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SOIL BIOLOGY

Dependence of Soil Properties under Alpine Lichen Heath Community on the Soil Water Content and the Presence of *Vaccinium vitis-idaea*

M. I. Makarov[a, *], **R. V. Sabirova**[a], **M. S. Kadulin**[a], **T. I. Malysheva**[a], **A. I. Zhuravleva**[b], **V. G. Onipchenko**[a], **and A. A. Aksenova**[a]
[a] *Lomonosov Moscow State University, Moscow, 119991 Russia*
[b] *Institute of Physicochemical and Biological Problems of Soil Science, Russian Academy of Sciences, Pushchino, 142290 Russia*
**e-mail: mmakarov@soil.msu.ru*

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Abstract—An increasing participation of dwarf shrubs and shrubs in plant communities of alpine meadows and a tendency to a decrease in summer precipitation in mountain regions determine the relevance of assessing the role of ectomycorrhiza and ericoid mycorrhiza, as well as the soil moisture status, in nutrient availability for plants and microorganisms. The properties of a mountain-meadow soil (Umbric Leptosol), including labile forms of carbon, nitrogen, and phosphorus and the soil biological activity were studied under the alpine lichen heath in the Teberda Reserve at different soil water contents and in the presence or absence of *Vaccinium vitis-idaea* in the plant community. The soil under *V. vitis-idaea* was characterized by higher acidity, and the response of its properties to changes in the soil water content was less pronounced. In the absence of this dwarf shrub, soil properties pronouncedly differed in response to changes in the water content. Under herbaceous vegetation, the content of inorganic nitrogen, the activity of N-mineralization and nitrification, microbial biomass, and soil respiration decreased with a drop in soil moisture, whereas the concentration of labile organic carbon and nitrogen and the activity of exoenzymes increased. Such changes attest to a shift in the organic matter transformation from mineralization to depolymerization, which is more typical of ectomycorrhiza- and ericoid mycorrhiza-dominated ecosystems.

Keywords: ericoid mycorrhiza, soil moisture, carbon, nitrogen, phosphorus, microbial biomass, enzymatic activity

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INTRODUCTION

The participation of dwarf shrubs and shrubs in phytocenoses of the arctic / subarctic tundra and alpine meadows has increased in recent decades [12, 15, 28]. For example, 40-year-long observations of the dynamics of alpine biogeocenoses in the Teberda Reserve have shown a rise in the portion of *Vaccinium vitis-idaea* L. in the aboveground biomass of the alpine lichen heath community (ALH) [13].

Changes in the composition of plant community may result in variations in soil properties due to specific features of assimilation and dissimilation of chemical elements and compounds by particular plant species [24]. For example, plants, which form different types of mycorrhiza, exert different impacts on the soil organic matter and mineral nutrients and thus on the main parameters of ecosystem functioning: the carbon and nitrogen cycles. This is related to different enzymatic activity of fungi, which form ectomycorrhiza (ECM) and ericoid mycorrhiza (ERM), on the one hand, and arbuscular mycorrhiza (ARM), on the other hand. Fungi, forming ECM and ERM, produce oxidative and hydrolytic enzymes, which can depolymerize soil organic matter and mobilize mineral nutrients, while ARM fungi are characterized by much smaller production of enzymes and their lower activity [2, 16, 26, 33].

Laboratory experiments show an active decomposition of complex organic compounds (lignin and polyphenols) and N mobilization from chitin and polyphenol-protein complexes by fungi forming ECM and ERM [8, 27, 29]. Nevertheless, the quantitative assessment of the efficiency of these processes in natural ecosystems is still debatable. The production of exoenzymes by mycorrhizal fungi under natural conditions is regulated by various factors, which affect the exchange of plant carbon for fungal nitrogen. They include the physiological status of the both symbionts and soil conditions [19, 22, 35]. In addition, mycorrhizal fungi represent several functional groups. The ability of some of them to affect soil organic matter is limited, while others can intensively mobilize nutrient elements [9, 32].

