

Prevalence and Intensity of Mycorrhiza Formation in Herbaceous Plants with Different Types of Ecological Strategies in the Middle Urals

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Abstract—The prevalence of arbuscular mycorrhizas and abundance of mycorrhizal fungi in the roots of herbaceous plants with different types of Grime–Ramenskii's ecological strategies (competitors, ruderals, and stress tolerators) have been studied in the Middle Urals. The closest association with arbuscular fungi has been observed in species with a competitive strategy. Compared to them, stress-tolerant species are characterized by lower abundance of mycorrhizal fungal hyphae in the root system, while ruderal plants include a relatively large proportion of nonmycotrophic species showing no interaction with arbuscular fungi.

Keywords: arbuscular mycorrhiza, herbaceous plants, ecological strategies.

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The ability to form mycorrhizal symbiosis is an important biological property of species and, in certain cases, taxonomic or ecological groups of plants (for a recent review, see Brundrett, 2009). The basic types of mycorrhizas are specific for different plant life forms. Thus, ectomycorrhizas are characteristic of most tree species of the boreal and temperate zones, and endomycorrhizas, of most herbaceous species and some tropical trees. Mycorrhizas have been studied in plants differing in the functional type, life form, duration of ontogeny, and successional status. Primary successions often begin with the establishment of nonmycotrophic or weakly mycotrophic species, which are gradually replaced by mycotrophic plants (Gemma and Koske, 1990; Lambers et al., 2008). Succession may involve changes in the prevailing types of mycorrhiza morphotypes (Ahulu et al., 2005) and plant–fungus relationships (Pezzani et al., 2006), with the outcome of competition between mycotrophic and nonmycotrophic plants depending not only on the presence or absence of mycorrhizal fungi in the soil (Heijden et al., 1998) but also on the level of their host-plant specificity (Heijden et al., 2003; Puschel et al., 2007). Grime et al. (1988), presenting data on the ability to form mycorrhiza in plants with different strategies, consider this property along with the fundamental characteristics of species, such as the life form and duration of ontogeny. As shown in subsequent studies (Cornelissen et al., 2001; Heijden and Cornelissen, 2002), the relative growth rate (a parameter used to identify the type of Grime–Ramenskii's ecological

strategy) consistently increases upon transition from plants with ericoid mycorrhizas to ectomycorrhizal trees and endomycorrhizal plants.

In this paper, we analyze specific features of association with arbuscular fungi in Middle Ural seed plants with different ecological strategies. The reason for undertaking such a study is as follows. It is accepted that the Grime–Ramenskii's system of strategies describes the modes of plant adaptation to environmental conditions in most general terms (Mirkin et al., 1999), can be appended with new data, and has a definite operational and prognostic value (Mirkin et al., 1999; P'yankov and Ivanov, 2000; P'yankov et al., 2001). Meanwhile, we know little about specific features of interactions between plants with different life strategies and arbuscular fungi. In available publications, the authors analyze plant morphophysiological properties correlating with a certain type of Grime–Ramenskii's strategy in dependence on the type of mycorrhizal association (Cornelissen et al., 2001; Heijden and Cornelissen, 2002) and mycorrhiza formation in plants of different life forms and life cycles (Selivanov, 1981; Wilson and Hartnett, 1998; Hartnett and Wilson, 2002; Roumet et al., 2006).

MATERIAL AND METHODS

Our data on the prevalence and intensity of mycorrhiza formation (Betekhtina and Kondratkov, 2003; Betekhtina, 2004; Betekhtina et al., 2004) were obtained mainly in the vicinity of the Biological Sta-

tion of the Ural State University (56°37'N, 61°04'E), near Yekaterinburg. With this purpose, we studied generative plants of 100 species (5–15 ind. per sample) collected in their typical habitats in the middle of the growing season. Characteristics of mycorrhiza formation in 105 plant species from technogenic habitats (spoil banks of coal mines and power plants) were taken from relevant publications (Chibrik et al., 1980; Chibrik and Salamatova, 1985; Glebova, 1992; Glazyrina et al., 2007). Among a total of 170 species studied in natural and technogenic habitats, we selected 73 seed plants for which, according to published data (Grime et al., 1988; Frank and Klotz, 1990), it was possible to determine the type of Grime–Ramenskii's primary ecological strategy: competitive (C), stress-tolerant (S) or ruderal (R) according to Grime (1979), or violent, patient or explerent, respectively, according to Ramenskii (1971) (Table 1). Species forming mycorrhizas mainly of ericoid (Ericaceae, Pyrolaceae, Vacciniaceae) or orchid types (Orchidaceae) were excluded from analysis.

