ISSN 1067-4136, Russian Journal of Ecology, 2015, Vol. 46, No. 5, pp. 417–424. © Pleiades Publishing, Ltd., 2015.
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The Ratio of Mycorrhizal and Nonmycorrhizal Plant Species in Primary Technogenic Successions

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Received August 15, 2014

Abstract—An analysis has been made of 58 original estimates of the ratio between mycorrhizal and nonmycorrhizal herbaceous plant species during primary endoecogenetic successions in technogenic habitats of the forest–steppe and taiga zones of the Urals. It has been found that the proportion of species forming arbuscular mycorrhizas similarly increases in the course of substrate overgrowing in both zones. At the stage of simple plant group, the proportion of mycorrhizal species is about 50–65%; at the stage of phytocenosis, 75–85% in technogenic habitats and 80–90% in natural habitats. The influence of different factors on this proportion decreases in the following series: successional stage > habitat type (by origin) > period of overgrowing > natural zone.

Keywords: technogenic successions, primary successions, overgrowing of spoil dumps, mycorrhiza, mycorrhizal plants, herbaceous plants

DOI: 10.1134/S1067413615050203

Successions in technogenic biotopes are almost perfect models of community and ecosystem formation created as a result of "spontaneous experiments." Their development depends both on macroscale factors (climatic and zonal conditions) and on local geomorphological and physicochemical conditions. Since the properties of technogenic substrates are usually unfavorable, succession management in such biotopes is only possible by regulating plant–substrate connections. This is a basic premise behind all land reclamation measures. Although the idea of succession management by correcting soil–plant interaction is somewhat trivial, it has an important but rarely considered aspect: it indicates the necessity to take into account modes of soil nutrition. Among them, mycorrhiza is the most important and widespread: The majority of plant species (over 80%) absorb soil nutrients in symbiosis with mycorrhizal fungi (Selivanov, 1981; Wang and Qiu, 2006).

According to current views, mycorrhization has a close functional connection with formation of the structure, diversity, and stability of plant communities (Miller, 1979; Gemma and Koske, 1990; Ahulu et al., 2005; Pezzani et al., 2006; Püschel et al., 2007; Lambers et al., 2008; Veselkin, 2012a, 2012b). Specialists have been always aware of the importance of taking into account the phenomenon of mycotrophism when solving applied problems. For example, a surge of interest in the study of mycorrhizas in the Soviet Union during the 1950s and 1960s was explained by current requirements of agriculture and forestry related, in particular, to the problem of afforestation in the steppe zone. We have long been studying mycorrhizas in technogenic habitats of the Urals (Chibrik et al., 1980; Lukina, 1997, 2009; Veselkin, 2004, 2006; Glazyrina et al., 2007; Lukina and Ryazanova, 2012), considering this research important for solving a complex problem of developing a theoretical basis for disturbed land reclamation. In particular, we aim to confirm the premise that mycorrhization is an important indicator of the maturity of plant communities (Chibrik et al., 1980) and a factor providing for successful adaptation of plants in technogenic habitats (Veselkin, 2006; Lukina and Udartseva, 2009).

The purpose of this study was to analyze original empirical data on technogenic successions in order to reveal trends in the occurrence frequency of plants differing in mycorrhizal status. The successional dynamics of the ratio between mycorrhizal and nonmycorrhizal plants was analyzed with regard to two factors: the way of formation (origin) and zonal position of technogenic habitats.

MATERIAL AND METHODS

In geographic terms, original estimates of the proportions of mycorrhizal plants in technogenic communities were distributed as follows: the steppe zone, two estimates; the forest–steppe zone, 24 estimates; and the taiga zone, 32 estimates (Table 1). Hence, the data on the first two zones were pooled and regarded as pertaining to the forest–steppe zone, or habitats with arid conditions, in contrast to humid conditions in the taiga zone (without differentiating it into subzones). With respect to the way of formation, habitats were divided into four groups (1) coal overburden dumps, (2) gob piles of coal waste at coal mines, (3) cinder dumps of heat and power plants (HPPs), and (4) dumps of different waste materials, including dredge spoils, calcareous rock waste, and sludges and solid spoils of metal industries. The main types of habitats were surveyed in both zones. As a rule, several habitats within the same industrial region were surveyed on one occasion each. In two cases (gob piles of Bulanash coal mines and cinder dump of Verkhnii Tagil heat and power plant), the level of mycorrhization in the same habitats was estimated twice with an interval of 20–26 years. Plant samples (5–10 ind. each) were taken from typical sites (with ordinary parameters) in order to representatively characterize the state of vegetation in a given habitat. Thus, the extreme sites of each habitat and sites where the vegetation developed at an increased rate due to local conditions were excluded from consideration.