We have already suggested that an increased participation of *V. vitis-idaea,* forming ERM, in plant community of ALH may change soil properties related to mobilization of organic matter and mineral nutrients under the effect of exoenzymes of mycorrhizal fungi. To test this hypothesis, we have compared the mountain-meadow soil under ALH with and without the dwarf shrub. The rise in the content of extracted carbon, nitrogen of microbial biomass, and available phosphorus and in microbial activity in the presence of *V. vitis-idaea* conforms to the idea of increased availability of biogenic elements for nutrition of soil microorganisms and plants [4].

In addition, the soil in the variant with *V. vitis-idaea* was better moistened, which could be related to specific features of its water-physical properties determining the settlement of this dwarf shrub and could also affect the organic matter composition and the functioning of the microbial community. A tendency to a decrease in precipitation of the warm season and the predicted increase in the number and intensity of droughts in mountain regions [14, 18] make the assessment of the role of the soil moisture factor in the availability of nutrients particularly relevant.

We studied soil properties under an ALH along the water content gradient on different sites but with equal water contents in the soils in the presence and absence of *V. vitis-idaea* on each site. The aim was to verify the effect of the dwarf shrub and of soil water content on the organic matter transformation and on the content of labile forms of carbon, nitrogen, and phosphorus.

OBJECTS AND METHODS

The object of the study was represented by a light-loamy mountain-meadow soil (Umbric Leptosol) under the ALH at the Malaya Khatipara High-Altitude Experimental Station in the Teberda State Biospheric Reserve (2800 m a.s.l.). In July 2018, two ALH plots were chosen for the study: on a steep (15°) southeastern slope and on the upper part of an eastern slope. Vegetation spots without *V. vitis-idaea* (control) and with dwarf shrub were chosen on the plots, and soils were sampled from them.

During the sampling, the volumetric soil water content at the depth of 10 cm was controlled using a TRIME-EZ sensor (IMKO Micromodultechnic GMBH, Germany): for a comparative analysis, it had to be approximately the same in the two variants (with and without the dwarf shrub). Soil moisture was significantly lower on the first plot (about 15%), and samples from the second plot characterized soils at two different moistening levels (about 21 and 27%). Thus, we obtained three pairs of variants control—*V. vitis-idaea* at different moisture contents: about 15% (site 1), 21% (site 2), and 27% (site 3).

Ten soil samples were taken from a depth of 0–5 cm for each variant. They were frozen and transported to a laboratory for further analysis.

In the thawed samples, we determined the acidity (pH of water suspension), the content of available inorganic phosphorus (P_{min}) by the Kirsanov method (extraction by 0.2 M HCl), and available C and N compounds (extraction by 0.05 M K_2SO_4). The concentrations of C of organic compounds (C_{org}), ammonium N ($N{-}NH_4^+$), nitrate N ($N{-}NO_3^-$), and total N (N_{extr}) were determined in the extract. The amount of N of organic compounds (N_{org}) was calculated as the difference between the concentrations of N_{extr} and inorganic N forms ($N{-}NH_4^+ + N{-}NO_3^-$).

Among the parameters, characterizing biological soil properties, C and N of microbial biomass (C_{micr} and N_{micr}) were determined by the fumigation-extraction method [10, 34]. Carbon and nitrogen were extracted from samples fumigated by chloroform vapor using 0.05 M K_2SO_4. Concentrations of C_{micr} and N_{micr} were calculated as the difference between C_{org} and N_{extr} in fumigated and initial samples (we did not apply the coefficients, which take into account incomplete extractability of microbial biomass components).

The mineralization activity of organic nitrogen compounds (N-mineralization) and nitrification activity were determined after the incubation of soil samples for 20 days at 22°C and field moisture (in a SANYO MIR-153 thermostat). The N-mineralization was calculated as the difference between the concentrations of N of inorganic compounds ($N{-}NH_4^+ + N{-}NO_3^-$) in the soil after and before the incubation. The nitrification was determined as the difference between the corresponding concentrations of $N{-}NO_3^-$.

Basal respiration (BR) of soil was determined after incubation of samples for 24 h at 22°C. The respiration rate was given in mg $C{-}CO_2$/kg per hour. The microbial metabolic quotient (qCO_2) was calculated as the BR-to-C_{micr} ratio [1].

