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Chemical Composition of *Juniperus sibirica* Needles (Cupressaceae) in the Forest–Tundra Ecotone, the Khibiny Mountains

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Abstract—The needles of juniper growing in spruce and birch forests of the Khibiny Mountains have been analyzed to evaluate the pattern of changes in their chemical composition (ADF, lignin, cellulose, lignin/cellulose, lipids, phenolic compounds, proanthocyanidins, flavonoids, N, C, and also Ca, Mg, K, Mn, Zn, P, S, Al, and Fe). It has been shown that the concentrations of lignin, lipids, phenolic compounds, Ca, Al, and Fe in the needles increase with age, while those of flavonoids, soluble and bound proanthocyanidins, N, P, K, Mg, Zn, and Mn decrease. The needles of juniper from spruce and birch forests differ in the contents of nutrient elements, which is explained by differences in the composition of soils. The contents of lignin, cellulose, and lipids in aging needles are lower in birch forests than in spruce forests.

Keywords: Juniperus sibirica, needles, forest–tundra ecotone, lignin, phenolic compounds, flavonoids, tannins, nutrient elements

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The variety of common juniper growing in the Khibiny Mountains has been described as *Juniperus communis* L. var. *saxatilis* Pall. (Khantemirova and Semerikov, 2009), but there are many synonyms to this name, including *J. sibirica* Burgsd., *J. nana* Willd., *J. alpina* S.F. Gray, *J. pygmaea* K. Koch, *J. montana* (Aiton) Lindle & Gordon (Farjon, 2001). Here, this plant is named *Juniperus sibirica* Burgsd.

Latitudinal and altitudinal gradients can be regarded as natural long-term analogs of climate change (Aerts, 2006). Ecological conditions for plant growth in the Khibiny change significantly upon transition from the base to the top of the mountain massif (from the forest to the tundra belt), which may have an effect on the chemical composition of juniper needles. It has been shown that their chemical composition (in *J. communis*) changes with latitude and elevation (Martz et al., 2009) and also depends on other factors, including season (Adams, 1987; Peñuelas et al., 2002), habitat, species, plant organ, and nutrient status of soils (Adams, 1987; Thomas et al., 2007; Lesjak et al., 2011). In turn, changes in the chemical composition of juniper needles may have an effect on the processes of litter decomposition and, hence, on the physicochemical properties of soils (Murphy et al., 1998; García-Morote et al., 2012). DeLuca and Zackrisson (2007) have shown that the soil under juniper shrubs accumulates increased concentrations of N and P, compared to open areas. These authors consider that juniper plays an important role in facilitating nitrogen fixation by mosses in the tundra and thereby contributes to the recovery of arctic and alpine ecosystems after natural or anthropogenic disturbances.

To gain a deeper insight into the role of juniper in biogeochemical cycles and ecosystem functioning in forest-tundra ecotones, it is necessary to analyze its needles for the contents of not only mineral elements but also of structural components such as lignin and cellulose.

In this study, needles of different age classes of *J. sibirica* growing in the forest–tundra ecotone of the Khibiny Mountains (Murmansk oblast) were analyzed for the contents of lignin, cellulose, lipids, and certain groups of phenolic compounds and nutrient elements.

MATERIAL AND METHODS

The Khibiny have a specific microclimate with abundant precipitation (1.5–2 times higher than in the plains), annual average temperatures of about –2.0°C, and average January and July temperatures of –12.3°C and 10.3°C. The mountain taiga belt consisting mainly of Siberian spruce (*Picea obovata*) forests with green mosses, small, or tall herbs extend from the foothills to elevations of 300–400 m. Forests and sparse tree stands at elevations above 400 m are composed by mountain birch *Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti.

Studies were performed on Mt. Saami, the eastern Khibiny (67°70′ N, 33°79′ E), in dogwood–dwarf shrub–moss spruce forests and dwarf shrub–moss birch forests with dominance of boreal dwarf shrubs and green mosses in the ground vegetation layer, which also contain large proportions of Swedish dwarf dogwood (*Cornus suecica*), small herbs, and grasses. Juniper occurs as small islands in these forests.

