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# COMPARATIVE ASSESSMENT OF THE DECOMPOSITION RATE OF PLANT LITTERFALL IN SPRUCE AND PINE FORESTS AT THE NORTHERN DISTRIBUTION LIMIT

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A comparative assessment of the processes of the initial stages of decomposition of plant residues (pine needles, spruce needles, leaves of boreal shrubs, moss thalli) in lichen-shrub pine forests and shrub-green-moss spruce forests formed under natural conditions at the northern limit of distribution was carried out. The characteristics of the litterfall initial composition, the rate of decomposition, and changes in the chemical composition of plant residues in the process of destruction caused by the forest type were studied. The higher initial content of Corg in the plant tissues of pine forests is associated with favourable lighting conditions under the forest canopy, while the high content of Mn in the tissues of ground cover plants in spruce forests is due to the direct influence of spruce needle litterfall rich in this nutrient. The results of the study clearly demonstrated that the forest type has a significant impact both on the initial quality of the litterfall of the same plant species and on the rate of decomposition: in the spruce forest, spruce needles and lingonberry leaves with a higher content of nutrients (Mg, Mn, P) and narrow ratios of elements (C:N, C:P) were characterised by more active decomposition processes. However, green moss litter, despite its high quality in spruce forests, decomposed more actively in pine forests, which may be due to a large amount of precipitation in pine forests. Thus, differences in the rate of decomposition of plant residues are influenced by a combination of the plant material quality, temperature conditions, and precipitation amount associated with the forest type.

**Keywords:** forest type, decomposition of litter, plant residues, quality of litter

The litterfall of woody plants and ground cover plants, such as leaves, needles, buds, shoots, fruits, roots, etc., dying off over a certain period of time, is one of the most important components affecting the formation of

biogeochemical cycles in forest ecosystems. Plant litterfall is a source of organic carbon and mineral nutrition elements that become available to biota during its decomposition and mineralization.

The decomposition rate of litterfall and carbon entry into the soil largely depend on the hydrothermal conditions of soils (Kuznetsov, 2010; Kuznetsov, Osipov, 2011), the activity and composition of soil biota (Vorobyova, Naumova, 2009; Högberg et al., 2017), the fractional composition of incoming litterfall (Bobkova, 2000; Fang et al., 2015), and climatic conditions (air temperature and precipitation) (Pausas, 1997; Portillo-Estrada et al., 2016). According to modern concepts, climate is considered the leading factor on a regional scale, while the quality of litterfall is considered local, whereas the activity of destructive organisms is regulated by climate and the quality of litterfall (Bradford et al., 2016) determined by concentrations of nutrients and secondary metabolites. Thus, at the early stages of decomposition, N, P and water-soluble organic compounds have the greatest effects, whereas the main determinant of decomposition dynamics at later stages is lignin (Berg, 2000; Wardle et al., 2003; Zhang et al., 2008; Rahman et al., 2013; Larionova et al., 2017). The stoichiometric ratios of elements and substances (C:N, lignin:N) in decomposing litterfall are also related to the quality of plant material: the narrower is the ratio, the higher is the rate of destruction (Berg, McClaugherty, 2008; Rahman et al., 2013; Tu et al., 2014; Lukina et al., 2017). The initial chemical composition of the litter, which determines its quality, and, accordingly, the process of its decomposition, exhibits specific features. In four different species of pine (*Pinus pinea*, *P. laricio*, *P. sylvestris* and *P. ni-*

*gra*), the decomposition rate was regulated by the initial content of nutrients (N, K, Mn) (De Marco et al., 2007). Pine needles (*P. contorta*) contained more C and N and less lignin compared to spruce needles (*Picea engelmannii*), which indicates a higher quality of plant material, but carbon losses were higher for spruce (Leonard et al., 2020). Another study showed that spruce needles litterfall with a higher content of nutrients and relatively narrow C:N and lignin:N ratios decomposed noticeably faster than the pine needles litter, whereas the litterfall of silver birch leaves (*Betula pendula*) in pine forests, with a lower ratio of N:P, decomposed faster compared to the downy birch litterfall (*B. pubescens*) in spruce forests (Ivanova et al., 2019).

Woody plants are able to form forest types with their own special habitat conditions and soil fertility, namely through litter the chemical composition of which affects microbial activity and soil composition (Rakhleeva et al., 2011; Aponte et al., 2013; Chavez-Vergara et al., 2014; Kolmogorova, Ufimtsev, 2018; Pomogaybin, Pomogaybin, 2018; Tsandekova, 2018). The canopy of the forest stand, depending on the species composition and structure and closeness of the crowns, changes the composition of atmospheric precipitation and affects the level of illumination (Lukina et al., 2008; Kishchenko, 2019). Forest ecosystems in the Murmansk region represent the stages of succession, during which there is a change of tree species (pine, spruce, birch), which forms different environmental conditions in ecosystems on soil-forming rocks of similar

composition. Thus, spruce, to a greater extent than pine, acidifies sediments passing through the crowns and prevents them from penetrating under the crowns of trees, creating a more pronounced mosaic. Due to the greater closeness of the crowns, spruce prevents sunlight from penetrating under the forest canopy. In spruce forests, soil fertility is significantly higher than in pine forests, which are formed on the same soil-forming rocks and positions in the landform (Lukina et al., 2002, 2006, 2008, 2010; Tsvetkov, 2004; Orlova et al., 2011). This can also determine differences in the composition of the litterfall of the same plant species in different types of forests and affect the rate of their decomposition.

The purpose of this paper is to assess the influence of forest type on the initial composition and decomposition rate of litterfall in the spruce and pine forests dominant in the North Taiga subzone.

