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ECOLOGY

Trophic Role of the Moose (*Alces alces* L.) Population and Its Effect on the Nitrogen and Carbon Cycles in a Southern Taiga Spruce–Birch Forest

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Abstract—The results of a two-year study conducted to assess the outcomes of a long-term forest isolation experiment are presented. A section of a spruce–birch forest in Yaroslavl oblast (6S4B, 100 years old, quality class I) was isolated from the presence of moose for 25 years. It is established that net mineralization of nitrogen compounds in the 0- to 12-cm soil horizon measured from May to October under field conditions was more intense in the unfenced area in comparison with the isolated area (15 ± 0.4 and 10.4 ± 0.5 g N/m^2, respectively). Carbon dioxide emissions from the soil in that same time period were lower in the unfenced area (319 ± 47 g C/m^2) than in the isolated area (552 ± 82 g C/m^2). On the isolated site, 19 mg of nitrogen is mineralized in the soil per gram of $C\text{-}CO_2$; while on the control site, it is 47 mg of nitrogen per gram of $C\text{-}CO_2$. In the isolated variant, the distribution of ammonium concentrations in the upper (0–4 cm) soil horizon is normal, while in the control variant, it is lognormal due to the presence of elk.

Keywords: net mineralization of nitrogen compounds, ammonification, nitrification, CO_2 emission from soil, moose, southern taiga

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INTRODUCTION

In ecosystems, animals are involved in the cycles of the main biogenic elements as consumers of various orders, but their role in these processes remains insufficiently understood as yet. The state of knowledge about the role of animals in cycles of various elements differs as well. In the carbon cycle, the role of animals is formulated in the biosphere concept (Schmitz et al., 2014), while in the nitrogen cycle, it is demonstrated for individual processes in individual ecosystems (Hobbs, 1996). In boreal forests, the trophic role of ungulates, including deer and elk, is the most extensively researched area. These animals selectively consume certain species (poplar, willow, aspen, and rowan), thus giving advantages to other species that are not of trophic interest to them; sometimes, this occurs through complex competitive relationships (Smirnov, 1987; Persson et al., 2000; Goetsch et al., 2011; Jensen et al., 2011; McGarvey et al., 2013; Murray, 2013; Burkea et al., 2019).

A number of studies have examined the effect of dendrophagous ungulates on the physicochemical soil properties (Pastor et al., 1993; Jensen et al., 2011; Burkea et al., 2019).

In forests of the temperate zone, the key role in the biospheric cycle belongs to nitrogen, a deficiency of which hinders the productivity of forest phytocoenoses. The most productive process in the nitrogen cycle is mineralization of nitrogen compounds by soil microorganisms; this process is complexly interrelated with the phytocoenosis growth, functioning of plant mycorrhizal complexes, nitrogen fixation, atmospheric nitrogen emissions, soil fauna, vertebrates, and gaseous and infiltration losses (Sponseller et al., 2016). In forests of North America and in some areas of Western Europe, mineralization of nitrogen compounds representing the centerpiece of the nitrogen cycle is well-researched (Razgulin, 2008, 2017; Chapman et al., 2013).

In Russia, with its infinite diversity of forest soils and colossal size of forested areas, in situ data on net mineralization of nitrogen compounds are provided in just a few studies (Razgulin, 2017); overall, this topic remains poorly researched.

According to K.A. Smirnov (Smirnov, 1987, 2007, 2017; Smirnov and Sudnitsyna, 2003), the role of dendrophagous ungulates in the southern taiga subzone of European Russia is determined by their population density and trophic load on phytocoenoses. As the food pressure increases, the direct and indirect impacts of ungulates can affect all ecosystem levels: from the soil to the upper forest story. This leads to structural changes in the phytocoenosis and redistribution of the matter and energy flow in the ecosystem. Despite the large number of works dedicated to the moose, this aspect of its life activity remains poorly researched; just a few studies examine effects caused by ungulates on the carbon and nitrogen cycles in forest ecosystems (Pastor et al., 1993; Persson et al., 2009; Popma and Nadelhoffer, 2020).

This study assesses the effects of the moose population on the following parameters: (1) content of organic carbon (C_{org}) and nitrogen forms in the soil; (2) productivity of net mineralization of nitrogen compounds in the soil; and (3) carbon dioxide production. The possible effects include stimulation, suppression, or lack of effect on the above processes.

MATERIALS AND METHODS

The studies were conducted in Rybinsk district, Yaroslavl oblast. The experimental site is located on the slope of the Nakhta River in a well-drained spruce–birch forest (stand composition: 6S4B, 100 years old, quality class I, forest stand density: 0.7). The undergrowth consists of spruce (*Picea abies*) up to 8 m high and some aspen (*Populus tremula*). The underwood consist of rowan (*Sorbus aucuparia*), honeysuckle (*Lonicera xilosteum*), alder buckthorn (*Frangula alnus*), common hazel (*Corylus avellana*), and red currant (*Ríbes rúbrum*). The ground cover is very diverse, including wood stitchwort (*Stellária nemórum*), asarabacca (*Ásarum europaéum*), wood sorrel (*Óxalis acetosélla*), wood millet (*Milium effusum*), and wonder violet (*Víola mirábilis*). Overall, more than 40 plant species belonging to the nemoral and boreal groups and the group of secondary forest species occur in the study area (Smirnov and Sudnitsyna, 2003).