In all cases, analysis for presence/absence and abundance of arbuscular fungi in plant roots was performed with dry herbarium samples by the standard procedure (Selivanov, 1981) involving maceration of the roots in a KOH solution and staining of the mycelium with aniline blue. To characterize the strength of plant–fungus association, we used two parameters: the prevalence of mycorrhiza formation in a certain plant group (P) determined from the proportion of mycotrophic species (i.e., species in which at least part of plants are mycorrhizal) and mycorrhization intensity (C), or the proportion of cells invaded by arbuscular fungi in the parenchyma of the primary root bark. The latter parameter was calculated only for mycotrophic species.

To compare the proportions of mycotrophic species, we used the χ^2 test for 2×2 tables, estimating the significance of differences by the Fisher bilateral test. Mycorrhization intensities were compared by the Kruskal–Wallis H test.

RESULTS AND DISCUSSION

The list of Middle Ural plants characterized with respect to Grime–Ramenskii's primary strategies and mycorrhiza formation was dominated by competitors (38 species), while stress tolerators were represented by only 11 species (Table 2). Such a disproportionate representation of different strategies is evidence for nonrandom selection of species for analysis. On the other hand, however, this fact is partly accounted for by objective factors. In particular, stress tolerators, unlike ruderals, are sparse in technogenic habitats.

The ratio of nonmycotrophic and mycotrophic species in the groups of C-, S-, and R-strategists varied slightly and did not differ statistically between natural and technogenic habitats (Table 2). The proportion of mycotrophic species reached the highest values (78–

100%) in the groups of competitors and stress tolerators, being lower in the group of ruderals (56–69%). Statistical evidence for differences in the prevalence of mycorrhiza formation was also obtained by comparing the groups of C- and R-strategists from natural habitats and the pooled sets of data on natural and technogenic habitats. Thus, among 38 C-strategists analyzed in the Middle Urals, nonmycotrophic plants were represented by two species (*Geranium silvaticum* and *Ranunculus acris*); among 11 S-strategists, also by two species (*Carex caryophylla* and *Luzula pilosa*); whereas the group of 24 R-strategists included nine such species (*Alisma plantago-aquatica*, *Capsella bursa-pastoris*, *Chenopodium album*, *Fumaria officinalis*, *Melandrium album*, *Polygonum aviculare*, *Spergularia arvensis*, *Stellaria media*, and *Viola tricolor*).

Since the list of studied stress-tolerant plants is relatively short, one should be cautious when extrapolating the above trend beyond this particular list. Hence, we consider it important that the proportions of mycotrophic species in groups with C-, S-, and R-strategies in the Middle Urals are similar to those in Britain: 95 vs. 85%, respectively, among competitors ($\chi^2 = 1.82$, $P = 0.1770$); 82 vs. 75% among stress tolerators ($\chi^2 = 0.25$, $P = 0.9995$); and 63 vs. 65% among ruderals ($\chi^2 = 0.07$, $P = 0.7960$). It can be seen that, in any group, the difference between the data for the Urals and Britain lacks statistical significance. This is an additional argument for the conclusion that the prevalence of arbuscular mycorrhizae among herbaceous explerents (R-strategists) is lower than in the groups of violent (C-strategists) and patients (S-strategists). As noted previously (Francis and Read, 1995; Cornelissen et al., 2001), the ruderal strategy may be a form of the "arbuscular fungus avoidance" strategy.