## MATERIALS AND METHOD

The research was carried out at permanent observation sites (POS) in the Murmansk region in lichen-shrub pine forests (10P) on illuvial-ferruginous podzols (Rustic podzols) in 1997–1999 and in green-mossy-shrub spruce forests (8S2B) on illuvial-humus podzols (Carbic podzols) under automorphic conditions in 1996–1998. More detailed descriptions of the objects of research are given in early papers (Lukina, Nikonov, 1996, 1998; Lukina et al., 2017; Ivanova et al., 2019). The

main soil-forming rocks in the study area are glacial deposits—moraine and water-glacial—as well as sandy and sandy loam rocks according to granulometric composition (Belov, Baranovskaya, 1969; Pereverzev, 2004). During the succession of coniferous forests, when pine forests are replaced by spruce forests, patterns of changes in the chemical composition of soils are observed: in spruce forests, the content of available compounds of biophilic elements in the entire soil profile increases, while the C:N ratio decreases in organogenic horizons and humus accumulation is observed. In pine forests, the organogenic horizons of the undercrown spaces are characterised by higher acidity than those of the intercrown ones, whereas in spruce forests, the opposite pattern is observed. An increase in the content of acidic components is observed in the mineral horizons of soils, in particular, an increase in the content of fulvic acids was noted in the illuvial horizons with a decrease in the content of humic acids (Orlova et al., 2011).

Experiments to study the processes of decomposition of litterfall on POSs in different types of forests were carried out in compliance with the uniformity of methods and statistical data processing. Samples of the active fraction of the litterfall (leaves and needles) of the dominant vascular plant species (*Pinus sylvestris*, *Picea abies*, *Vaccinium vitis-idaea*, *V. myrtillus* and *Empetrum hermaphroditum*) and samples of the ageing brown part of mosses (*Pleurozium schreberi*) were taken in September 1997 at a monitoring station in

pine forests, and in October 1996 in spruce forests. For decomposition, plant material (10 g of dry matter) was placed in bags made of synthetic material with a pore size of 30  $\mu\text{m}$ , which were placed on the soil surface (in the litter L subhorizon) in the undercrown and intercrown spaces at monitoring sites. Samples were taken annually in October, 1 and 2 years after the start of each experiment. In just two selection periods, 32 packages were selected in pine forests, and 49 packages were selected in spruce forests.

Before chemical analysis, the plant material was milled and subjected to wet oxidation with concentrated  $\text{HNO}_3$ . The concentrations of metals (Ca, Mg, K, Mn) were determined by atomic absorption spectrometry on the Analyst 800. For content determination, the following methods were used: the Kjeldahl method for the total nitrogen content, the Tyurin method for the organic carbon ( $\text{C}_{\text{org}}$ ), and colorimetry for the phosphorus (Vorobyova, 1998). The lignin content was determined by treatment a sample of  $\text{H}_2\text{SO}_4$  (72%) after pre-boiling in a solution of cetyltrimethylammonium bromide in a 0.5 M solution of  $\text{H}_2\text{SO}_4$  (Rowland, Roberts, 1994).

Calculations were done for the absolute dry weight. The mass loss was calculated as the difference between the weight of the samples before laying and 1 or 2 years after and expressed as a percentage. The enrichment coefficient demonstrating the change in the composition of plant material during decomposition was calculated for each element as the ratio of concentration after the first or sec-

ond year of decomposition to the initial concentration. Losses of nutrition elements and lignin, taking into account the rate of mass loss, were expressed as a percentage and calculated as the difference between the products of the concentration of the component per weight of the sample before the experiment and 1 or 2 years after, respectively. The quality of the litterfall was characterised based on the content of lignin (secondary metabolites), nutrients (N, Ca, Mg, K, P, Mn), and stoichiometric ratios of C:N, C:P, lignin:N, and N:P.

The statistical analysis of the data was carried out using various methods. The influence of forest type (spruce and pine) on the initial chemical composition of plant material was analysed for individual plant species using the V-test (Husson et al., 2017) in the statistical programming environment R (R Core Team ..., 2017). At the same time, the data matrix for the chemical composition of the litterfall was supplemented with available data on the composition of living plants: pine and spruce needles in their last years of life, perennial leaves of lingonberry, crowberry, and perennial and dead shoots of green mosses *P. schreberi* and *Hylocomium splendens*. The decomposition parameters (loss of mass and elements, enrichment coefficient) in pine and spruce forests were compared for each fraction of the litterfall (pine and spruce needles, lingonberry and crowberry leaves, mosses) using the Mann-Whitney U-test in the Statistica program. The possible influence of intra- and interbiogeocenotic variability of soil and air temperatures in spruce and pine forests

was analysed using data obtained in the period from 2015 to 2021 using temperature loggers under tree crowns, in intercrown spaces, and on trees.

## RESULTS AND DISCUSSION

*The initial composition of plant material* — non-decomposed litterfall and living plants (their perennial parts) — characterises the quality of plant material for subsequent decomposition by its destructor organisms.

A comparison of the composition of individual fractions of the litter, as well as living plant material of the corresponding plant species, showed that spruce needles in the last years of life are richer in nutrients Ca, Mg, Mn, P and are characterised by lower ratios of C:P and N:P ( $p < 0.05$ ), which confirms the previously obtained data (Sukhareva, Lukina, 2014), whereas pine needles are characterised by a higher content of C and N (Table 1), which is consistent with the results of other authors (Leonard et al., 2020). At the same time, it should be noted that, unlike the previous results, the concentrations of K in this study turned out to be higher in perennial spruce needles. Higher nitrogen content in pine needles in the last years of life (7–8 years) compared with the spruce needles aged 11–13 years was explained earlier (Sukhareva, Lukina, 2014) by age differences: N, like K and P, refers to mobile nutrition elements (Helmisaari, 1990; Rautio, 1998), that is, translocation of its compounds into younger tissues and depletion of older needles oc-

curs. On the contrary, the content of other mobile nutrients, which belong to the elements of mineral nutrition, namely K, P, and Mg (elements of medium mobility), turned out to be higher in spruce needles. The content of non-mobile elements of mineral nutrition, which include Ca and Mn, as expected, is significantly higher in ageing spruce needles.