The studied soil is sod–medium podzolic light loamy. The discernible litter layer (A_0) is 1 cm thick. Below is a grayish black humus horizon (A_1) spreading to a depth of 15 cm. Then goes the reddish pale eluvial part of the profile (A_2) underlain by moraine loam at a depth of 70–80 cm.

In 1992, a portion of the study area 15 × 30 m in size was enclosed with a fence (poles 2.5 m high every 0.4 m with five rows of wire) preventing moose from penetrating past the fenced perimeter. An adjacent site of the same size was used as the control (no fencing).

In the years 2017–2018, the following parameters were measured simultaneously on both sites in the period from May to October:

(1) Net mineralization of nitrogen compounds in two soil horizons (A_0–A_1 (0–4 cm) and A_1 (4–12 cm)) using the sample incubation method without plants. Samples were placed in nylon mesh bags and exposed in situ in the soil profile for 27–30 days with an eightfold replication for each horizon. The samples were deployed checker-wise from the top to the foot of the slope to cover the entire sampling area. Nitrogen accumulation was computed as the difference between the products of the horizon weight per 1 m^2 and the element content at the end and at the beginning of exposure (Razgulin, 2009).

(2) Ammonia emissions using the isolated chambers method. The chamber area was 60 cm^2. The measurements were performed with a tenfold replication using the principle of absorption of trace amounts of this gas by sulfuric acid after 10–13 days (Razgulin and Stepanov, 2009).

(3) Carbon dioxide emission in four isolated chambers (40 × 40 × 10 cm) with steel frames embedded in the soil to a depth of 15–20 cm. Air samples were collected into vacuumized flasks with a threefold replication every 10–13 days during the season. Overall, five nitrogen mineralization measurements and nine ammonia and carbon dioxide emission measurements were performed each year.

(4) Litterfall in five litterfall collectors 1.5 × 0.9 m in size; the contents were removed three times in the period from August to November.

After the exposure, large (more than 1 mm in diameter) inclusions were removed from the samples in the laboratory. Then samples from the upper horizon were separated using 5- and 3-mm sieves; samples from the lower horizon, using 3- and 2-mm sieves. The samples were mixed, placed in plastic bags, and stored in a refrigerator at 4°C. To determine the exchangeable ammonium content, soil samples equivalent to 4 g of dry weight for the upper horizon and to 8 g of dry weight for the lower horizon were extracted for 24 hours with 100 mL of a 2% potassium chloride solution with the addition of 1 drop of toluene. Then the suspension was shaken for 1 h on a rotator, centrifuged, and filtered, and the ammonia content was determined using the diffusion-isothermal ammonia distillation method in all replications. The content of nitrates was measured in an aqueous extract using the Griess reagent after reducing them to nitrites on copper-coated cadmium (Razgulin, 2009). The nitrate nitrogen content was determined in a mixed sample of eight components.

The carbon dioxide content was measured using a gas analyzer with Reberg absorbers; the excess of barium hydroxide was titrated with hydrochloric acid. Argon was used as the carrier gas (Razgulin, 2017).

The organic carbon content and the total nitrogen content were determined in the soil, in rowan leaves, and in fallen needles once per growing season with a fourfold replication using the loss on ignition method and the Kjeldahl method, respectively.

The bulk density of the A_0–A_1 and A_1 horizons was measured with an eightfold replication.

In Tables 1 and 2, the content of carbon and nitrogen forms in the soil, as well as the amount of litter, are

Table 1. Average seasonal content of mineral nitrogen, organic carbon, and organic nitrogen in soil horizons on the unfenced (Uf) and fenced (F) sites

Parameter	Horizon		Year 2017	Year 2018
NH_4^+, mg N/100 g	A_0-A_1,	Uf	6.28 ± 0.86	4.82 ± 0.65
		F	5.78 ± 0.87	4.7 ± 0.26
	A_1,	Uf	1.72 ± 0.13	1.22 ± 0.11
		F	1.44 ± 0.27	1.02 ± 0.14
NO_3^-, mg N/100 g	A_0-A_1,	Uf	0.46 ± 0.08	0.71 ± 0.08
		F	0.26 ± 0.06	0.74 ± 0.11
	A_1,	Uf	0.30 ± 0.07*	0.58 ± 0.12
		F	0.09 ± 0.02	0.29 ± 0.06
C_{org}, %	A_0-A_1,	Uf	10 ± 0.3	9.3 ± 0.4
		F	11.3 ± 0.3	9.1 ± 0.3
	A_1,	Uf	3.3 ± 0.1	3.2 ± 0.2
		F	3.5 ± 0.1	3.1 ± 0.2
N_{tot}, %	A_0-A_1,	Uf	0.53 ± 0.05	0.50 ± 0.05
		F	0.62 ± 0.06	0.42 ± 0.06
	A_1,	Uf	0.15 ± 0.01	0.15 ± 0.01
		F	0.17 ± 0.01	0.16 ± 0.01

