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DEGRADATION, REHABILITATION, AND CONSERVATION OF SOILS

Biochemical Stability of Water-Soluble Organic Matter in Tundra Soils of the Khibiny Mountains during Postfire Succession

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Abstract—The dynamics of the content of water-soluble organic matter (WSOM) and its resistance to microbiological transformation in the Entic Folic Podzol of the postfire succession in the dwarf-shrub mountain tundra of the Khibiny Mountains are studied. A medium-intensity fire does not cause a statistically significant decrease in the soil WSOM content as compared to the reference plot. The activity of WSOM mineralization is mainly determined by the WSOM properties rather than by the microbial community. The dynamics of biodegradation is adequately described by a two-component first-order exponential model with a statistically significant existence of fast-mineralized (mean residence time, <1 day) and slow-mineralized (mean residence time, 33 to 111 days) pools. The maximum share of the fast pool is typical of the soil immediately after a fire and smoothly decreases during further postfire succession. During biodegradation, a biokinetic selection of the aromatic hydrophobic compounds most resistant to microorganisms is observed, while the simple nitrogen-containing components of WSOM are the first to be consumed by microorganisms.

Keywords: biodegradation, mineralization, wildfire, Entic Folic Podzols

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INTRODUCTION

Water-soluble organic matter (WSOM), a complex mixture of components and metabolic products of plants, microorganisms, and soil fauna [14], plays a key role in the cycle of carbon and other elements, first and foremost, nitrogen and phosphorus. WSOM is involved in the regulation of manifold chemical and biological soil processes, including the intensity of soil respiration, as well as determines the soil redox regime and acid–base balance [14, 39, 58]. In its nature, WSOM is a heterogeneous group of organic substances differing in their resistance to microbial transformation. The microbial transformation here should be understood as (1) the processes involved in degradation of organic molecules with carbon incorporation into microbial cells and (2) their complete degradation with evolution of CO_2 as the final product [39]. Depending on the origin, 10 to 93% of soil WSOM can be metabolized by microorganisms [21, 32–34, 57]. The WSOM resistance to biodegradation is an important feature that controls the dynamics of this soil organic matter fraction, which directly influences the balance of carbon binding and mobilization by soils. As has been shown [32, 42], the soil WSOM pool is dividable into two fractions that differ in their mineralization rate. A better insight into the role of WSOM in the total carbon sequestration in soils requires determining the ratio of these fractions and the mean residence time (MRT) of carbon.

Although WSOM is the metabolic product of all soil organisms and these sources are hardly separable [14], the WSOM content and properties are to a considerable degree determined by the vegetation cover [37, 38, 56]. As has been shown, the WSOM content in forest soils is higher as compared with pastures or farmlands [27, 50, 56]. However, the WSOM of forest soils is more resistant to microbial degradation as compared with the agricultural ecosystems and the degree of this resistance depends on the composition of tree species [11, 36, 49]. A change in the phytocenosis entails a change in the taxonomic composition of microorganisms, which influences the WSOM availability for degradation in the soil [15, 33].

Soil pollution as well as natural and anthropogenic catastrophes influences the WSOM content and resistance to biodegradation. A detailed understanding of the processes underlying the WSOM formation and degradation during anthropogenic impacts on soil is important to predict the rate of restoration and the changes in the biological processes involved in carbon cycle as one of the fundamental soil characteristics. In particular, a twofold decrease in the resistance to microbial transformation was observed for the WSOM of the spruce stand litter in the Kola Peninsula situated

in the area affected by nonferrous metallurgy plants as compared with the WSOM of the litter in a reference site [11]. As has been earlier shown, the oil pollution of peat gley soil and its reclamation using wastewater residue influence not only the total WSOM content in the surface horizons, but also its biochemical stability [8]. The research into the effects of wildfires on forest soil WSOM gives rather contradictory data. In particular, the impact of fire raises the moisture-repellant ability of the soil surface layer, thereby increasing the surface runoff and loss of large WSOM volumes [52]. While a considerable decrease in the content of dissolved organic carbon in the postfire peatlands has been reported [18, 55], some data demonstrate a short-term increase in the WSOM content after fire [19]. In addition to the change in the total WSOM amount, its composition also changes [18]. Note that a thermal impact causes formation of condensed aromatic compounds, which, as a rule, are more resistant to microbial activity. On the other hand, these compounds are gradually oxidized and acquire higher water solubility with time after fire [26, 44]; their availability to biodegradation increases as well [40].