The activity of hydrolytic enzymes was determined by the method of fluorimetrically labeled substrates [21]. This method is based on the fact that enzyme-selective substrates with attached fluorescent compound represented by methylumbelliferone (MUF) or 7-amino-4-methylcumarin (AMC) undergo hydrolysis when interacting with the soil extract. The amount of the released fluorescent compound was determined fluorometrically. MUF-labeled substrates were used to determine the activity of β-D-glucosidase (MUF-β-D-glucopyranoside), chitinase (MUF-N-acetyl-β-D-glucosaminide), and phosphatase (MUF-phosphate). AMC-labeled substrate was used to evaluate the activity of leucin aminopeptidase (L-leucine-7-amino-4-methylcoumarin). The amounts of fluorescing MUF and AMC formed as a result of substrate decomposition were measured on a FilterMax F5 multi-modal microplate reader at the wavelength of emission excitation of 355 nm and of emission of 460 nm. Measurements were performed within 60-, 120-, and 180-minute periods after the substrate application. The enzyme activity was given in μM MUF(AMC)/g per hour.

The C_{org} and N_{extr} concentrations were determined on a TOC-V_{CPN} analyzer. Inorganic forms of nitrogen and phosphorus were colorimetrically analyzed on a GENESYS™ 10UV spectrophotometer. We determined $N{-}NH_4^+$ by the salicylate-nitroprusside method, $N{-}NO_3$ after reduction of NO_3^- to NO_2^- on a cadmium column with subsequent reaction with sulfanilamine and N-(1-naphthyl)-ethylenediamine-dihydrochloride, P_{min} by reduction of molybdenum of phosphomolybdic acid by ascorbic acid according to the approach by Murphy and Reilly modified by Watanabe and Olsen. The CO_2 concentration was determined on a Kristall-2000 gas chromatograph.

The data were statistically analyzed using the STATISTICA 8.0 software and checked for the distribution normality (the Shapiro-Wilk test) and equal variances (the Cochran, Hartley, and Bartlett test). The properties, which deviated from the normal distribution and did not have equal variances, were log-transformed. Then, we performed the two-way ANOVA to assess the effect of soil water content on the studied properties (three variants), the presence/absence of *V. vitis-idaea* (two variants), and the interaction of these factors. The effect of factors and their combination was considered significant at $P < 0.05$. If the effect of a factor or a combination of factors was significant, the Fischer test was used to evaluate the significance of the impact of the presence or absence of *V. vitis-idaea* on soil properties for each site. The effect of changes in soil moisture on studied soil properties in the control variant and the variant with *V. vitis-idaea* was evaluated in the same way.

RESULTS AND DISCUSSION

Umbric Leptosol of the ALH is characterized by acid reaction; high content of C_{micr}, N_{micr}, and C_{org}; the domination of N_{org} in extractable N compounds and of $N{-}NH_4^+$ in inorganic N compounds; and a low content of P_{min}. These properties of soil on the studied plots are typical for the ALH [4, 7].

Most of the studied soil properties are significantly affected by *V. vitis-idaea,* changes in the soil water content, and the combination of these factors (Table 1).

Soil acidity. This is the only studied property, which significantly changes, when *V. vitis-idaea* is present in the plant community, independently of the soil water content (Fig. 1). An increase in the soil acidity under *V. vitis-idaea* corresponds to the data of our previous study [4] and to the concept that the aboveground and underground debris of heather dwarf shrubs favor the formation of acid products during their transformation [17]. In addition, fungi with ERM secrete acid organic compounds into the soil [25]. Changes in the soil moisture in the control variant and under *V. vitis-idaea* do not affect soil acidity.

The contents of inorganic forms of nitrogen and phosphorus and the activity of N-mineralization and nitrification. Despite the fact that the concentrations of $N{-}NH_4^+$ and $N{-}NO_3^-$,differ in soils of the ALH by an order of magnitude [5], the regularities of their variation under the impact of *V. vitis-idaea* and soil moisture are similar. At the low water content, they do not differ in the soil of the control variant and under *V. vitis-idaea*, but when the water content increases, they become significantly smaller in the soil under the dwarf shrub. This is due to the fact the soil water content does not affect $N{-}NH_4^+$ and $N{-}NO_3^-$ contents in the presence of *V. vitis-idaea,* whereas their concentration in the soil of the control variant increases with the rise in the soil moisture (Fig. 1).