Living perennial lingonberry leaves in spruce forests, unlike leaves in pine forests, are characterised by significantly lower ratios of elements (C:N, C:P, N:P) and a higher content of nutrients (Mg, Mn, P), which is consistent with data on the composition of leaves current year (Isaeva, Sukhareva, 2013). However, the carbon content is higher in perennial lingonberry leaves in pine forests ( $p < 0.05$ ).

The litterfall and material of perennial living organs of crowberry and mosses showed distinct differences in chemical composition depending on the type of forest only in relation to Mn and C: the content of manganese is higher in spruce forests, while carbon content is higher in pine forests. It is noteworthy that live ageing pine needles also contain more carbon than spruce needles, which turned out to be rich in manganese. It is known that the assimilating organs of Scots pine show a higher intensity of photosynthesis processes compared to spruce (Tuzhilkina, 1984; Suvorova, 2006; Molchanov, 2020; Yang et al., 2020). A higher carbon content in the plant tissues of shrubs and mosses in pine forests may be associated with a higher intensity of photosynthesis of plants under the canopy of pine trees: dense low-hanging crowns of spruce

**Table 1.** Chemical composition of living and dead perennial parts of plants in North Taiga pine and spruce forests

Parameter	Average		Standard deviation		General average	General standard deviation	p	n		
	S-BGC	P-BGC	S-BGC	P-BGC				S-BGC	P-BGC	
Spruce and pine needles in the last years of life*										
Ca	mg/kg	13 878	4077	3904	941	11 321	5497	0	51	18
Mg		674	495	249	112	628	235	0.01	51	18
K		3527	3212	604	340	3445	563	0.04	51	18
Mn		2149	977	923	295	1844	958	0	51	18
P		1139	928	243	104	1084	234	0.001	51	18
N		8805	10 162	1248	1579	9159	1459	0.001	51	18
C <sub>org</sub>	%	52	56	4	6	53	5	0.01	51	18
C:N		61	56	10	8	59	10	0.07	51	18
C:P		478	607	97	96	511	112	0	51	18
N:P		8	11	2	2	9	2	0	51	18
Lingonberry — perennial leaves (living parts)										
Ca	mg/kg	6535	6878	1420	1063	6699	1260	0.37	23	21
Mg		1291	1089	306	127	1195	257	0.01	23	21
K		3917	3629	482	507	3780	509	0.06	23	21
Mn		2091	1704	371	426	1907	439	0.004	23	21
P		952	725	204	81	844	194	0.0001	23	21
N		8832	8397	1716	2275	8625	1991	0.47	23	21
C <sub>org</sub>	%	51	55	3	3	53	4	0.001	23	21
C:N		60	69	10	17	64	14	0.03	23	21
C:P		556	760	106	85	653	140	0	23	21
N:P		9	12	1	3	10	2	0.002	23	21
Crowberry — perennial leaves (living parts)										
Ca	mg/kg	8167	8755	1285	1455	8342	1345	0.22	26	11
Mg		2381	2710	273	300	2479	317	0.004	26	11
K		4571	3823	1279	593	4349	1163	0.07	26	11
Mn		1016	995	464	187	1009	399	0.88	26	11
P		959	1038	180	113	982	166	0.19	26	11
N		9610	10 895	2388	2900	9992	2579	0.17	26	11
C <sub>org</sub>	%	57	58	3	1	57	3	0.64	26	11
C:N		63	56	16	15	61	16	0.23	26	11
C:P		613	561	109	63	597	100	0.14	26	11
N:P		10	11	2	3	10	2	0.66	26	11



Parameter	Average		Standard deviation		General average	General standard deviation	p	n		
	S-BGC	P-BGC	S-BGC	P-BGC				S-BGC	P-BGC	
Crowberry — perennial leaves (dead parts)										
Ca	mg/kg	8132	8453	605	847	8315	744	0.43	6	8
Mg		1950	1774	332	86	1850	234	0.16	6	8
K		3106	2034	1296	293	2493	998	0.05	6	8
Mn		1212	678	293	49	907	331	0.003	6	8
P		720	1020	175	22	891	189	0.003	6	8
N		7577	9204	2685	825	8507	1959	0.12	6	8
C <sub>org</sub>	%	57	62	5	5	60	5	0.08	6	8
C:N		81	69	19	10	74	15	0.14	6	8
C:P		825	613	161	49	704	152	0.01	6	8
N:P		10	9	1	1	10	1	0.04	6	8
Mosses — living parts										
Ca	mg/kg	2519	2315	543	292	2481	508	0.38	26	6
Mg		974	743	502	80	931	461	0.27	26	6
K		5160	4280	1136	776	4995	1122	0.08	26	6
Mn		558	483	266	128	544	246	0.50	26	6
P		1168	852	268	121	1109	275	0.01	26	6
N		7338	5784	2013	728	7046	1932	0.08	26	6
C <sub>org</sub>	%	45	51	2	4	46	4	0.0001	26	6
C:N		65	91	18	18	70	20	0.01	26	6
C:P		400	616	89	120	440	127	0.0002	26	6
N:P		6	7	1	1	6	1	0.33	26	6
Mosses — dead parts										
Ca	mg/kg	4288	4456	1129	1095	4384	1069	0.77	6	8
Mg		668	1884	139	788	1363	855	0.01	6	8
K		3434	2645	855	887	2983	932	0.12	6	8
Mn		922	615	302	135	747	264	0.03	6	8
P		952	898	135	122	922	126	0.43	6	8
N		6656	8600	497	2602	7767	2177	0.10	6	8
C <sub>org</sub>	%	45	51	4	8	49	7	0.14	6	8
C:N		69	62	8	10	65	9	0.17	6	8
C:P		485	566	82	39	531	72	0.04	6	8
N:P		7	9	2	2	8	2	0.04	6	8