The goal of this work was to assess the resistance of soil WSOM to microbial transformation at different stages of postfire succession.

OBJECTS AND METHODS

Tundra plots in the Khibiny Mountains (Murmansk Oblast, Russia) immediately after a medium-intensity fire (2 weeks after the fire) and the ecosystems with different durations of postfire self-restoration of their plant cover and soils (1, 2, 3, 7, 12, and 60 years) were examined. The plots exposed to the north or northeast situated at an altitude of 600–650 m above the sea level were selected. The fires were dated according to the archive data of the Avrorin Polar Alpine Botanical Garden-Institute and own observations. Dwarf shrub ecosystems, most vulnerable to wildfires (because of their location in the driest sites on ridge slopes and slow mineralization of the organic matter in combination with abundant dwarf shrubs and lichens, were selected as control plots. The studied ecosystems were comprehensively described earlier [9, 10].

The soil of the control plot is Entic Folic Podzol [29]. The soils at all stages of postfire succession have organic horizons retaining the signs of a pyrogenic impact. The lower part of the soil profile has properties typical for Entic Folic Podzol. The samples for analyses were taken from the surface organic (pyrogenic) soil horizons.

The total carbon (C_{tot}) and nitrogen contents in samples were determined using an Elementar Vario EL III analyzer. WSOM was extracted from fresh soil samples with deionized water at 20°C at a soil to water ratio of 1 : 10. Before determining WSOM concentration, the solutions were centrifuged at 4500 rpm for 20 min and filtered through a membrane filter (pore size, 0.45 μm; cellulose acetate, OE 67; Schleicher and Schuell). The concentrations of WSOM carbon (C_{WSOM}) and nitrogen were determined using an automated liquiTOC Elementar (Germany) analyzer.

The differences in soil microbial activity at individual stages of postfire succession were assessed according to the mineralization rate of glucose solution (10 mg C/L). In order to prevent the inhibition of microorganisms growth by the availability of mineral components, the solution was supplemented with ammonium nitrate and potassium phosphate in a 1 : 20 : 200 stoichiometric ratio of C : N : P, which corresponds to a real ratio of these elements in extracts. The ready solutions were inoculated with 100 μL of soil suspension and incubated for 10 days at a constant temperature of 20°C. The soil suspension for inoculation was prepared by incubating the soil weighed sample (~5 g) with a natural moisture content for 24 h at 20°C, supplementing it with 30 mL of deionized water, and mixing in a vortex for 1 min.

The mineralization constant for glucose was determined using the following one-component first-order exponential regression equation:

$$C_0 = (100 - a) + ae^{-kt},$$

where C_0 is the share of mineralized glucose relative to its initial concentration, %; *a,* share of mineralizable pool, %; *t,* incubation time, days; and *k,* mineralization rate constant, day^{-1}. Nonlinear estimation using the least square method was conducted using STATISTICA 10.0 (StatSoft, Inc. (2011) STATISTICA (Data Analysis Software System). The approximation accuracy of experimental curves was >0.95.

The degradation kinetics of WSOM was determined during the incubation of soil solutions. When necessary, soil extracts before the experiment were diluted with deionized water to the concentration of water-soluble carbon below 10 mg/L to level the initial experimental conditions and prevent the excessive growth of microbial biomass [24]. The solution of WSOM (200 mL) extracted from each examined soil was placed into 500-mL glass flasks and inoculated with soil suspension (100 μL). In the first variant of the experiment, samples were inoculated with the suspension of the soil used for extraction, which allowed the actual soil WSOM resistance to microbial degradation at different stages of postfire succession to be assessed. In the second variant, all extracts were inoculated with the suspension of control soil. This allowed the differences in the activity and composition of microorganisms in different soils to be leveled and the patterns of WSOM biodegradation to be estimated depending on its properties. After inoculation, the flasks were covered with Parafilm, permeable for gases but preventing water evaporation. The solutions were incubated for 42 days in the dark at a temperature of 20°C at a constant mixing in an orbital shaker with