The abundance of mycelium in the roots of mycotrophic plants, irrespective of their strategy type, was 2.7–3.5 times lower in technogenic than in natural habitats (figure). Analysis of differences in mycorrhiza formation conditioned by technogenic factors is beyond the scope of this paper, but some related circumstances are important for interpreting the data obtained. The decrease in the abundance of arbuscular fungi in the roots of herbaceous plants in technogenic habitats is an expected phenomenon (Vosatka and Dodd, 1998; Trubina, 2002; Betekhtina and Kondratkov, 2003; Glazyrina et al., 2007). It should be taken into account, however, that estimates of mycorrhization in natural and technogenic biotopes have been obtained by different researchers, which could have an effect on the recorded values of fungal abundance. Hence, it is impossible to discriminate between probable differences accounted for by habitat conditions (natural or technogenic), methodology (approaches used by different researchers), and the composition of vegetation (plant species lists for natural and technogenic habitats overlap only slightly). Therefore, the sets of data on different habitats should be analyzed independently of each other, or it is necessary to use

Table 1. Mycorrhization intensity (%) in 73 species of Middle Ural herbaceous plants with different Grime–Ramenskii’s primary ecological strategies: (C) competitive, (S) stress-tolerant, and (R) ruderal species

No.	Species	Ecological strategy	Habitats	
			natural	technogenic
Mycotrophic species				
1	<i>Achillea millefolium</i> L.	C**	38	12
2	<i>Aegopodium podagraria</i> L.	C**	56	
3	<i>Amoria hybrida</i> (L.) C. Presl	C**		9
4	<i>Arctium lappa</i> L.	C**		1
5	<i>Artemisia dracunculus</i> L.	C**		86
6	<i>Artemisia vulgaris</i> L.	C**	52	10
7	<i>Bromopsis inermis</i> (Leys.) Holub	C**		43
8	<i>Calamagrostis arundinacea</i> (L.) Roth	C**	48	
9	<i>Calamagrostis epigeios</i> (L.) Roth	C**		26
10	<i>Carex ovalis</i> Good.	S*		14
11	<i>Carum carvi</i> L.	C**	58	
12	<i>Chamaenerion angustifolium</i> (L.) Scop.	C*		6
13	<i>Cirsium setosum</i> (Willd.) Bess.	C*	54	21
14	<i>Dactylis glomerata</i> L.	C**	22	
15	<i>Deschampsia cespitosa</i> (L.) Beauv.	C**	24	10
16	<i>Elytrigia repens</i> (L.) Nevski	C**	38	26
17	<i>Erigeron acris</i> L.	R**	28	22
18	<i>Erodium cicutarium</i> (L.) L’Her.	R**	22	
19	<i>Euphorbia helioscopia</i> L.	R*	38	
20	<i>Festuca pratensis</i> Huds.	C**	34	9
21	<i>Festuca rubra</i> L.	C**	20	6
22	<i>Filipendula ulmaria</i> (L.) Maxim.	C**	56	
23	<i>Galium album</i> Mill.	C**	30	4
24	<i>Galium odoratum</i> (L.) Scop.	S**	6	
25	<i>Geranium pratense</i> L.	C**	50	
26	<i>Geum urbanum</i> L.	S*		6
27	<i>Hylotelephium triphyllum</i> (Haw.) Holub	S*	31	
28	<i>Lathyrus pratensis</i> L.	C**	86	14
29	<i>Leontodon autumnalis</i> L.	R*		20
30	<i>Lepidium ruderales</i> L.	R**		2
31	<i>Lepidothea suaveolens</i> (Pursh) Nutt.	R*	20	
32	<i>Leucanthemum vulgare</i> Lam.	C**	66	11
33	<i>Lycopsis arvensis</i> L.	R*	18	
34	<i>Maianthemum bifolium</i> (L.) F. W. Schmidt	S**	56	
35	<i>Medicago lupulina</i> L.	R*		5

Table 1. (Contd.)