* Differences between (Uf) and (F) are statistically significant at $p < 0.1$ (also applies to Table 2). ** Differences between (Uf) and (F) are statistically significant at $p < 0.05$ (also applies to Table 2).

provided in relation to dry weight and presented as mean values and their errors. Mineralized nitrogen and carbon dioxide production over the study period are presented as sums and their errors.

Table 3 shows the 2-year average values of nitrogen mineralization activity expressed in mg N/100 g soil/day (Am) and the process efficiency, when the activity is expressed per C_{org} (mg N/g C/day, N_c) and N_{tot} (mg N/g N/day, N_n) of soil. The distribution of ammonium concentrations and ammonification activity in the soil, as well as the carbon dioxide emission values were calculated from the data of measurements for 2 years. Statistical calculations were performed using the Statistica 10 software*.

RESULTS AND DISCUSSION

In most cases, the sites studied did not differ from each other in the average seasonal content of mineral nitrogen forms in the soil. In 2017 alone, the amount of nitrates in the A_1 horizon in the soil of the fenced site was statistically significantly lower (at $p < 0.1$) than that on the control site. The year-to-year differences between the two variants in the content of ammonium nitrogen in the upper and lower soil horizons were small; by contrast, the differences in the content of nitrates were significant: from 1.5 to 3 times (Table 1).

No significant differences between the sites in the C_{org} and N_{tot} content in the soil were detected: these parameters turned out to be quite stable, both in the experiment and over the years of research (Table 1).

Earlier, the absence of differences in the chemical composition of soils on experimental and control sites was noted for broad-leaved and mixed forests of the United States and Canada with large (14–40 ind. per 1000 ha) and small (2–4 ind. per 1000 ha) ungulate populations. Animals do not affect the content of Na, K, Ca, and Mg; the capacity of the soil adsorption complex; or the total content of C, N, P, and ammonium in the soil (Pastor et al., 1993; Ellis and Leroux, 2017; Burkea et al., 2019).

The presence of animals increases the adsorption complex capacity and the content of K and Mg in the soil only in a mixed forest (Michigan, United States) with a large deer population (130–830 ind. per 1000 ha). However, no differences in the content of mineral and total nitrogen were registered, and the C_{org} concentrations in the soil were lower than on the isolated site (Jensen et al., 2011).

Table 2. Ammonification (Af) and nitrification (Nf) productivity, amount of mineralized nitrogen (Nm), ammonia emissions (Ea), carbon dioxide production, and litterfall amount in the soil on the unfenced (Uf) and fenced (F) sites

Parameter	Soil horizon		Year	
			2017	2018
Af, g N/m^2	A_0-A_1,	Uf	6.0 ± 0.3	5.4 ± 0.7**
		F	5.9 ± 0.2	1.9 ± 0.7
	A_1,	Uf	3.4 ± 0.3**	3.5 ± 0.5
		F	2.3 ± 0.2	4.5 ± 0.6
Nf, g N/m^2	A_0-A_1,	Uf	2.3 ± 0.03**	2.8 ± 0.1**
		F	1.1 ± 0.04	1.8 ± 0.2
	A_1,	Uf	2.9 ± 0.07**	3.8 ± 0.4**
		F	1.3 ± 0.06	2.5 ± 0.24
Nm, g N/m^2	Entire	Uf	14.7 ± 0.4**	15.5 ± 1**
	profile	F	10.6 ± 0.5	10.7 ± 1
Ea, mg N/m^2		Uf	3.9 ± 1.5	1 ± 0.2
		F	2.4 ± 0.2	0.6 ± 0.2
CO_2 production, g C/m^2		Uf	357 ± 53**	281 ± 40
		F	729 ± 100	375 ± 56
Litterfall, g/m^2		Uf	194 ± 11	183 ± 14
		F	193 ± 11	199 ± 11

Table 3. Average seasonal activity (A_m) and efficiency (N_c and N_n) of nitrogen mineralization in soil horizons of unfenced and fenced sites

Site, soil horizon	A_m, mg N/100 g/day	N_c, mg N/g C/day	N_n, mg N/g N/day
HO, A_0–A_1	0.25 ± 0.04*	0.026 ± 0.004	0.49 ± 0.08
A_1	0.059 ± 0.01	0.018 ± 0.001	0.39 ± 0.06
O, A_0–A_1	0.168 ± 0.06	0.016 ± 0.006	0.32 ± 0.12
A_1	0.053 ± 0.006	0.016 ± 0.002	0.33 ± 0.04

* Data are expressed as the mean values and their standard deviations.