The characteristic rocks of the eastern Khibiny are foyaites, which consist mostly of potassium and sodium feldspars and nepheline. This accounts for specific features of soil-forming rocks, namely, low contents of silica and high contents of aluminum and potassium. Subbrown soils dominate in the Khibiny; there also occur humus-rich podzolic soils with a shallow eluvial horizon. Juniper needles were collected in spruce forests growing on illuvial-humus (humus-rich) podzolic soils (O-E-Bh-C) and in birch forests on illuvial0humus subbrown soils (O-Bh-C).

Samples of juniper needles and soils were taken from spruce forests (forest belt, 300–350 m a.s.l.) and birch forests (forest–tundra, 400–450 m a.s.l.) in late June to early August 2009. Soil sampling was performed in two elementary biogeoranges, juniper and dwarf shrub–moss ones. The term “elementary biogeorange” (EBGR) refers to the elementary spatial, structural, and functional unit of biogeocenotic cover in which soil–vegetation–soil biota relationships are accomplished. The boundaries of EBGR and, hence, its shape and area are determined from the distribution of dominant plants, and its name is given accordingly. This unit represents the basal level in the structural hierarchy of forest biogeocenotic cover: EBGR—parcel—biogeocenosis—small river basin—etc. (Orlova, 2013).

In spruce and birch forests, three 25 × 25-m test plots were established to collect combined samples of needles and soils from three juniper EBGRs and combined soil samples from three dwarf shrub–moss EBGRs. The needles were sorted into three age classes: (current-year, 1-year, or older), dried at room temperature, and ground up. Soil analysis was performed with fine earth samples from different genetic horizons. Soil pH was measured potentiometrically in water extracts at water : soil ratios of 1 : 25 for organogenic horizons and 1 : 2.5 for mineral horizons. Exchangeable and hydrolytic acidity was determined after extraction with 1 N KCl and 1 M CH_3COONH_4 (pH 7.0), respectively, at the same ratios as above. The concentrations of accessible compounds of nutrient elements were measured after treating the samples with 1 M CH_3COONH_4 (pH 4.65). To determine the total contents of these elements, the samples were sintered with sodium carbonate and borax. The contents of chemical elements in plant samples were determined after wet ashing with concentrated nitric acid.

Potassium in soil and plant samples was determined by atomic emission spectrometry; Ca, Mg, Al, Fe, Zn, Cu, Ni, and Mn, by atomic absorption spectrometry (Perkin Elmer AAnalyst 800 spectrometer); S and P, by a colorimetric method; total C and N, by the Tyurin and Kjeldahl methods, respectively.

The contents of lignin and cellulose were determined by treating the samples with 72% H_2SO_4 after preliminary boiling in a cetrimonium bromide (CTAB) solution (10 g of CTAB in 1 L of 0.5 M H_2SO_4) (Rowland and Roberts, 1994). The residual matter not dissolved in the CTAB solution was designated acid-detergent fiber (ADF). Ground needles were extracted with 80% ethanol, and the extract was washed with hexane to remove resins, wax, pigments and other accessory substances. The total fraction extracted with hexane was designated as lipids. The total phenolic content in the samples was determined with the Folin–Ciocalteau reagent (Sigma, Switzerland), as described (Swain and Hillis, 1959), measuring the absorbance at 730 nm in a KFK-3 spectrophotometer. Gallic acid was used as a standard. The contents of soluble and cell wall-bound condensed tannins (proanthocyanidins) were determined by a photocolorimetric method at 555 nm after treating the extract and dry residue with an n-butanol : HCl mixture (95 : 5 v/v) (Ossipova et al., 2001), using condensed tannins from *B. pubescens* ssp. *czerepanovii* leaves as a standard. Total flavonoids were measured photocolorimetrically at 410 nm in the extract treated with 0.05 M $AlCl_3$ solution min ethanol (Buzuk et al., 2007) and expressed as quercetin equivalent.

