the variant with a mixture of AM plants, the loss of biomass and C was more than two times higher, while the loss of N was 10% of its initial content in the mixture of roots. When analyzing unpublished data obtained by us when studying the litter of forest plots and grass litter in meadow plots, a close regularity of the N content was revealed: the litter of forest plots differed, on average, by the higher N content (1.77%) than the litter of meadow communities (1.18%), with a comparable content of C (37.90 and 36.60%, respectively). Therefore, meadow communities differ from forest communities in the N-composition of not only the semi-decomposed roots, but also the leaf litter. The relative enrichment of N during decomposition of the litter of EM plants is aimed at maintaining a high N content in decomposition-resistant organic compounds. Since the main source of N in EM plants is OM litter, the accumulation of N in the root litter can be of great importance for the nitrogen nutrition of woody plants in the next growing season.

According to some data, the content of C and N may be of value for assessing the decomposition of plant roots only if different species of the same life form are compared (Mao et al., 2011). We studied the rate of decomposition of a mixture of grass roots by comparing it with the rate of decomposition of a mixture of roots of woody plants, and the chemical composition of tissues and fungi of grass roots of AM and EM of woody plants was fundamentally different. Roots with EM have a higher fraction of fungal structures (20–40%) than AM roots, in which this share is only 3–17% (Langley and Hungate, 2003). The main structural polymer of fungi is chitin, which is rich in N (its mass is 7%), but it is resistant to decomposition (Swift et al., 1979). EM fungi contain hydrophobic proteins that cover the outer walls of hyphae and make them waterproof, which slows down their enzymatic decomposition (Fernandez et al., 2016). In addition, EM roots may be more resistant to decomposition due to the dense structure of the mushroom cover (Beidler and Pritchard, 2017). Indeed, the experimentally studied mixture of EM roots was characterized not only by weak losses of C, but also by significantly lower losses of N. The latter may indirectly indicate resistance to decomposition of hyphae of EM fungi.

In the modern literature, there is practically no data on the rate of decomposition of the root mixture in technogenic substrates depleted in N, such as ash, as well as accurate quantitative data on the losses of C and N during decomposition of the root mixture with different types of mycorrhiza. It has been stated that root decomposition usually depends on the presence of N in the soil, which is positively related to the concentration of N in the root, as well as the activity and number of destructors (Fog, 1988; Manning et al., 2008). Moreover, the question of the relationship between the root decomposition and the availability of substrate N still does not have a clear answer. In some studies, it was found that the decomposition rate increases significantly with increasing availability of N (Van der Krift et al., 2001; King et al., 2002), while in others there was no similar dependence (King et al., 1997; Ludovici and Kress, 2006).

Our results on the rate of decomposition of a mixture of roots with different types of mycorrhiza will help to reveal the general patterns of accumulation of one of the most important biogenic elements—C and N—in a technogenic substrate and its transformation into a technogenic soil with fertility. The root decay of EM species is a large pool of organic C and N, which is slowly mineralized and is important for the accumulation of these elements in ecosystems at the initial stages of succession when populating substrates depleted in N (in ash). It was previously shown that the type of mycorrhiza is of great importance for the C and N cycles due to indirect absorption and decomposition of nutrients in the plant–fungus–soil system (Averill et al., 2014). In our work, a direct effect of the mycorrhiza type on the direction of changes in the content of C and N in the litter of roots during decomposition at the initial stages of soil formation was established.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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