The number of species studied in each habitat varied from 9 to 52 (in most cases, 20–30 species). All these were herbaceous species with arbuscular mycorrhiza (woody species and plants with mycorrhizas of orchid and ericoid types were not considered). Analysis for arbuscular mycorrhizal fungi in the roots was performed after ethanol fixation or in herbarium material by the standard method involving maceration in KOH and staining with aniline blue (Selivanov, 1981). Since the presence or absence of the fungi was estimated visually, the status of plants was defined as mycorrhizal or nonmycorrhizal; the terms “mycotrophic” or “nonmycotrophic” were not used, since they characterize mainly the degree of plant adaptation to mycorrhization (Selivanov, 1981).

The course of succession was characterized in two ways: taking into account the period of overgrowing, or the age of habitat (in years), and by identifying qualitative successional stages (based on the coverage of aboveground plant parts) according to Voronov’s scheme modified by Kurochkina and Vukhrer (1987): (I) simple plant group, (II) complex plant group, (III) phytocenosis in a technogenic habitat. Characteristics of successional stages in some habitats were absent. On the whole, original estimates were available for 58 habitats, 26 in the forest–steppe zone and 32 in the taiga zone; the period of overgrowing was known for 51 habitats (21 forest-steppe and 30 taiga habitats); and successional stages were determined for 48 habitats (26 and 22 habitats, respectively). For comparison, we used 26 published estimates of the ratio between mycorrhizal and nonmycorrhizal species in zonal communities (stage IV), 9 in the steppe and forest–steppe zones and 17 in the taiga zone.

Statistical processing was performed with the STATISTICA 6.0 program package. The results of preliminary tests for normality of distribution and homogeneity of variance (Levene test) were satisfactory, which allowed us to use parametric methods for assessing the significance of differences between means (ANOVA) and correlation analysis. In all cases, the proportion of mycorrhizal species in a habitat was taken as a statistical unit. Different models were considered that included characteristics of habitats and their combinations as predictors and the proportion of mycorrhizal species as a resultant variable. To select optimal models, we used the methodology of multimodel inference (Burnham and Anderson, 2002) and Akaike’s information criterion (*CAIC*). To compare the quality of the models, the absolute values of *CAIC* were converted into normalized relative likelihood values, or Akaike weights (W), which indicate the probability that a given model is the best among the whole set of candidate models.

RESULTS

Successional dynamics of the proportion of mycorrhizal species in different natural zones. In both zones, the proportions of species with arbuscular mycorrhizas were found to consistently increase upon transition from the stage of simple plant groups to complex groups and then to phytocenoses (Fig. 1). Two-way ANOVA of the whole set of data on technogenic and natural plant communities confirmed that both successional and zonal differences in this parameter were statistically significant ($F_{\text{stage }(3;73)} = 27.38$, $P < 0.0001$; $F_{\text{zone }(1;73)} = 9.20$, $P = 0.0035$). The proportion of mycorrhizal species in technogenic habitats increased from 50–65% in a simple plant group to 75–85% in a phytocenosis, compared to 80–90% in natural communities. Zonal differences were manifested in the fact that the proportion of mycorrhizal plants in technogenic habitats proved to be 10–20% lower in the forest–steppe zone (under arid conditions) than in the taiga zone, especially at early stages of overgrowing. The effect of interaction between factors “natural zone” and “successional stage” lacked statistical significance ($F_{\text{stage × zone }(3;73)} = 1.15$, $P = 0.3343$).

Similar results were obtained when the significance of zonal and successional sources of variation in the ratio of mycorrhizal and mycorrhizal plants was analyzed in a truncated data set from which natural habitats were excluded: $F_{\text{stage }(2;47)} = 18.32$, $P < 0.0001$; $F_{\text{zone }(1;47)} = 8.07$, $P = 0.0069$; $F_{\text{stage × zone }(2;47)} = 0.17$, $P = 0.8480$. Thus, qualitative changes in plant communities during the overgrowing of technogenic substrates in both zones are accompanied by a 1.3- to 1.5-fold increase in the proportion of mycorrhizal plants: from 50–65% at the stage of simple plant groups to 80–90% at the stage of phytocenosis.