Therefore, even long-time isolation (from 12 to 37 years) does not make it possible to confirm the unambiguous effect of ungulates on the chemical composition of the soil.

No significant differences in the soil bulk density were registered between the unfenced and isolated areas; in the upper horizon, it was equal to 0.585 ± 0.07 and 0.673 ± 0.05 g/cm^3, respectively; in the lower part of the profile, it was equal to 1.08 ± 0.04 g/cm^3 on both sites. The absence of differences between the experimental variants in the bulk density of the soil was noted earlier as well (Burkea et al., 2019).

In 2017, the ammonification productivity in the unfenced area in horizons A_0–A_1 and A_1 was 6 ± 0.3 and 3.4 ± 0.3 g N/m^2, respectively; while the nitrification productivity was 2.3 ± 0.03 and 2.9 ± 0.07 g N/m^2, respectively. In total, 14.6 ± 0.4 g N/m^2 was mineralized; the contribution of nitrification was 5.2 ± 0.07 g N/m^2 (35%) (Table 2).

In the soil of the isolated site, 5.9 ± 0.5 and 2.3 ± 0.2 g N/m^2 were ammonified in the same horizons, and 1.1 ± 0.04 g N/m^2 and 1.3 ± 0.06 g N/m^2 were nitrified. The total amount of mineralized nitrogen was 10.6 ± 0.5 g N/m^2; the contribution of nitrification was 22%.

In 2018, ammonification in the upper and lower soil horizons on the unfenced site amounted to 5.4 ± 0.7 and 3.5 ± 0.5 g N/m^2, respectively; while nitrification reached 2.8 ± 0.1 and 3.8 ± 0.4 g N/m^2, respectively. The total amount of mineralized nitrogen was 15.5 ± 1 g N/m^2; the contribution of nitrification was 42%.

In the upper and lower soil horizons on the isolated site, ammonification was 1.7 ± 0.7 and 4.5 ± 0.6 g N/m^2, respectively; while nitrification was 1.8 ± 0.2 and 2.5 ± 0.2 g N/m^2, respectively. Overall, 10.5 ± 1 g N/m^2 was mineralized; the contribution of nitrification was 40%.

In the control variant, year-to-year changes in the mineralization of nitrogen compounds in the forest soil were insignificant; while on the experimental site, they reached 2–3 times in the upper soil horizon (Table 2).

Overall, the two-year average ammonification productivity on the unfenced site in horizons A_0–A_1 and A_1 was 5.7 ± 0.3 and 3.4 ± 0.3 g N/m^2, respectively; while the nitrification productivity was 2.5 ± 0.03 and 3.3 ± 0.07 g N/m^2, respectively.

In the isolated variant, 3.8 ± 0.5 and 3.4 ± 0.2 g N/m^2 were ammonified in the same horizons, and 1.4 ± 0.04 and 1.8 ± 0.06 g N/m^2 were nitrified. In total, 15 ± 0.4 and 10.4 ± 0.5 g N/m^2 were mineralized in the soil profile of the control and experimental sites, respectively. This difference is statistically significant at $P < 0.05$. The decrease in the process productivity observed in the isolated area ensured a 1.5-fold decrease in ammonification in the A_0–A_1 horizon and a 1.7-fold decrease in the nitrified nitrogen content in the entire profile in comparison with the unfenced area. Net mineralized nitrogen constituted 7 and 5.3% of the total nitrogen reserve (N_{tot}) in the upper and lower soil horizons in the unfenced area and 3.7% in both horizons in the isolated variant.

When moving down the soil profile, the activity of nitrogen mineralization (A_m) naturally decreases, but the efficiency of the process (N_c and N_n) in both soil horizons of the experimental site was similar, which was also noted earlier in areas with a low trophic influence of the moose (Razgulin, 2017). The presence of the moose led to an increase in nitrogen mineralization efficiency (N_c) in the upper soil horizon of the control site by 1.4 times as compared with the lower horizon (Table 3).

Total ammonia losses over the study period (i.e., in 2017 and 2018) amounted to 3.9 ± 1.5 and 2.4 ± 0.2 mg N/m^2 in the unfenced area and to 1 ± 0.2 and 0.6 ± 0.2 mg N/m^2 in the isolated area. In both years of research, these values were higher in the unfenced area, but the differences were not statistically significant (Table 2).

Carbon dioxide production in the forest soils was higher in the isolated area in both years of research, but the values were statistically significantly different only in 2017 (Table 2).

In most cases, the distribution histograms computed for the ammonium content, ammonification activity in horizons of the forest soil, and carbon dioxide emissions show normal distributions of these values (Figs. 1–3). However, the presence of moose changes the ammonium content distribution in the upper soil horizon from normal in the fenced area to lognormal in the control area (Fig. 1). A left asymmetry is clearly manifested in the distribution of carbon dioxide emissions in the fenced area; it contains 70% of all data in the value class of 0–131 mg $C/m^2/h$ and is absent in the graph constructed for the unfenced area (Fig. 3).