Table 1. Dynamics of the total and water-soluble carbon contents in tundra soils during postfire succession (mean ± error of the mean)

Ecosystem	C_{tot}, %	C/N_{tot}	WSOM	
			mg C/kg	% of C_{tot}
0+	29.6 ± 4.0	22.9 ± 2.5	1456 ± 200	0.49
1+	20.3 ± 3.2	23.9 ± 1.1	659 ± 39	0.32
2+	10.3 ± 2.6	23.7 ± 1.5	769 ± 92	0.75
3+	12.2 ± 3.9	19.3 ± 0.3	644 ± 72	0.53
7+	16.4 ± 2.2	21.0 ± 1.5	792 ± 87	0.48
12+	24.6 ± 4.0	23.2 ± 1.3	980 ± 85	0.40
60+	36.7 ± 2.1	27.2 ± 1.1	1092 ± 171	0.30
Control	31.9 ± 2.7	26.5 ± 2.8	1521 ± 389	0.48

sampling on days 1, 2, 3, 5, 7, 10, 14, 28, 36, and 42 of incubation. The samples were analyzed as described above.

The ratio of the fast- and slow-mineralized pools in WSOM was determined using two-component first-order exponential regression equation,

$$C_0 = a\left(1 - e_1^{-kt}\right) + (100 - a)\left(1 - e_2^{-kt}\right),$$

where C_0 is the share of mineralized WSOM relative to its initial concentration, %; *a,* share of fast-mineralized pool in WSOM, %; $(100 - a)$, share of slow-mineralized pool in WSOM, %; *t,* incubation time, days; k_1 is the rate constant for fast-mineralized WSOM, day^{-1}; and k_2 is the rate constant for slow-mineralized WSOM, day^{-1}. Nonlinear estimation using the least square method was conducted using STATISTICA 10.0 (StatSoft, Inc. (2011) STATISTICA (Data Analysis Software System). The MRT for the fractions was computed as $MRT_1 = 1/k_1$ and $MRT_2 = 1/k_2$.

The absorption of WSOM solutions in ultraviolet range at a wavelength of 254 nm (A_{254}) was determined before and after incubation in a Specord 50 (Analytik, Jena, Germany) spectrophotometer. The degrees of WSOM hydrophobicity and aromaticity were calculated using the specific ultraviolet absorption coefficient

$$SUVA_{254} = \left(A_{254}/C_{WSOM}\right) \times 100,\ L/(mg\ m)\ [28, 54].$$

All incubation experiments were performed in triplicate. Results are presented as the mean ± one standard error; the data are calculated per absolutely dry soil (105°C, 12 h). Statistical analyses were conducted using STATISTICA 10.0 (StatSoft, Inc. (2011) STATISTICA (Data Analysis Software System). The effects of the fire factor on the soil and WSOM properties were assessed with one-way ANOVA. The significance of the differences between the samples was estimated using *t*-test and the correlation between the parameters, using Pearson's test. Several characteristics were additionally assessed with the principal component analysis. For all types of statistical processing, the differences at $p < 0.05$ were regarded as statistically significant.

RESULTS AND DISCUSSION

Dynamics of the Total Organic Matter and WSOM Contents in Soils

One-way ANOVA did not show any statistically significant effect of a medium-intensity fire on the total carbon content in the soil (Table 1). The main trends of the changes in the total carbon content and stock in postfire soils have been earlier described [9]. The total organic matter of Entic Folic Podzol is poorly enriched in nitrogen, which well agrees with the earlier published data for these soils [2, 6, 7]. A pyrogenic impact enriches the organic matter with nitrogen (statistically significant difference between the postfire and control variants at $p < 0.035$). The observed trends are similar to the earlier described patterns for forest ecosystems, which display the nitrogen enrichments of organic matter during the first years after a wildfire [1, 13]. The C : N ratio grows during the further postfire succession except for the soil of a 3+ burnt plot with an increased nitrogen content in soil organic matter. We explain this fact by an active colonization of this 3+ burnt plot by mosses [9] and an increase in fixation of atmospheric nitrogen since symbiotic organisms are the main players in nitrogen fixation in the acid and cold tundra and high mountain soils [48]. As has been earlier shown, the epiphytic cyanobacteria are the main contributors to nitrogen fixation under moss synusiae in the Khibiny Mountain tundra belt, while heterotrophic organisms have insignificant effect on the intensity of nitrogen fixation [3].