**Note:** S-BGC — spruce biogeocenosis; P-BGC — pine biogeocenosis; \* — data on the composition of spruce needles are presented in S-BGC, pine needles in P-BGC; p — probability of Type I error when calculating the V-test

intercept solar radiation much more effectively than high-raised sparse crowns of Scots pine (Kishchenko, 2019). Accordingly, with better illumination and less closeness of the crowns, plants of the ground cover produce organic matter more efficiently and accumulate more carbon in tissues (Atkina, 2000; Zubkova et al., 2022). In spruce forests, the increased Mn content in ground cover plants may be due to the effect of the litterfall of spruce needles rich in this nutrient on its content in soils.

The content of the other nutrients did not show clear dependencies on the type of forest. In the dead leaves of the crowberry, the K content is also higher in spruce forests, but the P content is higher in pine forests. According to the data obtained earlier at these research sites, the leaves of this year's crowberry are characterised by a higher content of K, Mn, and P in lichen-shrub pine forests compared with shrub-green-moss spruce forests (Isaeva, Sukhareva, 2013). The ratios of elements in the long-term dead leaves of the crowberry also showed differences: the C:P ratio was lower in spruce forests, and N:P was lower in pine forests. Green mosses (living perennial parts) in spruce forests are richer in phosphorus and in pine forests in carbon, which is consistent with the literature data on the composition of green mosses (Sukhareva, 2018). At the same time, the C:N and C:P ratios are lower in spruce forests. The dead parts of mosses were characterised by differences in the content of other elements: Mg is higher in pine forests, and Mn is higher in spruce forests; the C:P and N:P ratios are lower in spruce forests.

Thus, the content of nutrients and carbon in the ageing and dead leaves of shrubs, as well as in the tissues of mosses, varies depending on the type of forest, which is most clearly manifested in relation to Mn and  $C_{org}$ : in spruce forests, the plant material of shrubs and mosses is enriched with manganese; in pine forests, with carbon. This can be explained by differences in the growing conditions formed by the dominant woody plants: the fertility and soil moisture of spruce forests is higher than that of pine forests, under the same climatic conditions and on the same soil-forming rocks (Lukina et al., 2008). However, in pine forests, due to the sparsity of the crowns, more favourable lighting conditions are created for active photosynthesis of ground cover plants and, accordingly, more active carbon accumulation. It is also likely that the chemical composition of the ground cover plants is directly related to the composition of the litterfall of assimilating organs of woody edifier plants: the increased Mn content in the plants of the ground cover is influenced by its entry into the soil with the litterfall of spruce needles rich in manganese.

#### ***Rate of decomposition and changes in the chemical composition of plant residues during the destruction process***

Differences in the rate of mass loss may be due to the initial quality and environmental conditions. According to the mass loss rate after the first year of decomposition, the litterfall of the studied species is distributed as follows: lingonberry > spruce needles >



crowberry > mosses; after the second year: spruce needles > crowberry > lingonberry > mosses. In pine biogeocenoses, the decomposition rate ranges are as follows: after the first year: crowberry > lingonberry > pine needles > mosses; after the second year: pine needles > lingonberry > crowberry > mosses (Table 2). As in an earlier study conducted in spruce forests, with a relatively high initial value of the C:N ratio in moss litterfall in both spruce and pine forests, the rate of loss of their mass was lower than in other species (Lukina et al., 2017). Other studies have also shown that moss litterfall decomposes slowly (Wardle et al., 2003; Cornelissen et al., 2007; Hilli, 2013), which may be due to the high content of unidentified phenolic compounds in the cell walls of mosses and a wide C:N ratio in plant residues (Ligrone et al., 2008; Lukina et al., 2017).

Both after the first and after the second year of decomposition, spruce needles significantly lost mass faster than pine needles did (20% vs. 16% and 37% vs. 29%, respectively); more active K losses and accumulation of lignin ( $p < 0.05$ ) were observed (Tables 2, 3). In addition, in the first year of decomposition, spruce needles had demonstrated a more active accumulation of P. The spruce needles had a higher enrichment coefficient for Mn, P, and lignin after the first year, and for Mg, N, and lignin after the second one. The enrichment coefficient for K was higher for pine needles both after the first and after the second year of decomposition. Stoichiometric ratios C:N, C:P and lignin:N after the first and sec-

ond years of decomposition were lower for the spruce needles litter.