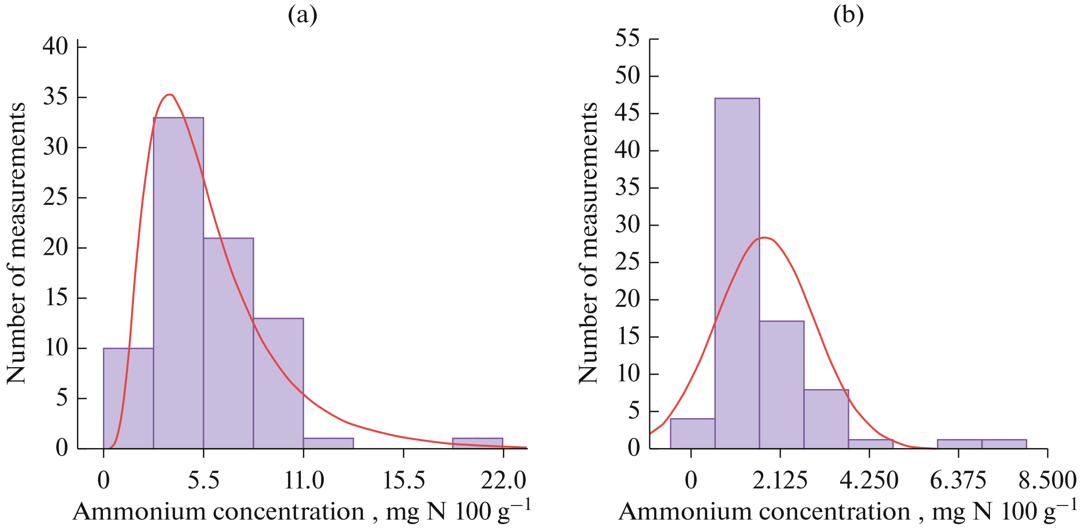
The data obtained indicate that an increase in nitrogen mineralization is accompanied by a decrease in carbon dioxide production on the control site (Table 2). This contradicts the data collected for an ecological series of southern taiga birch forests where an increase in net nitrogen mineralization during the growing season corresponds to an increase in carbon dioxide production that serves as an indicator of decomposition processes in the soil (Razgulin, 2017).

Other authors also note a decrease in the soil respiratory activity by 24–56% under the impact of ungulate grazing (Persson et al., 2009). On the other hand, the potential mineralization of soil carbon and nitrogen is higher in the presence of moose, but these differences are not statistically significant (Pastor et al., 1993). The litter decomposition rate in a mixed forest (Newfoundland, Canada) also did not differ in different variants of the isolation experiment (Ellis and Leroux, 2017).

It was believed that “urine and feces of ungulates can be factors strong enough to outweigh the decline in soil organic matter quality” (Stark, 2002) and stimulate the nitrogen cycle (Hobbs, 1996). In oligotrophic tundra in Finland, the C and N cycles are limited by low reindeer numbers. Higher grazing intensity stimulates C and N mineralization under both oligotrophic and eutrophic conditions (Stark, 2002). An increase in net nitrogen mineralization amid a decrease in soil respiratory activity under the impact of ungulate grazing was noted earlier for African savannas and landscapes of Yellowstone National Park, United States (Hobbs, 1996; Stark, 2002). However, repeated soil studies in semiarid prairies of the park did not show an unambiguous effect of ungulates on the nitrogen cycle, including gross mineralization of the element (Verchot et al., 2002).

Statistically significant differences in the productivity of net nitrogen mineralization in forest soils are manifested only in situations when the numbers of animals are high. For instance, in a broad-leaved forest (Michigan, United States), a moose population with a density of 34 and 46 ind. per 1000 ha reduced the amount of mineralized nitrogen in the 0- to 10-cm soil horizon in half compared with the fenced area: from 45–46 to 22–28 kg N/ha. No differences in the process productivity were identified between the control and experimental sites for a moose population with a density of 14 ind. per 1000 ha. The sites remained in isolation for 30 years. Elk selectively consume deciduous species, thus, giving a competitive advantage to coniferous ones. As a result, the cellulose