Table 1. Characteristics of habitats and estimates of occurrence of mycorrhizal species

No.	Locality, industrial facility, field	Habitat			Number of species studied	Proportion of mycorrhizal species, %	Reference[3]
		type[1]	period of over-growing, years	successional stage[2]			
	Steppe zone						
1	Kumertau, Kumertauskii open-pit mine	(1)	21	III	26	73	[1]
2	Same	(1)	13	II	25	48	[1]
	Forest-steppe zone						
3	Korkino, Korkinskii open-pit mine	(1)	21	III	23	74	[1]
4	Same	(1)	13	III	18	67	[1]
5	Krasnogorskii, Krasnosel'skii open-pit mine	(1)	21	III	26	73	[1]
6	Same	(1)	13	III	22	68	[1]
7	Emanzhelinsk, Baturinskii open-pit mine	(1)	24	III	23	100	[1]
8	Same	(1)	15	I	12	58	[1]
9	Korkino, Korkinskaya mine	(2)	28	II	29	66	[1]
10	Same	(2)	28	I	21	62	[1]
11	"	(2)	28	II	29	66	[1]
12	Korkino, Kalachaevskaya mine	(2)	–	II	30	67	[1]
13	Same	(2)	–	I	27	56	[1]
14	"	(2)	–	II	22	55	[1]
15	Kopeisk, Kapital'naya mine	(2)	28	II	34	62	[1]
16	Same	(2)	28	I	26	50	[1]
17	"	(2)	28	II	23	52	[1]
18	Kopeisk, Podozernaya mine	(2)	6	I	24	50	[1]
19	Same	(2)	6	I	13	38	[1]
20	"	(2)	6	I	17	41	[1]
21	Krasnoselka, Kulyarskaya mine	(2)	–	I	27	52	[1]
22	Same	(2)	–	I	19	47	[1]
23	Emanzhelinsk, Yuzhnaya mine	(2)	26	I	23	65	[1]
24	Same	(2)	26	I	19	42	[1]
25	Yuzhnoural'sk, Yuzhnoural'skaya HPP	(3)	25	II	21	52	[2]
26	Same	(3)	25	II	23	65	[2]
	Taiga zone						
27	Karpinsk, Veselovskii open-pit mine	(1)	20	III	26	73	[1]
28	Same	(1)	14	III	19	68	[1]
29	Karpinsk, Yuzhnyi open-pit mine	(1)	27	III	24	75	[1]
30	Same	(1)	20	III	35	66	[1]
31	Bulanash, Bulanash 2–5 mine	(2)	16	II	31	71	[1]
32	Same	(2)	16	I	20	60	[1]
33	"	(2)	16	II	24	58	[1]
34	"	(2)	42	III	21	90	[3]
35	Bulanash, Bulanash 2–5 mine	(2)	42	III	36	81	[3]
36	Bulanash, Bulanash 3 mine	(2)	16	II	29	72	[1]
37	Same	(2)	16	I	19	68	[1]
38	"	(2)	16	II	26	65	[1]
39	"	(2)	42	III	13	85	[3]
40	"	(2)	42	III	11	73	[3]

Table 1. (Contd.)

No.	Locality, industrial facility, field	Habitat			Number of species studied	Proportion of mycorrhizal species, %	Reference[3]
		type[1]	period of overgrowing, years	successional stage[2]			
41	Nevyansk, dredge spoil banks	(4)	13	–	52	92	[4]
42	Bilimbai, limestone deposit	(4)	19	–	29	100	[4]
43	Asbest, asbestos deposit	(4)	33	–	16	69	[4]
44	Bilimbai. dolomite deposit	(4)	13	–	36	78	[4]
45	Same	(4)	33	–	31	97	[4]
46	Nizhny Tagil, iron ore field	(4)	18	–	16	75	[4]
47	Same	(4)	33	–	9	89	[4]
48	Krasnoturinsk, Bogoslovski Aluminum Plant	(4)	–	–	28	82	[4], [5]
49	Krasnoturinsk, Bogoslovskaya HPP	(3)	35	–	24	96	[4], [5]
50	Kachkanar, Kachkanarsky Ore Mining and Processing Plant	(4)	–	–	13	85	[4], [5]
51	Verkhny Tagil, Verkhnetagilskaya HPP	(3)	20	III	25	92	[2]
52	Same	(3)	20	III	37	89	[2]
53	"	(3)	20	III	30	87	[2]
54	"	(3)	20	III	31	90	[2]
55	"	(3)	40	III	42	93	[6]
56	"	(3)	40	III	19	100	[6]
57	"	(3)	40	III	25	100	[6]
58	"	(3)	40	III	27	100	[6]