The content of water-soluble carbon in the soils of a postfire succession tightly correlates ($r = 0.81$, $p < 0.05$) with the total carbon content in soils. Wildfires do not cause any statistically significant decrease in the WSOM carbon in the soil as compared to the control plot. A long-term postfire change in the soil WSOM pool follows the dynamics of C_{tot} with its decrease in the first years after the fire and subsequent increase with the restoration of vegetation. These patterns were earlier considered in detail [9]. Similar to the total

organic matter, wildfire has no effect on the C : N ratio in WSOM (Fig. 1). In the first years after a fire, the C : N ratio increases because a stable vegetation cover is absent and there is no falloff. However, the nitrogen enrichment of WSOM smoothly increases starting from the 3rd year after fire. This fact agrees with the earlier observed dynamics of nitrogen fixation in the soils of postfire tundra ecosystems [10].

A direct fire impact causes a decrease in the specific ultraviolet absorption (statistically significant at $p < 0.001$; Table 2). This characteristic reflects the share of different (mostly hydrophobic) aromatic structures in WSOM [43]. The decrease in the share of aromatic compounds in WSOM caused by fire is explainable by the formation of soluble aliphatic products of hemicellulose and cellulose since a medium-intensity fire primarily affects the living ground cover and litter, while a direct impact on the soil organic horizon is as a rule less pronounced. The degradation of cellulose in the soil and litter of larch stands at a temperature of approximately 200°C was reported earlier [12]. An increase in the content of hexoses in WSOM may also result from lysis of microbial cells [17]. In the subsequent postfire succession, $SUVA_{254}$ value also increases because of a larger volume of falloff and its transformation to the WSOM carrying a higher share of aromatic compounds. According to earlier studies, WSOM mainly consists of the products of photosynthesis, confirming the assumption that WSOM is formed via litter degradation [22, 30, 47]. In addition, characteristic of the tundra plants is accumulation of large amounts of phenolic compounds in tissues and, correspondingly, in the litter, which is a mechanism underlying their adaptation to stressful environmental conditions, first and foremost, low temperature and poor availability of nutrients [51].

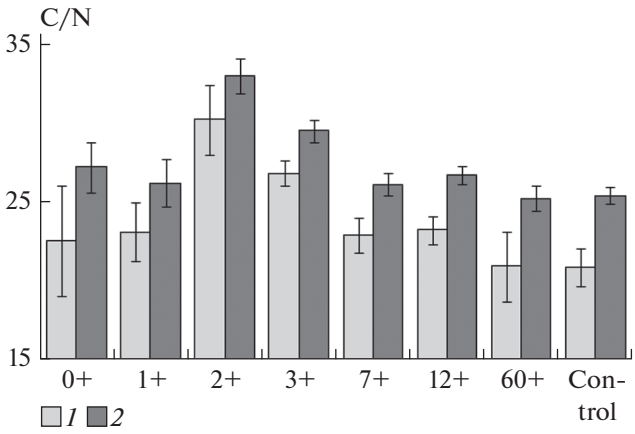

Fig. 1. The ratio of carbon and nitrogen in soil WSOM (*1*) before and (*2*) after incubation: 0+, soil 2 weeks after fire; 1+, 2+, 3+, 7+, 12+, and 60+, soil 1, 2, 3, 7, 12, and 60 years after fire, respectively; and control ecosystem.

Kinetics of WSOM Mineralization

Mineralization of glucose. Similar dynamics of glucose mineralization by microorganisms are characteristic of soils at different stages of postfire succession. The total share of glucose mineralized over 10 days of incubation amounted to 94.7 ± 2.0% for all examined soils. The mineralization rate constant for glucose (k) correlates with the carbon content in soil microbial biomass ($r = -0.84$, $p < 0.05$) and the MRT of mineralized fraction is 1.16 ± 0.12 days.