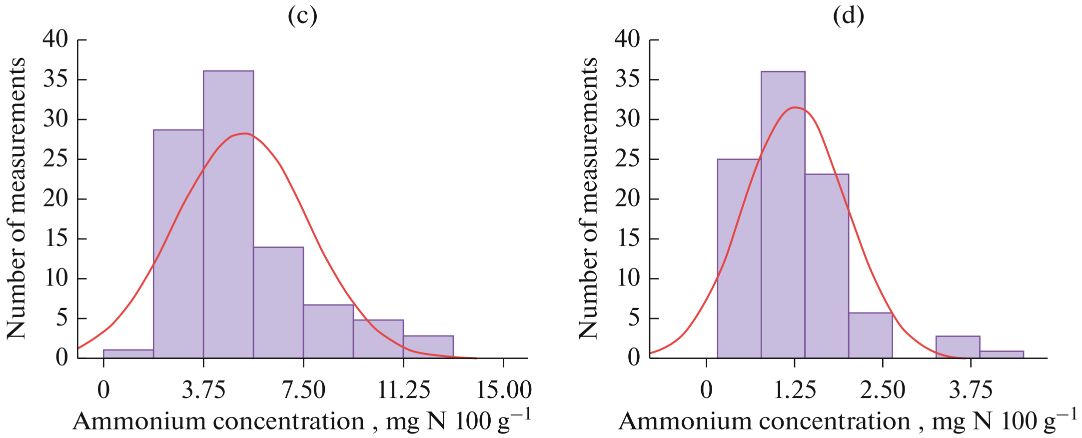
Unfenced site



Lognormal, Xi^2 = 6.75,
df = 2, p = 0.043, n = 79

Normal, Xi^2 = 33.76,
df = 1, p = 0, n = 79

Fenced site



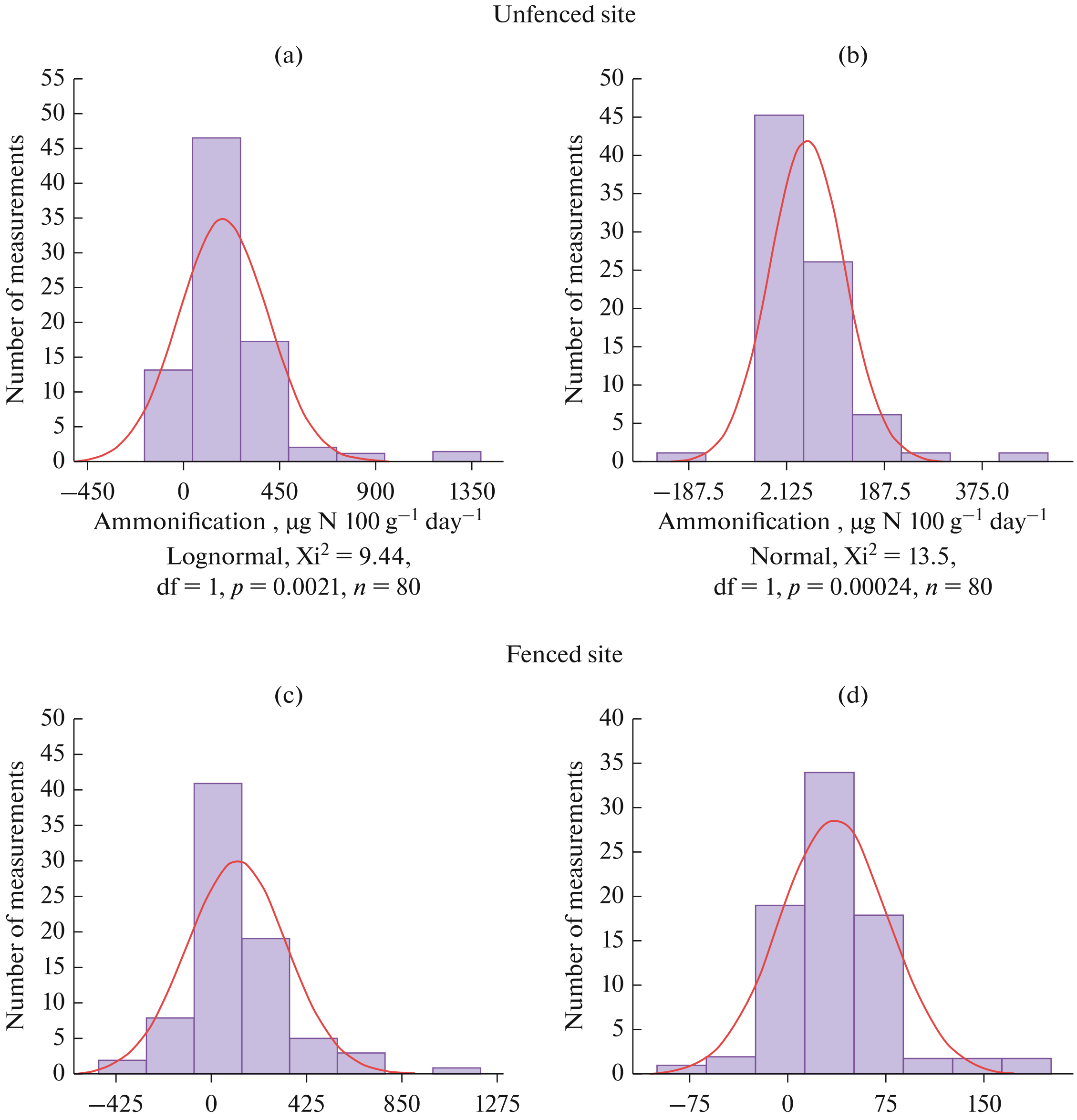
Normal, Xi^2 = 21.03,
df = 2, p = 0.00003, n = 95