[1] Types of technogenic habitats: (1) coal overburden dumps, (2) coal waste piles at coal mines, (3) cinder dumps, (4) dumps of different waste materials.

[2] Successional stages: (I) simple plant group, (II) complex plant group, (III) phytocenosis in technogenic habitat.

[3] References: [1] Chibrik et al., 1980; [2] Lukina, 1997; [3] Glazyrina et al., 2007; [4] Lukina, 2009; [5] Lukina and Udartseva, 2009; [6] Lukina and Ryazanova, 2012.

(–) No information available.

The dependence between the age of habitats (the period of overgrowing) and the proportion of mycorrhizal species is statistically significant only in the taiga zone: $r = 0.64$; $n = 22$, $P = 0.0014$ (Fig. 2). At any age, variation in this proportion is considerable.

Successional dynamics of the proportion of mycorrhizal species in habitats of different types. The trend toward the increase in the proportion of mycorrhizal species in plant communities is common to different types of habitats as well as to different natural zones (Fig. 3). Thus, such an increase (at different significance levels) was observed during separate analysis of data on coal overburden dumps (one-way ANOVA: $F_{(1;10)} = 7.65$, $P = 0.0199$), coal mining waste piles ($F_{(2;23)} = 19.11$, $P < 0.0001$), and cinder dumps ($F_{(1;8)} = 55.18$, $P < 0.0001$). It is also noteworthy that, as shown in Fig. 3, the type of substrate proved to have no significant effect on the ratio of mycorrhizal and nonmycorrhizal species at the stages of simple and complex plant groups, but the proportion of mycorrhizal species at the stage of phytocenosis was higher on cinder dumps than on overburden dumps and mining waste piles, with the difference being highly significant ($F_{(2;19)} = 13.92$, $P = 0.0002$).

As in case of data analysis by zones, the ratio between mycorrhizal and nonmycorrhizal plants in different types of habitats was not always strictly correlated with their age. The corresponding correlation coefficients were as follows: $r = 0.67$ ($n = 12$, $P = 0.0164$) for coal overburden dumps, $r = 0.67$ ($n = 21$, $P = 0.0009$) for coal mining waste piles, $r = 0.48$ ($n = 11$, $P = 0.1395$) for cinder dumps, and $r = 0.01$ ($n = 7$, $P = 0.9829$) for the mixed group combining dumps of other waste materials.

Relative significance of factors influencing the ratio of mycorrhizal and nonmycorrhizal plants. The proportion of mycorrhizal species in primary technogenic successions may depend on many parameters of communities and habitats. In our case, the most relevant parameters are the successional stage of community formation (factor "stage"), the period of overgrowing ("age"), and the type of habitat in terms of its genesis ("habitat type"). The data characterizing the relative significance (importance) of these factors are presented in Table 2. It can be seen that the model with the optimal quality-to-complexity ratio includes only two predictors, stage and habitat type. Its quality is markedly higher than that of the nearest model with three pre-