Lingonberry leaf litterfall decomposed significantly faster in the spruce forest in the first year; in the second year the differences leveled out, but differences in the chemical composition of the litterfall became more pronounced: the enrichment coefficients for Mg, K, and P were higher in the spruce forest, and, accordingly, in the pine forest, lingonberry leaves lost more Ca, Mg, K, and P ( $p < 0.05$ ). C:N and lignin:N ratios after the first and second years were lower in the spruce forest. During the study period, the leaves of the crowberry decomposed in spruce and pine forests at comparable rates (Table 2). However, in the first year the enrichment coefficients for Mg and K were higher in the spruce forest, and the losses of Mg and K were higher in the pine forest; conversely, the enrichment coefficient for C was higher in the pine forest, and the losses were higher in the spruce forest. In the second year the enrichment coefficients for K, Mn, and P were higher in the spruce forest, while the litterfall of crowberry leaves during decomposition lost more N and lignin in the spruce forest, and P in the pine forest ( $p < 0.05$ ). The ratios of C:N and lignin:N in the litterfall of crowberry leaves were narrower in the spruce forest throughout the study period.

The differences found for shrubs may indicate more active processes of transformation of the chemical composition of the litterfall in spruce forests compared with pine

**Table 2.** Loss of mass, nutrients, and lignin (in %), and stoichiometric ratios of elements during decomposition of active fractions of plant litterfall in North Taiga pine and spruce forests

Parameter	S-BGC		P-BGC		<i>p</i>	n	
	Average	Standard error	Average	Standard error		S-BGC	P-BGC
<b>1 year</b>							
Needles*							
Mass loss	20	1	16	1	0.01	5	5
Ca	12	1	8	8	1.00	4	4
Mg	15	3	12	1	0.19	4	4
K	45	1	24	2	0.03	4	4
Mn	-33	7	1	1	0.03	4	4
P	-32	2	-8	2	0.03	4	4
N	4	2	-2	7	0.47	4	4
C <sub>org</sub>	15	3	12	3	0.47	4	4
Lignin	-80	4	-10	3	0.03	4	4
C:N	48	3	99	8	0.03	4	4
C:P	538	20	1365	38	0.03	4	4
N:P	11	0.3	14	1	0.03	4	4
Lignin:N	32	0.4	45	3	0.03	4	4
Lingonberry							
Mass loss	20	1	16	0.3	0.01	5	5
Ca	5	0.1	10	4	0.31	4	4
Mg	5	4	16	1	0.03	4	4
K	36	4	35	2	0.67	4	4
Mn	8	5	-2	2	0.31	4	4
P	-4	7	8	1	0.31	4	4
N	2	3	-3	1	0.31	4	4
C <sub>org</sub>	14	6	7	4	0.67	4	4
Lignin	-172	6	-193	16	0.67	4	4
C:N	44	2	61	5	0.03	4	4
C:P	578	78	693	42	0.67	4	4
N:P	13	1	11	0.4	0.67	4	4
Lignin:N	42	0.4	52	3	0.03	4	4

Parameter	S-BGC		P-BGC		p	n	
	Average	Standard error	Average	Standard error		S-BGC	P-BGC
Crowberry							
Mass loss	20	3	17	2	0.21	5	5
Ca	14	6	6	2	0.67	4	4
Mg	21	0.3	29	2	0.03	4	4
K	41	4	53	3	0.03	4	4
Mn	10	5	9	3	0.89	4	4
P	9	8	13	4	0.89	4	4
N	10	3	5	6	0.31	4	4
C <sub>org</sub>	28	4	12	4	0.03	4	4
Lignin	7	3	6	1	0.89	4	4
C:N	40	1	62	7	0.03	4	4
C:P	499	14	626	59	0.11	4	4
N:P	12	1	10	0.4	0.03	4	4
Lignin:N	30	0.01	39	5	0.03	4	4
Mosses							
Mass loss	4	1	10	0.4	0.01	5	5
Ca	-7	3	8	10	0.31	4	4
Mg	11	7	32	12	0.31	4	4
K	43	4	54	8	0.67	4	4
Mn	1	9	35	6	0.11	4	4
P	5	4	28	4	0.03	4	4
N	-11	5	27	7	0.03	4	4
C <sub>org</sub>	-3	7	12	4	0.11	4	4
Lignin	2	3	4	6	0.89	4	4
C:N	69	4	77	0.3	0.19	4	4
C:P	623	35	684	42	0.47	4	4
N:P	9	0.2	9	1	0.47	4	4
Lignin:N	26	1	34	3	0.03	4	4

Parameter	S-BGC		P-BGC		p	n	
	Average	Standard error	Average	Standard error		S-BGC	P-BGC
<b>Year 2</b>							
Needles*							
Mass loss	37	1	29	0.5	0.01	5	5
Ca	15	5	4	1	0.06	4	4
Mg	20	5	29	3	0.19	4	4
K	80	1	50	1	0.03	4	4
Mn	-11	14	16	3	0.31	4	4
P	10	14	-1	2	0.89	4	4
N	11	2	19	2	0.06	4	4
C <sub>org</sub>	28	4	27	3	0.89	4	4
Lignin	-35	9	5	1	0.03	4	4
C:N	44	3	103	7	0.03	4	4
C:P	711	91	1215	39	0.03	4	4
N:P	17	3	12	0.4	0.31	4	4
Lignin:N	26	2	49	2	0.03	4	4
Lingonberry							
Mass loss	33	3	26	1	0.21	5	5
Ca	6	0.2	9	1	0.03	4	4
Mg	9	3	30	1	0.03	4	4
K	62	1	74	1	0.03	4	4
Mn	5	2	2	1	0.31	4	4
P	4	1	27	2	0.03	4	4
N	4	1	6	3	0.67	4	4
C <sub>org</sub>	28	6	19	3	0.67	4	4
Lignin	-131	27	-185	17	0.31	4	4
C:N	38	3	59	3	0.03	4	4
C:P	510	47	772	31	0.03	4	4
N:P	13	0.2	13	1	0.89	4	4
Lignin:N	36	4	55	5	0.03	4	4