Normal, Xi^2 = 12.2,
df = 2, p = 0.00213, n = 94

Fig. 1. Diagrams showing the distribution of ammonium concentrations in soil horizons under the spruce–birch forest: (a, c) A_0–A_1 horizon and (b, d) A_1 horizon.

content in the forest litter increases, while the leaf litterfall decreases, which reduces the decomposition of plant biomass and nitrogen mineralization (Pastor et al., 1993). In oligotrophic forests of Scandinavia, reindeer and elk grazing does not have an unambiguous effect on nitrogen mineralization. Both stimulation of this process and the absence of any effect were noted (Stark, 2002). In temperate forests, deer grazing increases nitrogen mineralization in landscapes with rich soils and reduces this parameter in ecotopes poor in nutrients. By contrast, carbon dioxide emissions decrease in rich soils and increase in areas poor in nutrients (Popma and Nadelhoffer, 2020). Apparently, the precise identification of effects exercised by ungulates on the nitrogen and carbon cycles is complicated by the endless diversity of forest ecosystems and therefore requires further research.

Data obtained in the course of this study indicate a clear decrease in net mineralization of nitrogen compounds in the soil affected by a low-density (three individuals per 1000 ha) moose population (Smirnov, 2007). According to Persson et al. (2000), one adult elk releases 40 kg of nitrogen per year; in the variant studied, this translates into 0.012 g N/m^2/yr. The actual input of nitrogen into the soil is even less, since the decomposition rate of moose ‘balls’ that constitute



(a) Lognormal, $Xi^2 = 9.44$, df = 1, $p = 0.0021$, $n = 80$

(b) Normal, $Xi^2 = 13.5$, df = 1, $p = 0.00024$, $n = 80$

(c) Normal, $Xi^2 = 11.28$, df = 1, $p = 0.00078$, $n = 79$

(d) Normal, $Xi^2 = 4.14$, df = 2, $p = 0.126$, $n = 80$

Fig. 2. Diagrams showing the distribution of ammonification activity in soil horizons under the spruce–birch forest: (a, c) A_0–A_1 horizon and (b, d) A_1 horizon.

40% of the total nitrogen excretion (Persson et al., 2000) is extremely low: 0.65% N per year (Pastor et al., 1993).

On the other hand, moose numbers are approximate values, while the control site had received additional nitrogen for 25 years, which could stimulate the nitrogen cycle. It is also known that experimental pruning of birch seedlings under mesocosmic conditions conducted to simulate the impact of ungulates reduces the aboveground and underground biomass of the seedlings but increases the mineralization of soil nitrogen compared to the control (Carline and Bardgett, 2005).

Rowan predominates on both sites studied constituting more than 50% of the aboveground undergrowth biomass (Smirnov and Sudnitsyna, 2003). In the unfenced variant, its height does not exceed 1.7 m and its flat funnel-shaped crowns are browsed by moose on a regular basis. The leaves have a black border, and the leaf weight is 2.3 times lower in comparison with the fenced area (Smirnov, 2007). On the experimental site, rowan forms a closed story 5–6 m