The same regularity is typical for the activities of N-mineralization and nitrification. In general, in the range of very low values (up to negative values for N-mineralization), the activities of these processes increase in the soil of the control variant with the rise in the soil water content and become significantly higher than those in the variant with *V. vitis-idaea* at the high water moisture (Fig. 2). It is known that plants forming ARM grow on soils better provided with inorganic nitrogen compounds [3, 20]. This regularity is interpreted as the dominating specialization of fungi with ARM on $N{-}NH_4^+$ and $N{-}NO_3^-$ absorption [30], or testifies to an insignificant contribution of ARM symbiosis to the nitrogen nutrition of plants [8, 31]. It has also been demonstrated that fungi with ARM may indirectly influence the transformation of organic matter and nitrogen-containing compounds via affecting the complex of free-living microorganisms [23]. However, the transformation of nitrogen compounds (nitrification, in particular) changes at different moisture contents in the soil of ALH under plants with ARM. In the presence of *V. vitis-idaea*, the N transformation activities remain stable. This corresponds to the data that the biological activity of soils (respiration) under plants with ARM responses more pronouncedly to changes in the soil moisture, while temperature becomes more important under plants with ECM (exoenzyme activity of which corresponds greater to plants with ERM) [35].

The P_{min} concentration in the soil is low, which is typical for ALH, and does not significantly depend on the presence of *V. vitis-idaea* in the plant community or on changes in the soil water content. A tendency for a difference between the control and the variant with *V. vitis-idaea* (higher P_{min} content in the soil under *V. vitis-idaea*) is only seen, when the soil moisture decreases (Fig. 1). The enhanced P_{min} mobilization in

Table 1. Results of the two-way ANOVA for the effect of *V. vitis-idaea*, soil moisture, and their combination on the properties of Umbric Leptosol of alpine lichen heath community

Property	Factor	*F*	*P*
pH	*V. vitis-idaea*	28.76	**0.000**
	Moisture	1.62	0.207
	V. vitis-idaea × moisture	0.901	0.412
P_{min}	*V. vitis-idaea*	3.966	0.051
	Moisture	0.869	0.425
	V. vitis-idaea × moisture	0.526	0.594
$N-NH_4^+$	*V. vitis-idaea*	3.639	**0.050**
	Moisture	4.077	**0.022**
	V. vitis-idaea × moisture	1.853	0.167
$N-NO_3^-$	*V. vitis-idaea*	19.52	**0.000**
	Moisture	8.770	**0.000**
	V. vitis-idaea × moisture	5.491	**0.006**
N_{org}	*V. vitis-idaea*	15.47	**0.000**
	Moisture	18.20	**0.000**
	V. vitis-idaea × moisture	5.041	**0.009**
C_{org}	*V. vitis-idaea*	5.247	**0.026**
	Moisture	1.960	0.151
	V. vitis-idaea × moisture	2.870	0.065
C_{org}/N_{org}	*V. vitis-idaea*	2.025	0.160
	Moisture	1.651	0.211
	V. vitis-idaea × moisture	1.201	0.309
C_{micr}	*V. vitis-idaea*	0.081	0.777
	Moisture	0.957	0.391
	V. vitis-idaea × moisture	2.447	0.096
N_{micr}	*V. vitis-idaea*	0.627	0.432
	Moisture	0.785	0.461
	V. vitis-idaea × moisture	3.603	**0.034**
C_{micr}/N_{micr}	*V. vitis-idaea*	6.355	**0.015**
	Moisture	4.425	**0.017**
	V. vitis-idaea × moisture	1.137	0.328
N-mineralization	*V. vitis-idaea*	7.635	**0.008**
	Moisture	1.181	0.314
	V. vitis-idaea × moisture	1.703	0.191
Nitrification	*V. vitis-idaea*	15.56	**0.000**
	Moisture	2.713	0.075
	V. vitis-idaea × moisture	3.559	**0.035**
BR	*V. vitis-idaea*	4.615	**0.036**
	Moisture	1.026	0.365
	V. vitis-idaea × moisture	2.658	0.079
qCO_2	*V. vitis-idaea*	4.217	**0.045**
	Moisture	0.170	0.844
	V. vitis-idaea × moisture	1.295	0.282

Table 1. (Contd.)