The results were processed statistically using the Statistica 9.0 program package. The significance of differences in the chemical composition of needles and soils between the samples from spruce and birch forests was estimated by Kruskal–Wallis ANOVA.

RESULTS AND DISCUSSION

Characteristics of Soils

In rustic podozols of spruce forests in the Knibiny, a shallow, light-colored eluvial horizon (E) occurs locally. The content of silica in it reaches a maximum (Table 1). The illuvial horizons are poor in silica and rich in aluminum, reflecting the composition of rock-forming mineral (nepheline).

Cambic podzols of birch forests are characterized by the eluvial distribution pattern of elements (silica, iron, potassium, calcium, magnesium, and phosphorus), with the content of aluminum showing a small peak in the illuvial horizon. Carbon contents in the illuvial horizons of rustic and cambic podzols reach 10% (Table 2). An explanation to the increased contents of organic matter in the illuvial soil horizons in the Khibiny is that aluminum compounds form a kind

Table 1. Total concentrations of elements and pH in soils of birch and spruce forests (a spur of Mt. Saami, the Khibiny Mountains)

Horizon	*n*	pH	Al	Fe	Si	K	Mg	Ca	Mn	P	S
			g/kg								
Birch forest											
O	3	4.48	2.65	0.87	5.35	2.67	0.23	0.45	0.03	0.20	0.02
B	3	5.24	9.10	4.12	22.71	5.77	0.93	1.75	1.95	0.19	0.01
Spruce forest											
O	3	4.11	2.50	1.40	8.69	2.73	0.30	0.63	0.07	0.13	0.01
E	3	4.30	6.32	4.42	28.22	8.17	0.61	1.35	0.27	0.03	0.01
BF	3	5.04	11.56	3.09	17.15	1.82	0.53	0.97	0.10	0.19	0.01

of geochemical barrier to migration-capable humic substances, which leads to intense impregnation of mineral horizons with fulvate humus (Manakov and Nikonov, 1979).

With respect to total concentrations of elements, the illuvial soil horizons in spruce forests, compared to birch forests, are relatively poor in base cations and rich in Al, while the organic horizons are richer in Ca, which is due to its high content in falling spruce needles (Orlova et al., 2013). The contents of P and Mn are higher in soils of birch forests, where these elements occur in various admixtures associated with the apatite mineral.

The soils of spruce and birch forests also differ in the contents of nutrient elements available to plants in the organic horizons; moreover, distinct differences are observed between EBGRs (Table 2). Soil acidity in subhorizons L, F, and H is markedly lower in the juniper than in the dwarf shrub–moss EBGR in both spruce and birch forests. On the other hand, the upper subhorizon (L) in the juniper EBGR is significantly richer in N and available P, K, and especially Ca, but these differences level off in the lower horizons. Differences in the C/N ratio between EBGRs are observed in all the three subhorizons. This ratio in the juniper EBGR is narrow, suggesting that organic matter decomposition under juniper shrubs is accelerated.

An abrupt decrease in the contents of accessible nutrients (especially Ca) in subhorizons F and H is due to their leaching by precipitation. The crown of juniper is funnel-shaped, which accounts for intense throughfall.

Chemical Composition of Juniper Needles

Nutrients. The age of needle classes is known to be one of the main factors of variation in the composition of assimilative organs in conifers. The concentrations of N, K, and P, which are capable of retranslocation within the plant, and of medium-mobility elements (Mg and S) in juniper needles decrease with age in both spruce and birch forests ($p < 0.05$), while those of low-mobility elements (Ca, Al, and Fe) and of C increase (figure). The results of this study confirm the increase in the concentration of zinc in aging needles, which was previously observed in conifers (Lukina et al., 2008). A decrease in Mn concentration in aging juniper needles from spruce and birch forests is a peculiar phenomenon, because Mn in conifers usually behaves as a low-mobility element (Lukina and Nikonov, 1996). A probable explanation is that, under conditions of the mountain ecotone, growing plant tissues have especially high requirements for manganese, since this element as a cofactor for flavin enzymes has a direct effect on chlorophyll synthesis.