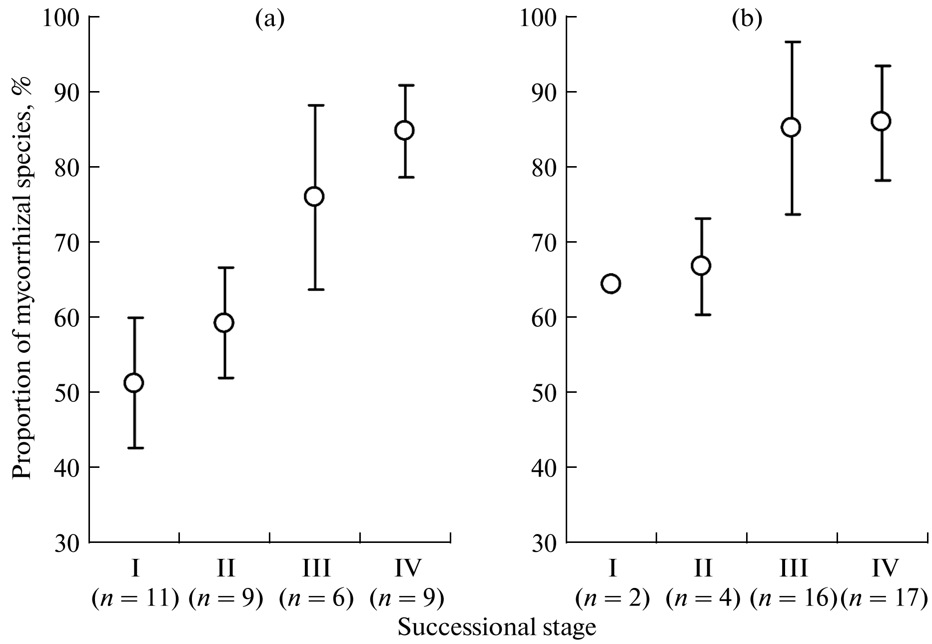

Fig. 1. Increase in the proportion of mycorrhizal species during primary successions in technogenic habitats of (a) forest–steppe and (b) taiga zones. Succesional stages: (I, II) simple and complex plant groups, (III, IV) phytocenoses in technogenic habitats and natural phytocenoses, respectively; (*n*) number of observations; vertical lines show standard deviation (here and in Fig. 3).

dictors (stage + habitat type + age), with the corresponding ratio of Akaike weights being 0.56/0.24 = 2.33. According to the values of relative total weight of variables, which characterizes their significance, the parameters of habitats form the following descending series: (1) the successional stage of community formation ($\Sigma W = 0.98$) > (2) the type of habitat in terms of its genesis ($\Sigma W = 0.89$) > (3) the period of overgrowing ($\Sigma W = 0.39$) > (4) natural zone ($\Sigma W = 0.25$).

DISCUSSION

The results presented above show that the proportion of mycorrhizal plants in communities of technogenic habitats depends primarily on the successional stage of community development. Since the stages of succession are distinguished on the basis of total plant coverage (Kurochkina and Vukhrer, 1987), it can be assumed that the proportion of mycorrhizal species increases with an increase in the abundance of plants and, consequently, in the complexity and closedness of communities. An important fact is that the ratio between mycorrhizal and nonmycorrhizal plants is much more strongly dependent on qualitatively distinguished stages of community development than on the period of overgrowing (age) of a habitat. This is evidence that changes in the ratio between species of different mycorrhizal status reflect qualitative rearrangements in communities and correlate with the level of their closedness and shaping of their internal environment.

The trend toward improvement of positions of mycorrhizal plants appears to be common to primary successions of different types: postvolcanic (Gemma and Koske, 1990; Ahulu et al., 2005), postglacial (Jumpponen et al., 2002), coastal (Püschel et al., 2007), and others (Miller, 1979; Pezzani et al., 2006). The main conclusion that follows from these studies is that the strength of plant association with mycorrhizal fungi and the importance of mycotrophic nutrition increase in the course of endoecogenetic successions. An indirect analysis based on comparison of independent data on the course of successions and on the mycorrhizal status of species involved in them provides evidence that the increase in the proportion of mycorrhizal species is also characteristic of secondary successions within the range of herbaceous vegetation (Veselkin and Betekhtina, 2011; Veselkin, 2012a, 2012b). Our data confirm that the vectorized increase in the occurrence of mycorrhizal plants during primary technogenic successions is a universal phenomenon in the two natural zones of intracontinental regions of Eurasia. We have analyzed a large number of direct estimates of mycorrhization, which allows for reliable conclusions. It is also important that our data make it possible to draw up a hierarchy of factors influencing the ratio of mycorrhizal and nonmycorrhizal plants.

The proportion of mycorrhizal species markedly differs depending on specific features of a given habitat. This may be due to a variety of factors, but the main role appears to be played by unfavorable physicochemical properties of technogenic substrates. Another important factor is that some of the surveyed biotopes have been recultivated.