Parameter	S-BGC		P-BGC		p	n	
	Average	Standard error	Average	Standard error		S-BGC	P-BGC
Crowberry							
Mass loss	34	3	25	2	0.06	5	5
Ca	26	6	16	4	0.31	4	4
Mg	42	3	40	3	0.67	4	4
K	61	3	72	2	0.11	4	4
Mn	14	1	17	2	0.31	4	4
P	20	3	30	3	0.03	4	4
N	14	2	0.3	2	0.03	4	4
C <sub>org</sub>	40	4	28	3	0.11	4	4
Lignin	22	3	13	0.3	0.03	4	4
C:N	35	2	48	2	0.03	4	4
C:P	459	18	644	40	0.03	4	4
N:P	13	0.1	13	0.3	0.89	4	4
Lignin:N	26	0.3	34	2	0.03	4	4
Mosses							
Mass loss	9	2	14	1	0.04	5	5
Ca	-18	2	13	9	0.03	4	4
Mg	20	8	37	12	0.67	4	4
K	62	4	71	3	0.06	4	4
Mn	-19	1	33	11	0.03	4	4
P	11	2	37	3	0.03	4	4
N	-6	1	16	17	0.89	4	4
C <sub>org</sub>	-2	10	23	7	0.06	4	4
Lignin	21	7	14	5	0.31	4	4
C:N	72	8	61	4	0.11	4	4
C:P	655	83	678	15	0.67	4	4
N:P	9	0.2	11	1	0.03	4	4
Lignin:N	22	2	29	4	0.31	4	4

**Note:** S-BGC — spruce biogeocenosis; P-BGC — pine biogeocenosis; \* — data on the composition of spruce needles are presented in S-BGC, pine needles in P-BGC; p — probability of Type I error for the Mann-Whitney U-test

forests, which can be explained by the initial concentrations of elements. Thus, a higher initial Mn content in spruce needles and ground cover plant tissues and its accumulation during decomposition can accelerate decomposition processes by increasing the content of the Mn peroxidase enzyme responsible for the decomposition of lignin (Orlova et al., 2011). An increased carbon content in plant tissues may indicate a high content of organic substances, such as lignin, resistant to decomposition. According to the results of earlier work, the mixed litterfall of evergreen plants of spruce forests (spruce needles, lingonberry and crowberry leaves) decomposed faster within two years than pine (pine needles, lingonberry and crowberry leaves), which was also associated with differences in the quality of plant residues: a higher content of nutrients and narrower C:N and lignin:N ratios in the litterfall and in the soils of spruce forests (Lukina et al., 2008; Ivanova et al., 2019).

Differences in the activity of decomposition processes in spruce and pine forests may be due not only to the initial quality of plant material. The main destructive organisms in boreal forests are saprotrophic fungi, which decompose litterfall most effectively (Hobbie et al., 1999; Bödeker et al., 2016). According to the literature data, the total biomass of microorganisms, including fungi, is higher in spruce biogeocenoses in comparison with pine ones (Nikonov et al., 2001; Polyanskaya et al., 2001), and the length of the fungal mycelium in organogenic soil horizons is also greater in spruce forests (Evdokimova, Mozgova, 2001). This

may be due to the relatively low soil moisture in pine forests (Nikonov et al., 2004).

An important factor that affects the rate of decomposition is soil temperature, which regulates the activity of destructive organisms; in particular, low temperatures limit the decomposition processes (Vorobyova, Naumova, 2009; Rief et al., 2012). However, according to measurements carried out in 2015–2021 using temperature loggers embedded under organogenic soil horizons, the average monthly temperatures in spruce forests were lower than those in pine forests, the difference reached 2 °C (Fig. 1). This leads to the conclusion that the quality of the litterfall may have a more significant effect on the rate of decomposition than the temperature of the soil.

The dead parts of green mosses, despite their higher quality in spruce forests, unlike all other species, decomposed more actively in pine forests over the study period ( $p < 0.05$ ) (Table 2). In the first year the enrichment coefficients for P and N were higher in spruce forests, and losses were higher in pine forests. At the same time, an active accumulation of N by moss residues was observed in the spruce forests. In the second year, green mosses, as well as in the first, lost P more actively in the pine forest. A possible reason may be a higher amount of precipitation in pine forests (32.6 mm versus 26.5 mm in spruce forests) (Ershov, 2021), contributing to the mechanical destruction of moss plant residues and the leaching of mobile elements. In addition, losses of Ca and Mn were observed in the pine forest, and their accumulation was noticed in