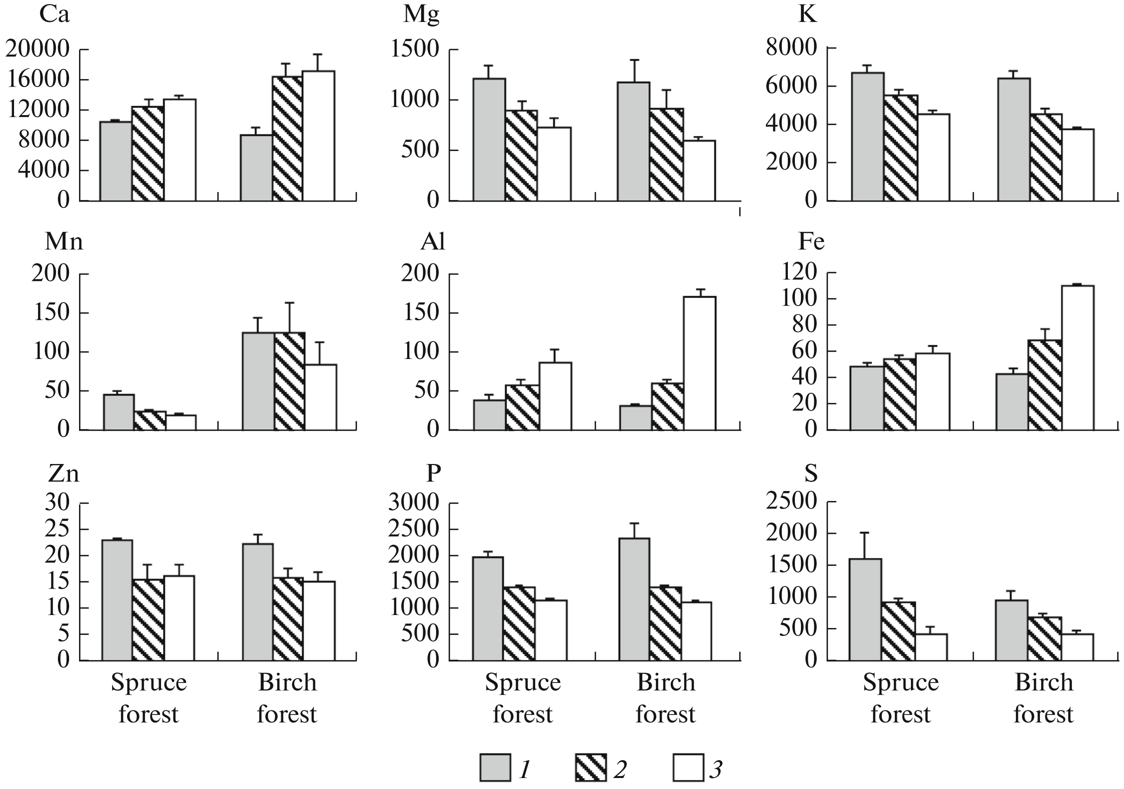
Differences in the contents of nutrients between the samples of juniper needles from spruce and birch forests may also be dependent on soil composition. In birch forest, Mn concentrations in the needles of all age classes are higher than in spruce forest ($p < 0.05$), which is explained by high contents of this element in rooting mineral horizons. Higher K concentrations in 1-year and older juniper needles from spruce forest ($p < 0.05$) are due to the high content of this active water migrant in the L subhorizon. Aging needles from birch forest are rich in Al and Fe, because the H subhorizons contain increased concentrations of their compounds available to plants. Thus, the contents of nutrient elements in juniper needles vary depending on their age and the composition of soils.