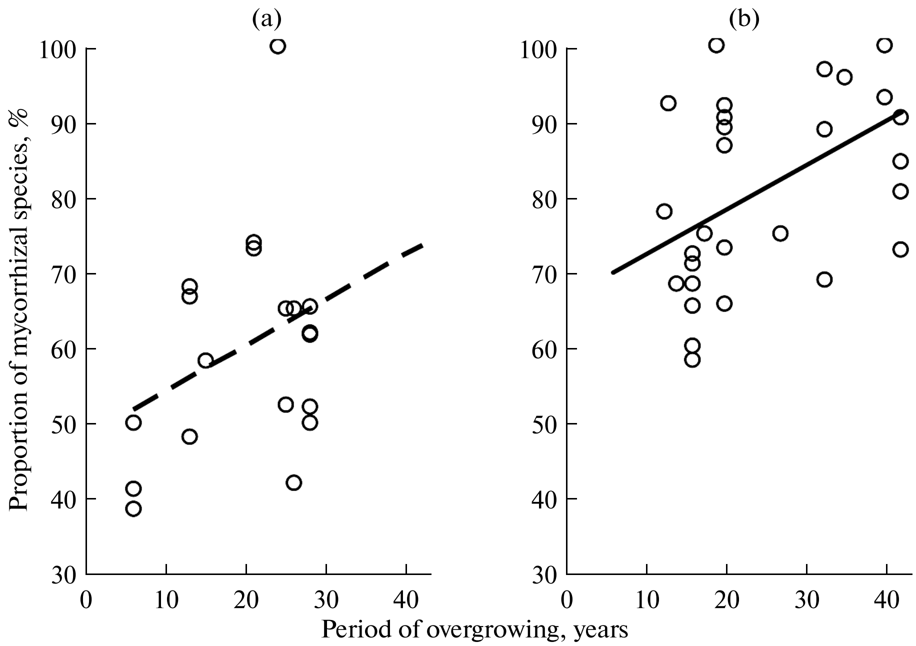

Fig. 2. Increase in the proportion of mycorrhizal species depending on the period of overgrowing of technogenic substrates in (a) forest–steppe and (b) taiga zones.

The improvement of the position of mycorrhizal species in the course of succession is a general trend, but its manifestation is slightly but significantly modified depending on whether the habitat is in the taiga or forest–steppe zone. At the initial stages of overgrowing, the proportion of nonmycorrhizal plants is higher in habitats with arid conditions than in humid habitats. At first glance, this contradicts the known data on higher prevalence of mycorrhizas in the forest–steppe and steppe zones, where they are found in 90 and 89% of species, respectively (Selivanov et al., 1964; Selivanov, 1981), compared to the southern taiga subzone, where the overall proportion of mycorrhizal species is 74% and that in the meadow cenoflora is 70% (Selivanov, 1981). However, this can be adequately explained in the context that the composition and pattern of plant communities in technogenic habitats are formed as xerophytic variants of those in zonal communities (Chibrik and El'kin, 1991), since in northern deserts mycorrhizae are formed in only 56% of species (Eleusenova and Selivanov, 1973). Discussing zonal features, it should be taken into account that the overgrowing of habitats for more than 20 years in the taiga zone leads to the formation of forest communities, and this is accompanied not only by the establishment of a specific system of intracenotic interactions between plants but also by rearrangements of mycorrhizal associations, since boreal tree species usually form ectomycorrhizas.

The results of this research may be discussed mainly in terms of geobotany or ecology, depending on what aspect is or greater interest. In the former case, discussion may concentrate on the group composition of phytocenoses (the ratio of mycorrhizal and nonmycorrhizal species) in relation to their successional development and under different environmental conditions; in the latter case, on the prevalence pattern of mycorrhizal associations, i.e., interactions between autotrophic (plants) and heterotrophic organisms (fungi). These approaches are not mutually exclusive. The geobotanical approach raises the major issue of the competitiveness of plants as related to their ability to form mycorrhizas. For example, predominance of mycorrhizal plants at the final successional stages can be explained, inter alia, by their competitive advantage over nonmycorrhizal plants (Betekhtina and Veselkin, 2011). In terms of functional ecology, it appears most important to analyze the contribution of mycorrhizas in the turnover of nutrient elements, i.e., their role in the development of ecosystem integrity and functional completeness. From both standpoints, the improvement of positions of mycorrhizal plants appears to be an important or even a crucial process connected with the accumulation of biomass and sophistication of communities and ecosystems in the course of primary successions.