No.	Species	Ecological strategy	Habitats	
			natural	technogenic
36	<i>Oxalis acetosella</i> L.	S*	22	
37	<i>Phleum pratense</i> L.	C**		8
38	<i>Phlomis tuberosa</i> (L.) Moench	C**		11
39	<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	C**		15
40	<i>Plantago major</i> L.	R*	66	15
41	<i>Poa annua</i> L.	R*	18	
42	<i>Poa pratensis</i> L.	C**		10
43	<i>Primula veris</i> L.	S*	2	
44	<i>Ranunculus polyanthemos</i> L.	C**	62	
45	<i>Setaria pumila</i> (Poir.) Roem. et Schult.	R**		3
46	<i>Solanum dulcamara</i> L.	C**		13
47	<i>Sonchus oleraceus</i> L.	R*		3
48	<i>Stachys palustris</i> L.	C**	40	
49	<i>Tanacetum vulgare</i> L.	C**		14
50	<i>Taraxacum officinale</i> Wigg.	R*	40	15
51	<i>Trientalis europaea</i> L.	S**	24	
52	<i>Trifolium medium</i> L.	C**	78	6
53	<i>Trifolium pratense</i> L.	C**		8
54	<i>Tripleurospermum inodorum</i> (L.) Sch. Bip.	R*	48	5
55	<i>Urtica dioica</i> L.	C*		11
56	<i>Veronica chamaedrys</i> L.	S*	30	
57	<i>Vicia cracca</i> L.	C**	72	0
58	<i>Vicia sativa</i> L.	R*	52	
59	<i>Vicia sepium</i> L.	C**	38	
60	<i>Vicia sylvatica</i> L.	C**		7
Nonmycotrophic species				
61	<i>Alisma plantago-aquatica</i> L.	R*	0	
62	<i>Capsella bursa-pastoris</i> (L.) Medik.	R*	0	0
63	<i>Carex caryophyllea</i> Latourr.	S*	0	
64	<i>Chenopodium album</i> L.	R*	0	0
65	<i>Fumaria officinalis</i> L.	R*	0	
66	<i>Geranium sylvaticum</i> L.	C**		0
67	<i>Luzula pilosa</i> (L.) Willd.	S*	0	
68	<i>Melandrium album</i> (Mill.) Garcke	R*	0	
69	<i>Polygonum aviculare</i> L.	R*	0	0
70	<i>Ranunculus acris</i> L.	C**		0
71	<i>Spergula arvensis</i> L.	R*	0	
72	<i>Stellaria media</i> (L.) Vill.	R*	0	
73	<i>Viola tricolor</i> L.	R**		0

* Grime et al. (1988). ** Frank, Klotz (1990).

Table 2. Proportions of mycotrophic species in groups of plants with (C) competitive, (S) stress-tolerant, and (R) ruderal types of primary ecological strategies

Habitats	Total number of species			Proportion of mycotrophic species, %			Significance of differences in the proportion of mycotrophic species*		
	C	S	R	C	S	R	C – S	C – R	S – R
The Urals, natural habitats	21	9	18	100	78	56	0.0828	0.0007	0.4059
The Urals, technogenic habitats	29	2	13	93	100	69	0.9995	0.0628	0.9995
The Urals, both natural and technogenic habitats	38	11	24	95	82	63	0.2136	0.0020	0.4354
The British Islands**	34	84	78	85	75	65	0.3267	0.0406	0.2282

Notes: * The observed significance level according to the Fisher bilateral test for 2 × 2 tables.

** Our calculations based on data by Grime et al. (1988).

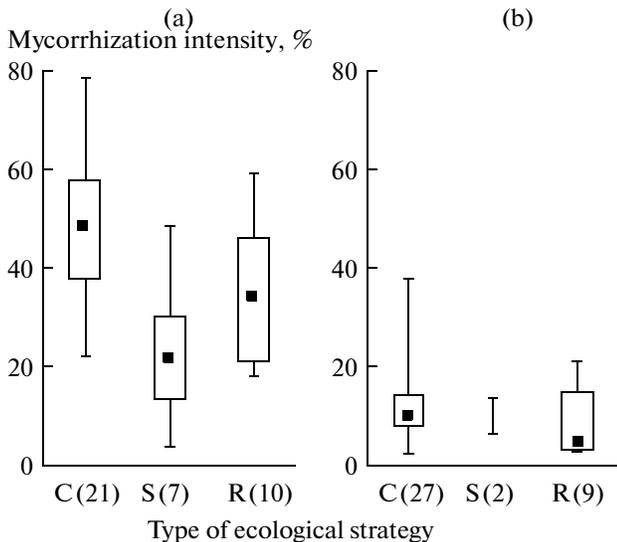
special approaches leveling off the differences between these sets.