WSOM mineralization. Over the incubation period (42 days), 45 to 75% of soil WSOM are transformed by microorganisms. This ratio of mineralized and nonmineralized components of WSOM in general matches the earlier published data [21, 32, 33, 46, 57] that 10–56% of the WSOM is mineralized. However, this rate may reach 75% [26] and even 93% [32, 33] in the case of fresh forest litter.

In the first years after a wildfire, the total share of mineralized soil WSOM (% of C_{WSOM}) smoothly decreases to reach its minimum in the 2+ burnt plot (Fig. 2). During the further succession, a drastic but short-term increase in the share of mineralized organic matter in the total WSOM pool is observed followed by another decrease in this share. As for the burnt sites aged 7–60 years, the share of mineralized WSOM smoothly increases to the values characteristic of the control plot (that have not experienced a fire) in 60+ soil. Analogous temporal dynamics were described for the pool of potentially mineralizable organic matter of these soils [9]. Similar to the potentially mineralizable soil organic matter, we relate the changes in the WSOM resistance to microbiological mineralization to the dynamics of vegetation cover on burnt sites. In particular, the absence of fresh organic matter input via plant live secretions and waste during the first years after a fire not only reduces the WSOM pool, but also decreases the share of readily mineralizable organic matter there. A 3+ burnt plot has a formed moss cover (primarily, *Polytrichum juniperinum*) with commenced active colonization by herbaceous plants (*Festuca ovina* and *Chamaenerion angustifolium*) and ericaceous

Table 2. Specific ultraviolet absorption of WSOM ($SUVA_{254}$), L/(mg m)

Ecosystem	Before incubation	After incubation
0+	0.99 ± 0.08	2.60 ± 0.47
1+	1.40 ± 0.15	2.38 ± 0.45
2+	1.93 ± 0.12	2.50 ± 0.16
3+	1.70 ± 0.20	3.47 ± 0.82
7+	2.38 ± 0.30	3.61 ± 0.84
12+	2.25 ± 0.45	3.80 ± 0.75
60+	2.00 ± 0.30	3.09 ± 0.29
Control	2.22 ± 0.25	4.52 ± 0.19

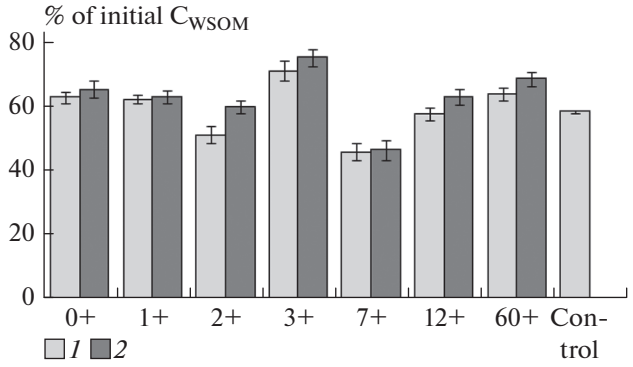

Fig. 2. The share of mineralized WSOM during postfire succession of soil when inoculated with (*1*) own microorganisms and (*2*) microorganisms of control soil.

dwarf shrubs, thereby replenishing the WSOM pool. Further, the composition of the plant community changes so that shrubs and lichens restore their prevalence and the share of grasses and mosses decreases. However, the latter are still more abundant as compared with the reference community, which creates the conditions for formation of the WSOM more susceptible to microbial degradation.

As was demonstrated by principal component analysis, two factors explain 80.2% of the sampling variance of the share of mineralized organic matter in the total WSOM pool (Fig. 3). The first factor explains 63.3% of the variations and most tightly correlates with C_{tot}, C/N_{WSOM}, C_{mic}, and C/N_{mic}, i.e., with the properties of soil itself, soil WSOM, and microbial biomass. The second factor explains 16.9% of the variance and correlates with $SUVA_{254}$.

A comparison of the shares of mineralized WSOM after inoculation with the soil used for extraction and control soil shows no statistically significant differences for most samples (Fig. 2) except for a 2+ burnt plot, which has the least microbial carbon content (912 ± 140 mg/kg [10]). Thus, the WSOM biochemical stability in the postfire soils of mountain tundra is determined at almost all stages of succession by the properties of the organic matter itself rather than the by the properties of the microbial community degrading it. Correspondingly, the remaining studied parameters will be regarded as the mean for two variants of experiment.