Thus, the overall change in the ratio of mycorrhizal and mycorrhizal species during primary technogenic successions is in favor of the former, so that plants absorbing soil nutrients in symbiosis with arbuscular mycorrhizal fungi predominate at late and final successional stages. This conclusion is equally true for plant communities of the forest–steppe and taiga zones of the Urals. The general trend toward the improvement of positions of mycorrhizal plants in the course of succession is only slightly modified depend-

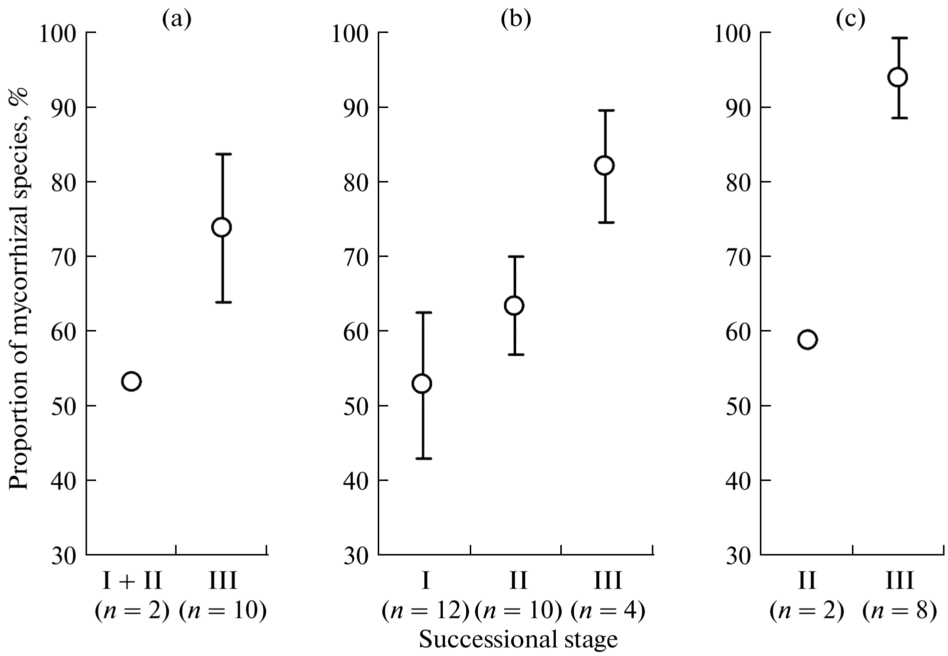

Fig. 3. Increase in the proportion of mycorrhizal species in the course of primary successions on (a) coal overburden dumps, (b) coal waste piles at coal mines, and (c) cinder dumps.

ing on specific edaphic and geomorphological features of different technogenic biotopes. As a hypothesis (that needs rigorous testing), we suggest that the proportion of mycorrhizal species may be regarded as a functionally important characteristic of not only phytocenoses (i.e., plant communities) but also of ecosystems as a whole, because there are grounds to consider that this characteristic is linked with the level of competition and parameters of ecosystem turnover.

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for Basic Research (project no. 14-04-90019) and

Table 2. Qualitative comparison of models describing the proportion of mycorrhizal species depending on characteristics of habitats

No.	Combination of predictors	*CAIC*	Δ*CAIC*	*W*
1	Stage + habitat type	319.11	0.00	0.56
2	Stage + habitat type + age	320.81	1.69	0.24
3	Stage + habitat type + zone	322.35	3.24	0.11
4	Stage + habitat type + zone + age	323.10	3.99	0.08
5	Stage + zone + age	328.49	9.37	0.01
6	Stage + age	328.76	9.64	0.00
7	Habitat type + zone + age	330.14	11.03	0.00
8	Stage + age	330.55	11.44	0.00
9	Stage	333.43	14.32	0.00
10	Habitat type + age	340.46	21.35	0.00
11	Habitat type + zone	342.28	23.17	0.00
12	Zone + age	346.92	27.80	0.00
13	Zone	354.39	35.27	0.00
14	Habitat type	354.65	35.53	0.00
15	Age	355.94	36.83	0.00

the Competitiveness Improvement Program of the Ural Federal University.

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Translated by N. Gorgolyuk