Property	Factor	*F*	*P*
Leucine amino-peptidase	*V. vitis-idaea*	4.726	**0.034**
	Moisture	8.169	**0.000**
	V. vitis-idaea × moisture	1.848	0.168
Glucosidase	*V. vitis-idaea*	4.099	**0.048**
	Moisture	5.745	**0.006**
	V. vitis-idaea × moisture	15.74	**0.000**
Chitinase	*V. vitis-idaea*	4.023	**0.049**
	Moisture	4.048	**0.023**
	V. vitis-idaea × moisture	4.266	**0.019**
Phosphatase	*V. vitis-idaea*	17.46	**0.000**
	Moisture	9.480	**0.000**
	V. vitis-idaea × moisture	4.116	**0.022**

the soil under plants with ERM and ECM [4, 6] corresponds to a higher acidity and phosphatase activity of the soil.

Carbon and nitrogen of the extracted organic matter. The concentrations of C_{org} and N_{org} do not change with changes in the soil water content in the presence of *V. vitis-idaea* and decrease with the rise in moistening of the control soil. Thus, at low soil moisture, C_{org} and N_{org} are equal in soils of the control and of the variant with *V. vitis-idaea* (similarly to inorganic nitrogen compounds). With an increase in the water content, the concentrations of C_{org} and N_{org} under *V. vitis-idaea* significantly exceed those in the control soil. On the contrary, in the greenhouse experiment, the increased release of exudates into the soil with a decrease in the soil moisture was typical for plants with ECM, but not for plants with ARM [19].

Concentrations of the extractable organic carbon and nitrogen depends on many factors, including the impact of mycorrhizal fungi. Theoretically, their influence may lead to the rise in C_{org} and N_{org} concentrations in soils under plants with ECM and ERM due to organic matter depolymerization under the impact of hydrolytic enzymes [16, 36] or due to release of more organic matter through mycorrhiza [25]. On the contrary, they may also enhance the C and N binding in stable organic matter due to the production of a large amount of polyphenols and the formation of polyphenol-protein complexes [11, 17, 20]. The experiments indicated that plants with ECM and ERM may increase the mobilization of organic matter [4, 6]; however, in some cases, the effect was absent, or the concentration of C_{org} could even decrease [6, 20].

Microbial biomass and biological activity. The concentrations of C_{micr} and N_{micr} in soil are stable parameters, the response of which to the appearance of ERM-symbiosis in ALH or to changes in the soil moisture is very weak according to the results of the two-way ANOVA. We have already shown by the example of soil of ALH [4] and tundra meadow soil in the Khibiny Mountains [6] that the concentrations of C_{micr} under herbs and heather dwarf shrubs are similar, but N_{micr} and the C/N ratio in the microbial biomass of the two studied soils are characterized by changes of different directions. The C_{micr}/N_{micr} ratio is one of few indicators, the change of which in the soil under *V. vitis-idaea* is more pronounced than in the control soil. At the high water content, this ratio is significantly higher in the soil under *V. vitis-idaea* than in the control soil (Fig. 2). The reason for this difference is not clear. A higher C/N ratio in microbial biomass in the presence of plants with ERM and ECM has been demonstrated by us for the soil of tundra meadow in the Khibiny Mountains. It is probably related to changes in the structure of microbial community [6].

Similar to microbial biomass, basal respiration remains stable during variations in the soil moisture under *V. vitis-idaea* but increases with the rise in the soil moisture in the control variant. This results in a significant excess of BR and qCO_2 in the soil under *V. vitis-idaea* at the low soil water content.