The rate of WSOM degradation in all variants of the experiment was the highest in the first 3–5 days of incubation and further considerably slowed down. This pattern has been earlier observed for other soils [4, 11, 24, 32, 53]. The data on WSOM degradation dynamics are well approximated ($R^2 > 0.95$) with a two-component first-order exponential regression equation, which suggests the existence of two pools differing in their kinetic characteristics, namely, fast-mineralized and slow-mineralized WSOM pools. The

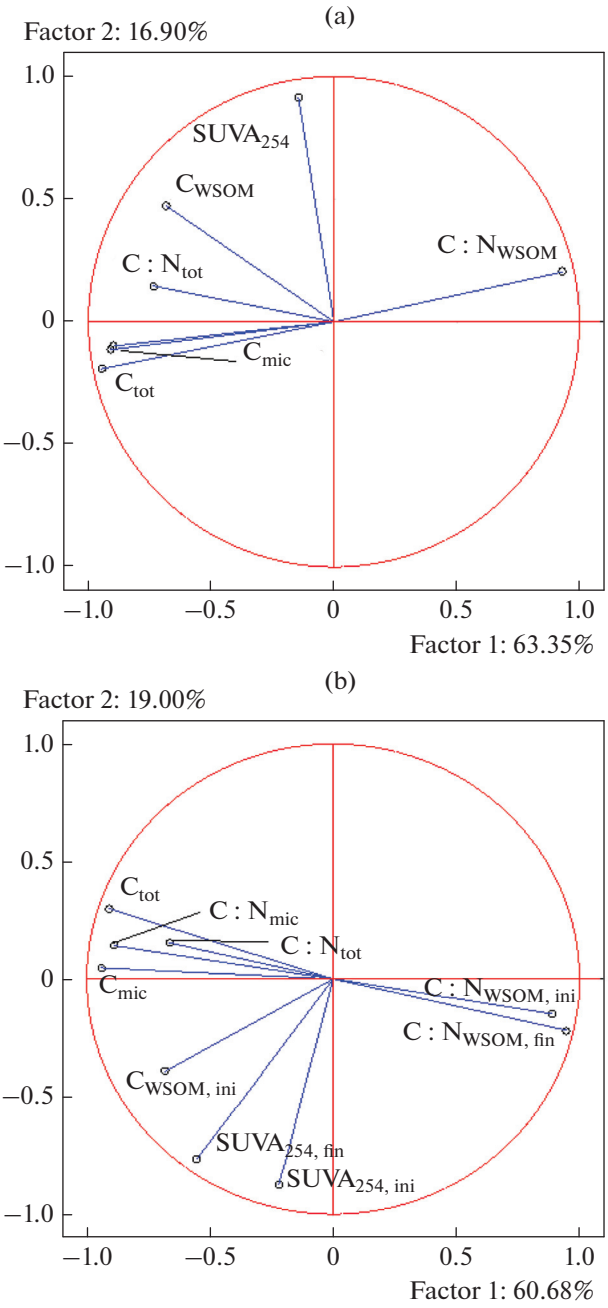

Fig. 3. Projection of the set of examined properties to the plane of two principal components with (a) the share of mineralized WSOM and (b) share of fast-mineralized WSOM pool as a grouping variable.

ratio of these pools and their mineralization rate constants are listed in Table 3. The maximum share of fast-mineralized WSOM pool is observed in the soil immediately after a fire. Thus, although the fire had no statistically significant effect on the total soil and WSOM carbon contents, this factor influences the ratio of the WSOM pools in a statistically significant manner. An increase in the share of fast-mineralized WSOM after a pyrogenic event is likely to be associ-