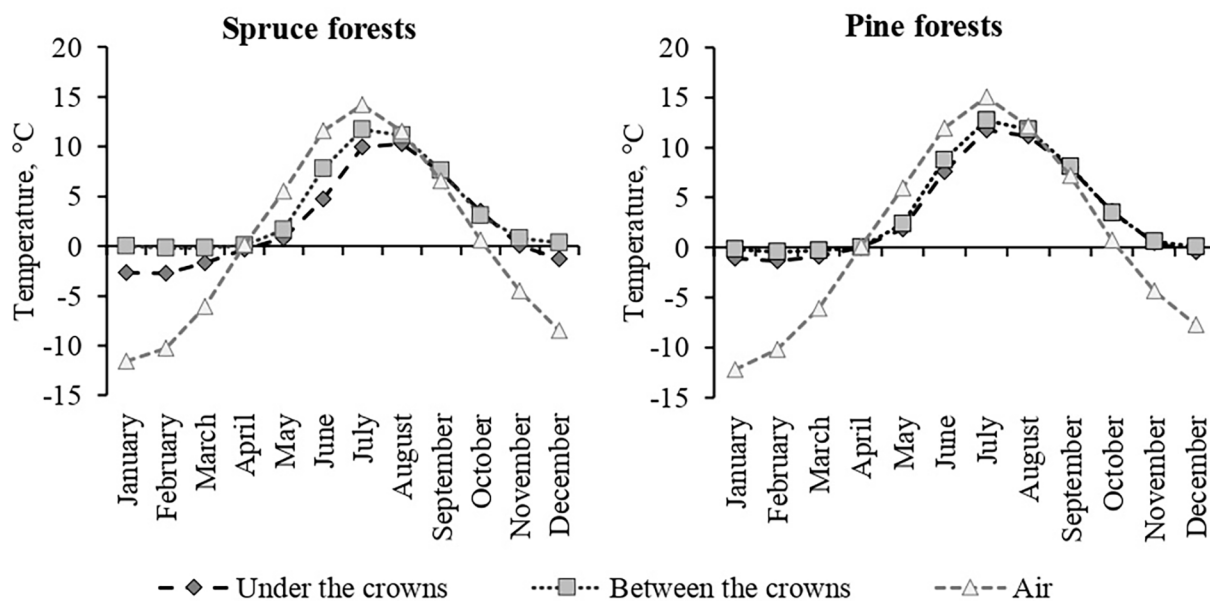


**Table 3.** Enrichment coefficient of active fractions of plant litterfall in North Taiga pine and spruce forests

Parameter	S-BGC		P-BGC		<i>p</i>	n	
	Average	Standard error	Average	Standard error		S-BGC	P-BGC
<b>1 year</b>							
Needles*							
Ca	1.10	0.01	1.09	0.08	1.00	4	4
Mg	1.06	0.05	1.05	0.02	1.00	4	4
K	0.69	0.01	0.91	0.03	0.03	4	4
Mn	1.67	0.10	1.18	0.01	0.03	4	4
P	1.65	0.03	1.28	0.03	0.03	4	4
N	1.20	0.02	1.22	0.08	0.89	4	4
C <sub>org</sub>	1.06	0.04	1.04	0.04	0.67	4	4
Lignin	2.27	0.03	1.31	0.04	0.03	4	4
Lingonberry							
Ca	1.19	0.02	1.07	0.04	0.11	4	4
Mg	1.18	0.07	1.00	0.005	0.03	4	4
K	0.80	0.06	0.78	0.03	0.89	4	4
Mn	1.16	0.08	1.21	0.02	0.89	4	4
P	1.30	0.10	1.10	0.01	0.11	4	4
N	1.22	0.02	1.23	0.02	0.31	4	4
C <sub>org</sub>	1.07	0.06	1.11	0.05	0.67	4	4
Lignin	3.39	0.02	3.49	0.18	0.89	4	4
Crowberry							
Ca	1.06	0.04	1.13	0.04	0.67	4	4
Mg	0.99	0.03	0.86	0.03	0.03	4	4
K	0.73	0.03	0.57	0.04	0.03	4	4
Mn	1.11	0.03	1.09	0.05	0.67	4	4
P	1.12	0.06	1.05	0.06	0.31	4	4
N	1.11	0.00	1.15	0.08	0.31	4	4
C <sub>org</sub>	0.89	0.02	1.05	0.04	0.03	4	4
Lignin	1.15	0.00	1.13	0.03	0.31	4	4
Mosses							
Ca	1.12	0.03	1.02	0.10	1.00	4	4
Mg	0.94	0.08	0.75	0.13	0.31	4	4
K	0.60	0.05	0.51	0.09	0.67	4	4
Mn	1.04	0.10	0.72	0.07	0.11	4	4
P	0.99	0.03	0.80	0.04	0.03	4	4
N	1.17	0.05	0.81	0.07	0.03	4	4
C <sub>org</sub>	1.07	0.06	0.98	0.05	0.67	4	4
Lignin	1.03	0.04	1.06	0.06	0.89	4	4

Parameter	S-BGC		P-BGC		p	n	
	Average	Standard error	Average	Standard error		S-BGC	P-BGC
<b>Year 2</b>							
Needles*							
Ca	1.35	0.07	1.36	0.02	0.89	4	4
Mg	1.28	0.07	1.00	0.03	0.03	4	4
K	0.32	0.01	0.70	0.02	0.03	4	4
Mn	1.78	0.23	1.18	0.03	0.11	4	4
P	1.43	0.23	1.42	0.03	0.89	4	4
N	1.41	0.02	1.14	0.03	0.03	4	4
C <sub>org</sub>	1.15	0.06	1.03	0.03	0.31	4	4
Lignin	2.16	0.14	1.34	0.02	0.03	4	4
Lingonberry							
Ca	1.38	0.06	1.23	0.02	0.11	4	4
Mg	1.33	0.02	0.95	0.02	0.03	4	4
K	0.55	0.01	0.35	0.02	0.03	4	4
Mn	1.40	0.09	1.33	0.03	0.89	4	4
P	1.41	0.07	0.99	0.03	0.03	4	4
N	1.40	0.05	1.28	0.06	0.31	4	4
C <sub>org</sub>	1.04	0.04	1.11	0.04	0.31	4	4
Lignin	3.34	0.24	3.86	0.20	0.31	4	4
Crowberry							
Ca	1.10	0.04	1.12	0.03	0.67	4	4
Mg	0.87	0.01	0.80	0.03	0.11	4	4
K	0.59	0.02	0.38	0.02	0.03	4	4
Mn	1.30	0.03	1.11	0.04	0.03	4	4
P	1.21	0.01	0.93	0.06	0.03	4	4
N	1.30	0.02	1.34	0.05	0.67	4	4
C <sub>org</sub>	0.89	0.03	0.97	0.06	0.67	4	4
Lignin	1.17	0.00	1.17	0.03	0.89	4	4
Mosses							
Ca	1.33	0.02	1.01	0.10	0.03	4	4
Mg	0.90	0.09	0.74	0.14	0.89	4	4
K	0.42	0.04	0.34	0.04	0.31	4	4
Mn	1.33	0.01	0.78	0.12	0.03	4	4
P	1.00	0.03	0.73	0.03	0.03	4	4
N	1.19	0.01	0.97	0.19	0.89	4	4
C <sub>org</sub>	1.14	0.11	0.90	0.08	0.06	4	4
Lignin	0.88	0.08	1.00	0.06	0.31	4	4