Thus, C_{micr} and N_{micr}, as well as other soil properties, which characterize the biological activity related to the functioning of living cells (N-mineralization, nitrification, and basal respiration) and the result of this activity (concentrations of $N{-}NH_4^+$ and $N{-}NO_3^-$), remain stable under changing soil moisture in the variant with *V. vitis-idaea* and increase with the rise in the soil water content in the control. This testifies to a greater sensitivity of the microbial community in the soil under plants with ARM to water availability and corresponds to previously obtained data on the response of biological activity of soils under ARM-dominated plants to the amount of atmospheric precipitation [35].

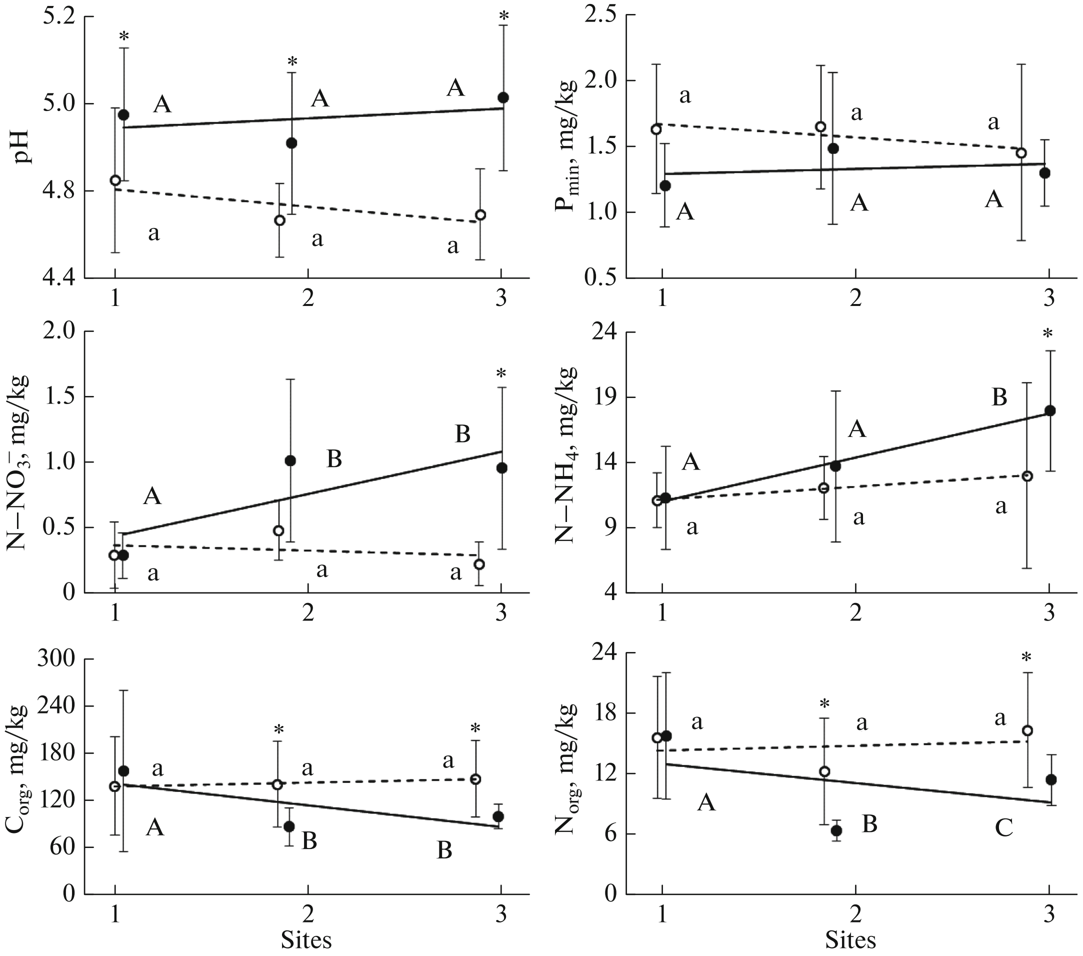

Fig. 1. Properties of Umbric Leptosol under the alpine lichen heath community. Here and in Fig. 2: black circle and solid trend line reflect the absence of *Vaccinium vitis-idaea* in plant community; white circle and dotted trend line reflect the presence of *V. vitis-idaea* (sites 1, 2, and 3 are characterized by the soil water content of 15, 21 and 27%, respectively). Symbol * shows a significant difference between the control and the variant with *V. vitis-idaea* at a fixed soil moisture. The same letter indices reflect the absence of significant variations under different soil moisture in the control (uppercase letters) and variant with *V. vitis-idaea* (lowercase letters).