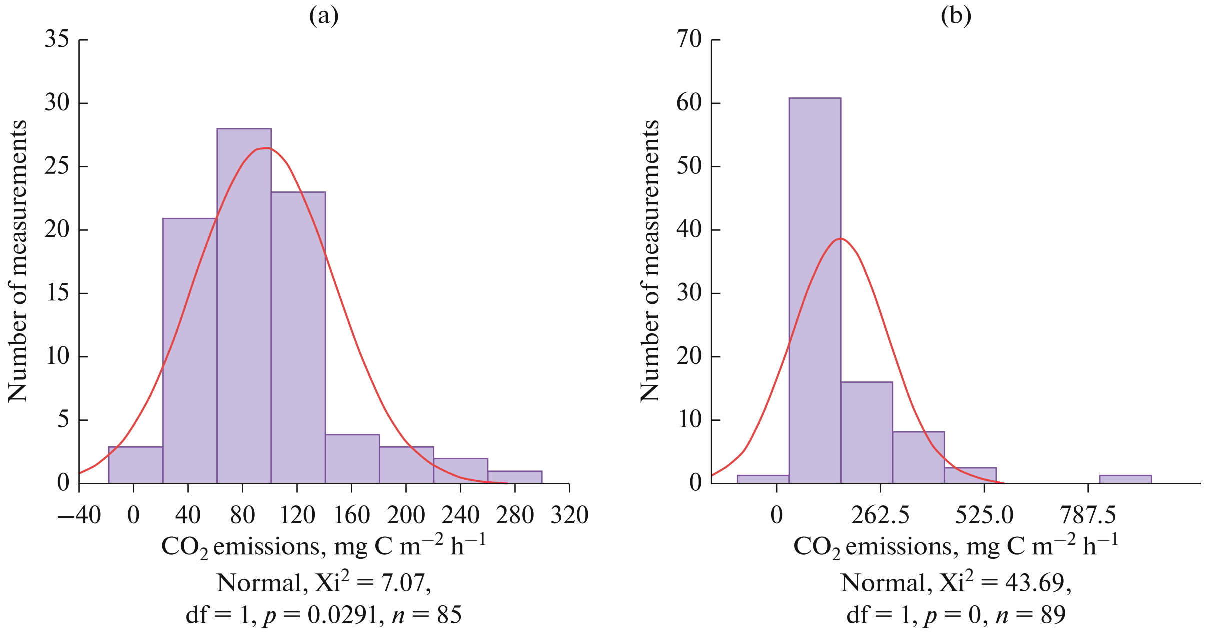


Fig. 3. Diagrams showing the distribution of carbon dioxide emissions from the soil under the spruce–birch forest: (a) unfenced site and (b) fenced site.

high with dense well-foliated crowns. On the unfenced site, trophic injuries of crowns reduce the production of photosynthesis and limit the amount of root exudates entering the soil (Stark, 2002). This, in turn, reduces the ectomycorrhization of thin roots (Rossow et al., 1997) and depresses the soil respiratory function (Stark, 2002), but may stimulate the mineralization of soil nitrogen compounds (Carline and Bardgett, 2005).

In 1999, the amount of litter on the control and isolated sites amounted to 191 and 249 g/m^2, respectively. The increase was due to coniferous litter the contribution of which amounted to 42 and 102 g/m^2, respectively (Smirnov and Sudnitsyna, 2003). In the years 2017–2018, the amount of litter was the same on both sites and close to the amount registered in 1999: 193 g/m^2 (Table 2). It is possible that birch has surpassed spruce on the isolated site, and the amount of coniferous litter decreased; however, the overall productivity of the phytocoenoses did not change and probably was close on both sites. Despite the differences in soil nitrogen mineralization, the total nitrogen content in green rowan leaves and in fallen needles was the same on both sites (1.65 ± 0.06% and 0.97 ± 0.05%, respectively), which was also noted earlier for leaf and coniferous litterfall (Smirnov and Sudnitsyna, 2003).

In forest ecosystems, large ungulates exercise a complex effect on the chemical composition of plants and litter quantity and quality. In a mixed forest, the amount of litter and the content of common C, N, and P forms in leaf litter on control sites (i.e., with the presence of moose) were less in comparison with experimental sites (Ellis and Leroux, 2017). In some studies, dendrophagous ungulates did not change the N_{tot} content in tree leaves (Pastor et al., 1993); while in others (with very high population densities), they reduced it (Jensen et al., 2011).

Simultaneous measurements of nitrogen mineralization and carbon dioxide emissions from the soil make it possible to estimate approximately the relationship between decomposition parameters and nitrogen mineralization. The use of carbon dioxide emissions from the soil as an indicator of decomposition processes is complicated by methodological difficulties and uncertainties. In this study, steel frames embedded in the soil to a depth of 15–20 cm cut roots of trees and shrubs; this brings the gas flow closer to basal respiration, but eliminates rhizospheric effects that develop on the root surface.

The average annual carbon dioxide production in the control and isolated variants amounts to 319 ± 47 and 552 ± 82 g C/m^2, respectively; the average annual productivity of mineralization of nitrogen compounds amounts to 15.0 and 10.4 g N/m^2, respectively. In other words, on the isolated site, 19 mg of nitrogen is mineralized in the soil per gram of C-CO_2 (Nm: C-CO_2); while on the control site, this amount is 2.5 times higher: 47 mg of nitrogen per gram of C-CO_2. Despite this, the fenced and unfenced sites are close to each other in phytocoenosis productivity.

CONCLUSIONS

Overall, the 25-year isolation did not lead to unambiguous changes in the content of organic carbon and mineral and total nitrogen in the soil of the experimental site.

The presence of moose increases the amount of mineralized soil nitrogen by 1.5 times compared to the fenced area, primarily due to greater contributions of ammonification in the upper soil horizon and nitrified nitrogen in the entire profile.

The presence of moose increases the share of mineralized nitrogen in the total nitrogen soil reserve (N_{tot}) from 3.7% in the entire profile on the isolated site to 7 and 5.3% in the upper and lower soil horizons in the control variant.

The average annual carbon dioxide emission on the isolated site is 1.7 times higher in comparison with the control.

The trophic role of the moose increases the efficiency of nitrogen mineralization in the upper soil horizon as compared to the lower horizon in the experimental site, with equal values of these parameters in the control site.

The moose population changes the distribution of ammonium concentrations in the upper soil horizon from normal in the isolated variant to lognormal in the control variant.

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COMPLIANCE WITH ETHICAL STANDARDS

The author declares that he has no conflicts of interest. This article does not contain any studies involving animals or human participants performed by the author.

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