Secondary metabolites. The results of our studies on the contents of lipids in juniper needles (Table 3) agree with data obtained by other researchers (Adams, 1987). The concentrations of soluble proanthocyanidins are similar to those in juniper needles from Evenkia (Narchuganov et al., 2010) but half lower than in the needles of *J. communis* growing in Turkey (165 mg/g) (Kamalak et al., 2004), while the concentrations of bound proanthocyanidins are similar to those in *J. communis* needles (Kamalak et al., 2004). The total proanthocyanidin content is more than half lower than in the needles of *J. communis* from Spain (197–230 mg/g) (Frutos et al., 2002). The total phenolic content in the needles is similar to that in *J. communis* from Finland (Martz et al., 2009) but higher than in

Table 2. Contents of nutrients in organic soil horizons of the juniper and dwarf shrub EBGRs in birch and spruce forests (a spur of Mt. Saami, the Khibiny Mountains)

EBGR	Horizon	C	N	Ca	Mg	K	Na	AL	Fe	Mn	Zn	P	S	C/N
		%	mg/kg											
Birch forest														
Juniper	L	46(2)	17690(1828)	9008(428)	727(81)	1503(64)	72(5)	229(58)	4(2)	490(61)	53(8)	344(48)	122(11)	27(4)
	F	39(2)	16722(1513)	2179(80)	185(35)	670(129)	62(6)	644(61)	31(4)	57(39)	12(6)	49(15)	106(10)	23(2)
	H	14(2)	6498(647)	185(47)	21(3)	121(44)	19(4)	2832(776)	514(145)	3(0)	2(0)	21(2)	49(4)	21(2)
Dwarf shrub–moss	L	53(2)	12240(1264)	4153(198)	505(57)	1261(53)	71(5)	364(92)	3(2)	509(63)	62(9)	166(23)	96(9)	43(6)
	F	48(1)	14119(267)	2338(161)	319(61)	1064(108)	71(23)	610(23)	18(5)	111(42)	40(8)	81(9)	116(11)	34(1)
	H	28(4)	9587(802)	685(367)	57(13)	303(79)	20(2)	1924(899)	127(43)	5(3)	11(3)	28(3)	57(9)	29(3)
Spruce forest														
Juniper	L	46(2)	26795(1642)	15156(1472)	1302(345)	2393(215)	113(8)	76(32)	3(1)	971(255)	114(48)	882(76)	150(11)	17(0)
	F	38(3)	18638(1193)	1954(86)	107(7)	447(190)	133(86)	381(2)	58(26)	19(13)	4(1)	43(20)	86(25)	20(0)
	H	14(5)	5133(1018)	896(248)	61(40)	126(61)	34(17)	540(114)	92(27)	9(2)	3.8(0.8)	19(4)	33(8)	26(4)
Dogwood–dwarf shrub	L	55(1)	16974(171)	7257(358)	897(67)	2088(292)	107(16)	95(36)	2(0)	1007(50)	131(23)	491(9)	120(11)	32(1)
	F	47(1)	15076(526)	2268(157)	254(33)	796(164)	112(68)	318(7)	23(13)	41(25)	34(13)	102(34)	114(33)	31(2)
	H	28(9)	7810(1751)	1223(274)	127(54)	328(50)	36(10)	371(30)	24(8)	6(1)	25(9)	29(4)	39(5)	35(4)

Mean values with standard errors (in parentheses) are shown ($n = 3$).



Contents of nutrients (mg/kg) in *Juniperus sibirica* needles of different age classes from spruce and birch forests: (*1*) current-year needles, (*2*) 1-year needles, (*3*) older needles (mean values with standard errors, $n = 3$).

J. sibirica from Evenkia (Narchuganov et al., 2010) and in *J. communis* from Italy (20–25 mg/g) (Peñuelas et al., 2002).