Enzymatic activity. Regularities of the activity of all the studied enzymes are similar. It is rather stable under changing soil moisture in the variant with *V. vitis-idaea* (only the activity of glucosidase increases with the rise in the soil water content) and decreases in the absence of *V. vitis-idaea* with the rise in the soil moisture (Fig. 2). Thus, the activities of glucosidase, chitinase, and phosphatase are significantly higher in the soil with *V. vitis-idaea* at the high water content. This corresponds to a significant increase in the concentrations of C_{org} and N_{org} under the impact of enzymes (glucosidase and chitinase) on high-molecular-weight components of organic matter with the production of small and more biogeochemically mobile (easily extractable) molecules [4]. Although there is a general tendency to changes in the activities of glucosidase, chitinase, and leucine aminopeptidase in the control soil at different moisture levels on the one hand, and in C_{org} and N_{org} concentrations, on the other hand, the increased activity of these enzymes at low moisture of control soil is not accompanied by higher concentrations of C_{org} and N_{org} compared with soil under *V. vitis-idaea*. The dynamics of phosphatase activity do not correspond to the dynamics of P_{min} in soil either. It was found that the P_{min} concentration increases in the soils under dwarf shrubs forming ERM [4, 6], but this was not accompanied by the rise in the C/P ratio in the extracted organic matter with an increase in the phosphatase activity [6]. This inconformity is probably related to the fact that a direct comparison of the dynamics of the studied mineral and organic phosphorus fractions is inappropriate because of their different biogeochemical lability.

Thus, the data obtained only partially confirm the concept of higher activity of exoenzymes of ERM, which is seen at increased moisture of the ALH soil. This is obviously a result of a lower activity of the cor-