Table 3. Kinetic parameters of potentially mineralizable soil WSOM pool

Ecosystem	Fast-mineralized pool			Slow-mineralized pool		
	share, %	k_1, day^{-1}	MRT, days	share, %	k_2, day^{-1}	MRT, days
0+	77	1.34 ± 0.10	0.75	23	0.031 ± 0.001	32.3
1+	64	1.36 ± 0.09	0.73	36	0.010 ± 0.001	100.0
2+	57	1.51 ± 0.10	0.66	43	0.009 ± 0.002	111.1
3+	52	1.58 ± 0.12	0.63	48	0.016 ± 0.002	62.5
7+	48	1.44 ± 0.10	0.69	52	0.019 ± 0.002	52.6
12+	54	1.40 ± 0.08	0.71	46	0.013 ± 0.001	76.9
60+	53	1.49 ± 0.08	0.67	47	0.010 ± 0.002	100.0
Control	36	1.55 ± 0.10	0.64	64	0.010 ± 0.001	100.0

ated with thermal depolymerization of part of soil organic components [23], in particular, dehydration of complex carbohydrates and lignin degradation [16]. During the further postfire succession, the share of fast-mineralized WSOM pool gradually decreases; however, it is still larger as compared with the control soil even 60 years after the fire.

As was demonstrated using principal component analysis, two factors explain 79.7% of the sampling variance of the share of fast-mineralized organic matter (Fig. 3). The first factor explains 60.7% of the variance and correlates best with C_{tot}, C/N_{WSOM} at the beginning and end of incubation, C_{mic}, and C/N_{mic}, i.e., with the properties of soil itself, soil WSOM, and microbial biomass. The second factor explains 19.0% of the variance and correlates with $SUVA_{254}$ at the beginning of incubation.

The mineralization rate constants for the fast-mineralized pool for all soils of the postfire succession are close amounting on the average to 1.46 ± 0.08 day^{-1}, suggesting that the MRT of this fraction does not exceed 0.68 ± 0.02 day. The MRT of the low mineralized WSOM pool ranges from 32 to 111 days, suggesting a biokinetic selection of the molecules most resistant to microbial degradation during WSOM incubation.

Dynamics of WSOM Properties during Incubation

Microbiological transformation decreases the nitrogen enrichment of soil WSOM (Fig. 1). This suggests that microorganisms initially consume the compounds more enriched in nitrogen, such as amino sugars, amino acids, and peptides, while nitrogen-poor organic compounds are more resistant to degradation. Note here that similar to carbohydrates, the soluble compounds of nitrogen are, as a rule, associated with the hydrophilic fraction of WSOM [31, 42], which is the first to be transformed by microorganisms [35, 36]. Presumably, selective mineralization of nitrogen compounds is a response of microbial community to their demand in nitrogen sources since these nutrients are most limited in the tundra ecosystems [7, 20]. The fact that any accumulation of mineral (ammonium and nitrate) nitrogen was unobservable during the incubation suggests that mineralized nitrogen is incorporated by microbial biomass.

$SUVA_{254}$ increases during WSOM biodegradation in soils of the entire postfire chronosequence, suggesting an increase in the share of hydrophobic substances with an aromatic structure. In particular, a tight correlation between $SUVA_{254}$ and accumulation of the phenolic fraction during WSOM biodegradation was earlier observed [11]. Aromatic compounds are usually regarded as biochemically stable; thus, their content negatively correlates with WSOM biodegradability [39, 41, 49].

CONCLUSIONS

Although a medium-intensity wildfire has no statistically significant impact on the WSOM content in soil, our data demonstrate that this factor influences WSOM properties enhancing an increase in the share of fast-mineralized pool. A gradual increase in the slow-mineralized WSOM pool during postfire succession assists carbon sequestration in soil. However, the share of fast-mineralized WSOM pool exceeds that in the reference soil even 60 years after the fire.

The biochemical stability of mountain tundra soil WSOM at most stages of postfire succession is primarily determined by the WSOM properties itself rather than by those of the microbial community degrading it.

WSOM properties considerably change during microbiological transformation; first and foremost, this consists in a decrease in the content of nitrogen-containing components and an increase in the share of hydrophobic aromatic compounds, which suggests that the microbiota first consumes simple aliphatic WSOM components, while aromatic substances remain relatively stable. Biodegradation involves a biokinetic selection of the WSOM components most stable to microbial activity, which further provides the restoration of the total carbon pool during postfire soil development.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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