Thus, the contents of proanthocyanidins in the needles of juniper from regions with colder climate are lower, while those of phenolic compounds are higher.

The recorded concentrations of flavonoids are the same as in the needles of *J. sibirica* from Serbia (Lesjak et al., 2011), and data on the contents of cellulose, lignin, and ADF also agree with the results reported by other authors (Peñuelas et al., 2002; Kamalak et al., 2004).

As in the case of nutrients, variation in the composition of secondary metabolites appears to depend on the age of needles. An analysis of our results has revealed significant age-dependent changes in the chemical composition of needles, including an increase in the contents of lignin, lipids, and, in spruce forest, phenolic compounds ($p < 0.05$ in all cases) (Table 3). Such an increase has been previously reported for phenolic compounds in the needles of *Pinus sylvestris* and *Picea abies* and lipids in the needles of the latter species (Fuksman et al., 2005) and for lignin in the needles of Douglas fir (*Pseudotsuga menziesii* Mirb. Franco) (Horner et al., 1987). No relationship between the age of needles and cellulose content has been revealed. The concentrations of soluble and bound proanthocyanidins and flavonoids decrease in *J. sibirica* needles of older age groups ($p < 0.05$). This agrees with the data by Slimestad and Hostettmann (1996) that the contents of flavonoids in aging *Picea abies* needles are lower and their composition is less diverse than in young needles.

The contents of lignin and cellulose in old *J. sibirica* needles decrease significantly ($p < 0.05$) with an increase in habitat elevation. A similar trend has been reported for their contents in the needles of *Picea rubens* Sarg. and *Abies balsamea* [L.] Mill in the northeastern United States (Richardson, 2004). The author notes that the decrease in lignin concentration at higher elevations may be of significance for the cycles of nutrients in the ecosystem where the rate of litter decomposition is limited by low temperatures. As suggested by Kitayama et al. (2004), this decrease may be an adaptive response that provides for accelerated recirculation of nutrients in environments with lower productivity (located at higher elevations).

It has been reported that the contents of chlorophylls and carotene in conifers increases with elevation (Oleksyn et al., 1998), and the same is true of terpenes (Martz et al., 2009) included in the lipid fraction. On the other hand, studies in the forest–tundra ecotones of the Northern Urals (Gerling and Zagirova, 2009) have shown that the rate of photosynthesis in the nee-

Table 3. Chemical composition of *Juniperus sibirica* needles of different age classes in spruce and birch forests

Component	Spruce forest			Birch forest		
	current-year needles (n = 3)	1-year needles (n =3)	3- to 7-year needles (n = 3)	current-year needles (n = 3)	1-year needles (n =3)	3- to 7-year needles (n = 3)
C, %	51.7 ± 0.9	53.0 ± 1.0	54.8 ± 0.5	47.7 ± 1.9	50.3 ± 1.5	51.7 ± 2.5
N, %	1.63 ± 0.04	1.25 ± 0.06	1.12 ± 0.04	1.48 ± 0.27	1.21 ± 0.03	0.93 ± 0.03
C : N	32 ± 1	42 ± 3	49 ± 2	35 ± 7	42 ± 2	55 ± 3
ADF, %	34.9 ± 1.5	37.7 ± 0.7	48.1 ± 0.8	36.3 ± 0.6	37.0 ± 0.9	38.6 ± 1.9
Lignin, %	16.2 ± 1.3	19.4 ± 0.3	26.9 ± 0.8	15.2 ± 0.8	17.2 ± 1.2	19.9 ± 1.6
Cellulose, %	18.6 ± 0.6	18.1 ± 0.4	20.8 ± 0.3	20.9 ± 0.5	19.5 ± 0.4	18.4 ± 0.6
Lignin/cellulose	0.87 ± 0.07	1.07 ± 0.01	1.30 ± 0.05	0.73 ± 0.06	0.88 ± 0.08	1.08 ± 0.08
Lignin/N	10 ± 1	16 ± 1	24 ± 1	11 ± 2	14 ± 1	22 ± 2
Lipids, %	7.7 ± 0.4	8.8 ± 0.3	13.0 ± 0.9	7.2 ± 0.2	9.2 ± 0.3	10.3 ± 0.1
Total phenolic content, mg/g	66.9 ± 1.9	69.9 ± 1.3	83.1 ± 3.1	65.8 ± 5.1	72.9 ± 4.4	78.9 ± 3.6
SPA, mg/g	76.1 ± 1.7	70.3 ± 6.5	65.0 ± 2.7	81.7 ± 2.5	75.8 ± 2.7	71.2 ± 2.8
BPA, mg/g	41.7 ± 0.8	36.7 ± 1.4	26.7 ± 0.1	42.2 ± 0.4	34.9 ± 0.8	25.9 ± 1.3
Total PA, mg/g	117.8 ± 2.5	108.0 ± 6.9	89.2 ± 4.6	123.9 ± 2.5	110.7 ± 2.3	97.1 ± 1.7
Flavonoids, mg/g	14.5 ± 1.3	12.2 ± 1.1	10.5 ± 0.9	15.3 ± 1.0	13.3 ± 0.4	11.3 ± 0.9