**Note:** S-BGC— spruce biogeocenosis; P-BGC — pine biogeocenosis; \* — data on the composition of spruce needles are presented in S-BGC, pine needles in P-BGC; p — probability of Type I error for the Mann-Whitney U-test



**Figure 1.** Soil and air temperature in spruce and pine forests, measured in the 2015–2021 using temperature loggers under tree crowns, in intercrown spaces, and on trees

the spruce forest; enrichment coefficients for Ca, Mn, and P were significantly higher in the spruce forest. After the first year, the lignin:N ratio in the spruce forests was significantly lower; after the second year the N:P ratio was lower (Table 2).

Thus, a combination of factors such as the quality of litterfall, the activity of microorganisms, the temperature conditions, and the amount of precipitation associated with forest type can determine the increased rate of decomposition and the intensity of changes in the chemical composition of plant material in spruce forests compared with pine forests.

## CONCLUSION

The results of the study show that the forest type has a significant effect on the rate of decomposition: in spruce forests the rate of decomposition of spruce needles is higher than that of pine needles in pine forests. The quality of plant material and, accordingly, the activity of microorganisms had a significant impact on the rate of decomposition of plant residues in various forest types. Spruce needles are characterised by higher quality: the content of Ca, Mg, K, P, and Mn is higher in ageing spruce needles compared with the content of these elements in pine needles in the last

years of life; the C:N and C:P ratios are lower in spruce needles. This explains the more active decomposition processes of spruce litterfall in spruce forests: 37% of the mass loss after two years of decomposition in the spruce forest versus 29% in the pine forest. Ageing, dying organs of shrubs and mosses ready to become litterfall showed ambiguous differences in the content of nutrients depending on the forest type: the quality of living ageing leaves of lingonberry and live parts of mosses was higher in spruce forests. Nevertheless, in the tissues of all plant species in spruce forests, there was more Mn, whereas pine forests had a higher level of C. This may be due to both the habitat conditions that are formed under the action of edifying trees (soil fertility, humidity, and temperature conditions) and the direct influence of woody plants: in pine forests, due to the sparsity of the crowns, more favourable lighting conditions are created for active photosynthesis and carbon accumulation by plants of the ground cover; increased Mn content in ground cover plants of spruce forests is associated with its entry into the soil with the litterfall of spruce needles, which are also rich in manganese. Accordingly, differences in the rate of decomposition of the litterfall of shrubs and mosses between forest types are not clearly manifested. The rate of decomposition of lingonberry leaves was higher in spruce forests after a year of decomposition, which may be due to the higher quality of plant material in the spruce forest: narrow ratios of elements

(C:N, C:P, N:P) and high content of nutrients (Mg, Mn, P). At the same time, the dead parts of green mosses decomposed more actively in pine forests, despite their higher quality in spruce forests, which may be explained by the large amount of precipitation in pine forests. Thus, differences in the rate of decomposition of plant residues of needles of woody plants, leaves of shrubs, and shoots of mosses are determined by a combination of factors such as the quality of plant material, temperature conditions, and precipitation associated with the forest type.

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## СРАВНИТЕЛЬНАЯ ОЦЕНКА СКОРОСТИ РАЗЛОЖЕНИЯ РАСТИТЕЛЬНОГО ОПАДА В ЕЛОВЫХ И СОСНОВЫХ ЛЕСАХ НА СЕВЕРНОМ ПРЕДЕЛЕ РАСПРОСТРАНЕНИЯ

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Проведена сравнительная оценка процессов разложения растительных остатков (хвоя сосны, хвоя ели, листья бореальных кустарничков, слоевища мхов) на начальных этапах в сосняках лишайниково-кустарничковых и ельниках кустарничково-зеленомошных, формирующихся в естественных условиях на северном пределе распространения. Изучались особенности исходного состава опада, темпы разложения и изменения химического состава растительных остатков в процессе деструкции, обусловленные формацией леса. Более высокое исходное содержание  $C_{орг}$  в тканях растений сосновых лесов связано с благоприятными условиями освещенности под пологом леса, тогда как высокое содержание Mn в тканях растений напочвенного покрова в ельниках обусловлено непосредственным влиянием богатого этим элементом питания опада хвои ели. Результаты исследования наглядно продемонстрировали, что формация леса оказывает значительное влияние как на исходное качество опада одних и тех же видов растений, так и на скорость разложения: хвоя ели и листья брусники с более высоким содержанием элементов питания (Mg, Mn, P) и узкими соотношениями элементов (C:N, C:P) в еловом лесу характеризовались и более активными процессами разложения. Однако опад зеленых мхов, несмотря на более высокое качество в ельниках, разлагался активнее в сосновых лесах, что может быть связано с большим количеством осадков в сосновых лесах. Таким образом, на различия в скорости разложения растительных остатков влияет сочетание качества растительного материала, температурного режима и количества осадков, связанных с формацией леса.

**Ключевые слова:** формация леса, разложение опада, растительные остатки, качество опада

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