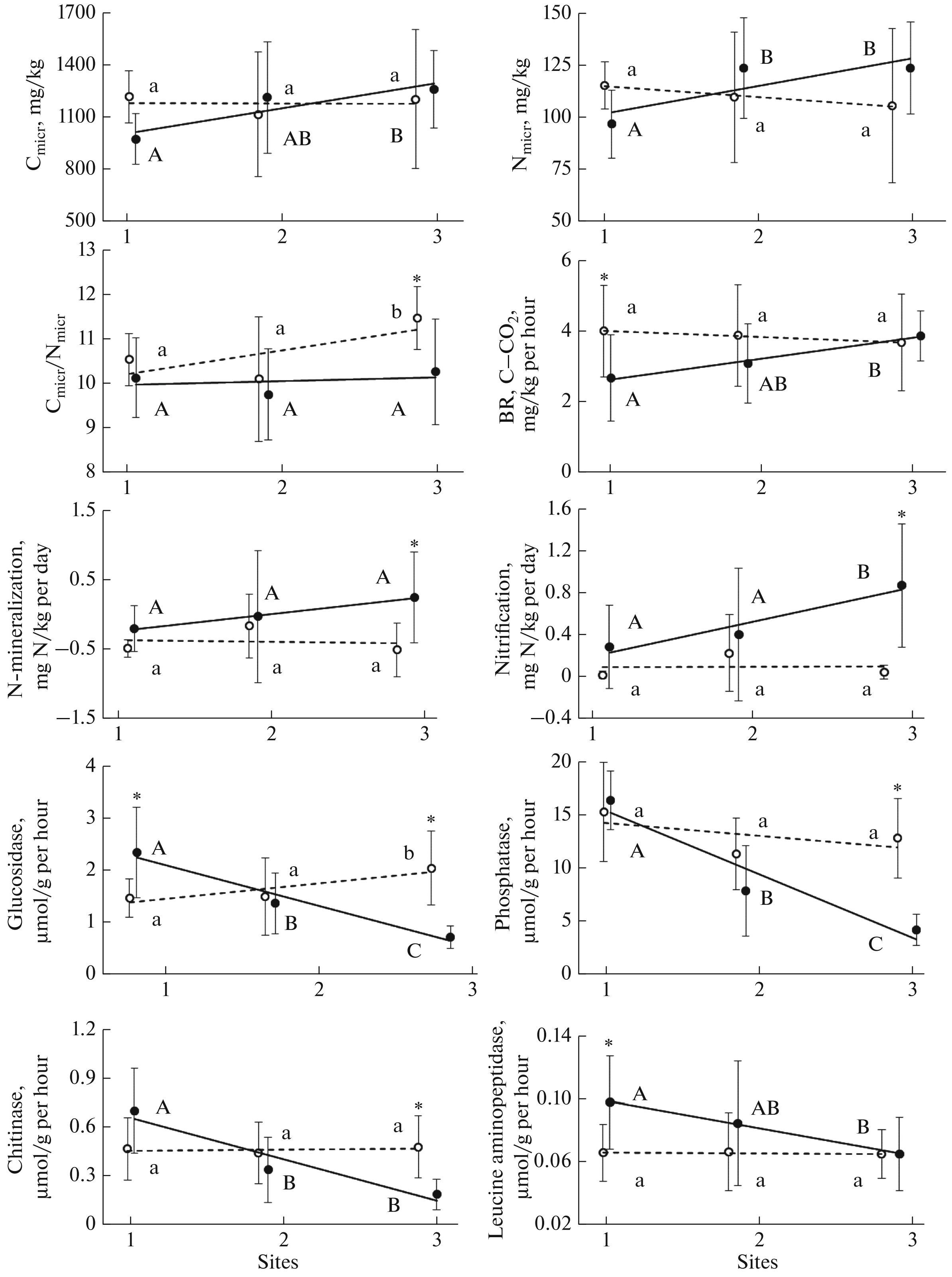

Fig. 2. Biological properties and biological activity of Umbric Leptosol of the alpine lichen heath community.

responding enzymes in the soil in the absence of *V. vitis-idaea*. When soil moisture decreases, the activity of enzymes under herbaceous vegetation, on the contrary, rises. The response of the enzyme system of mycorrhiza to changes in the soil moisture may be a result of adaptation to unfavorable dry conditions to ensure the microbial activity and plant nutrition. However, contrary to our result, the data obtained in the greenhouse experiment showed that the decrease in the soil water content is accompanied by a weaker response of exudate production by plants forming ARM [19]. It should be noted that the biological (microbial biomass, transformation of nitrogen compounds, and respiration) and biochemical (activity of exoenzymes) properties of soil change in different directions under changing soil moisture.

CONCLUSIONS

The acidity of ALH soil increases in the presence of *V. vitis-idaea*. The dynamics of other studied properties are more complicated and are determined both by the presence of *V. vitis-idaea* and the soil moistening. More stable content of labile C and N compounds and biological and enzymatic activity of soil with *V. vitis-idaea* under changing soil moisture attest to a lower sensitivity of fungi of ERM and saprotrophic microbial community associated with ERM to the availability of soil water. Lower $N{-}NH_4^+$, and $N{-}NO_3^-$ concentrations and N-mineralization and nitrification activities in soil under *V. vitis-idaea* at high moistening attest to a weaker dependence of the plant on the mineral compounds in nitrogen nutrition. The content of inorganic nitrogen and the activity of N-mineralization and nitrification, as well as microbial biomass and basal respiration of soil, decrease under herbaceous vegetation with a decrease in the soil water content. At the same time, the concentrations of labile organic carbon and nitrogen compounds and the activity of exoenzymes increase, which testifies to a shift in the transformation of organic matter from mineralization to depolymerization. The latter is more typical for ecosystems with the domination of ECM and ERM. This should be taken into account when forecasting changes in the functioning of alpine ecosystems related to increasing participation of dwarf shrubs and shrubs in plant communities and under a decrease in precipitation of the warm season in combination with the predicted increase in the number and intensity of droughts in mountain regions.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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