Mean values with standard errors are shown; SPA, soluble proanthocyanidins; BPA, bound proanthocyanidins.

dles of *J. sibirica* growing in the mountain tundra is lower than in the needles of *J. communis* from middle taiga forests; as a consequence, the development of chloroplasts in the mesophyll is retarded, and the contents of pigments are low. Our results agree with these data: the contents of lipids in old juniper needles are higher in samples from spruce forests than from birch forests ($p < 0.05$).

The contents of cell wall-bound proanthocyanidins, total phenolic compounds, and flavonoids hardly differ between the samples from spruce and birch forests ($p > 0.28$). The content of soluble proanthocyanidins in old needles slightly increases with elevation, but this increase is not conformed statistically ($p = 0.13$) because the results of measurements strongly vary within the plots. The results of some studies (Close and McArthur, 2002; Martz et al., 2009) provide evidence that the contents of certain groups of phenylpropanoids increase with elevation, which is usually explained by the dependence of their synthesis on illumination intensity (in particular, the amounts of UV radiation and ozone) and temperature. However, other authors (e.g., Sundqvist et al., 2012) have not revealed any elevation-dependent increase in phenolic contents and hypothesized that the response of plants to growing conditions largely depends in the species.

Thus, the results presented above show that variation in the contents of nutrients in the needles of juniper growing in spruce and birch forests depends on the age of needles and differences in the contents of these elements in root-habitable soil horizons. The concentrations of mobile N, P, K, Mg, S, and Zn decrease with age, whereas those of low-mobile Ca, Al, and Fe increase. Interestingly, the concentration of Mn in the needles also decreases with age, although Mn in conifers usually behaves as a low-mobility element. Differences in the concentrations of K, Al, Fe, and Mn between the needles of juniper growing in spruce and birch forests are explained by different contents of mobile compounds of these elements in organogenic and eluvial soil horizons.

The aging of juniper needles is accompanied by the accumulation of lignin, lipids, and phenolic compounds and decrease in the concentrations of flavonoids and soluble and bound proanthocyanidins.

In birch forests (growing at higher elevations), the contents of lipids, cellulose, and lignin in old juniper needles are significantly lower than in spruce forests, while the concentrations of total phenolic compounds, flavonoids, and soluble and bound proanthocyanidins are comparable between the two habitats.

Our results confirm that organic soil horizons sampled under juniper shrubs and in open areas differ in the contents of N and P and show that they also differ significantly in the contents of Ca, K, and Mg compounds available to plants, especially in the upper L subhorizon: the soils under juniper shrubs are richer in nutrients, while the C/N ratio in them is relatively narrow, which may be indicative of an accelerated rate of organic matter decomposition.

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