In both natural and technogenic habitats, the highest abundance of arbuscular mycelium in plant roots was observed in competitors, while the lowest abundance was characteristic of stress tolerators (figure). The average mycorrhization intensity in natural habitats was 1.8 times lower in S-strategists than in C-strategists, with the difference being statistically significant ($H_{(2, N=38)} = 8.32; P = 0.0155$). In technogenic habitats this difference was 1.5-fold but lacked statistical significance ($H_{(2, N=38)} = 0.63; P = 0.7263$), because the sample included only two stress-tolerant species. When the sets of data on natural and technogenic hab-

itats were pooled (after preliminary standardization within each set to level off habitat-dependent differences without altering the differences between plant species), competitors and stress tolerators also proved to differ in mycorrhization intensity, but at a low significance level ($H_{(2, N=76)} = 6.57; P = 0.0373$). No differences in this parameter were revealed between competitors and ruderals.

For integrated characterization of the association with fungi in plants with different strategies, it is convenient to use the term “association strength” (T) determined as a function of two parameters: $T = f(P, C)$, where P is the proportion of mycotrophic species and C is mycorrhization intensity. Plants with the C-strategy show the strongest association with fungi, since both the prevalence of mycorrhiza and the abundance of fungi in this group are high (Table 3). The association strength in S- and R-strategists is lower, but this is due to different factors, since there is no definite relationship between the two parameters of mycorrhiza formation. In the group of R-strategists, the lower strength of association with mycorrhizal fungi is explained mainly by a decrease in the proportion of mycotrophic species, with the abundance of mycelium in their roots being comparable to that in mycotrophic C-strategists. In the group of S-strategists, conversely, the reduced association strength is due primarily to low parameters of fungal abundance, while the ratio of mycotrophic and nonmycotrophic species in this group is the same as in C-strategists.

The data presented above make it possible to trace certain correspondence between vectors of change in environmental conditions within the Grime triangle (see Mirkin et al., 1999) and mycorrhization intensity. The ratio of mycotrophic and nonmycotrophic species is apparently dependent on stability of the environment, since the proportion of the former is large under relatively stable conditions (C- and S-strategies) but decreases in severely disturbed habitats (R-strategy). Mycorrhization intensity depends mainly on the richness of habitats, because relatively high levels of fungal



Mycorrhization intensity in mycotrophic plants with (C) competitive, (S) stress-tolerant, and (R) ruderal types of primary ecological strategies in (a) natural and (b) technogenic habitats of the Middle Urals. Black squares, rectangles, and vertical lines show median values and their deviation within 25 to 75 and 5 to 95 percentile ranges, respectively.

Table 3. The strength of association with arbuscular fungi in groups of species with (C) competitive, (S) stress-tolerant, and (R) ruderal types of primary ecological strategies

Ecological strategy	Proportion of mycotrophic species (<i>P</i>)*, %	Mycorrhization intensity (<i>C</i>)**, %	Strength of association with mycorrhizal fungi (<i>T</i>)
C	High (85–95)	High (38–58)	High
S	Medium (75–82)	Low (14–31)	Medium or low
R	Low (63–65)	Medium (21–46)	Medium or low

Notes: * The range of values in the Middle Urals and the British Islands (according to Grime et al., 1988).

** Interquartile range in natural habitats of the Middle Urals.

abundance are observed in C- and R-strategists, which grow in environments rich in resources, while low levels are characteristic of S-strategists, which are adapted to growing under stressful conditions, at a very poor resource supply.

The above considerations are not absolute for the reasons that have already been mentioned: (1) non-random compilation of species lists; (2) small numbers of species included in analysis, especially in the group of S-strategists, against the background of their considerable functional diversity (Rabotnov, 1985; Mirkin et al., 1999); and (3) the impossibility to discriminate between biotopic and methodological differences within the analyzed data set. The hypotheses proposed here need verification in special studies. Therefore, we consider it premature to discuss any factors responsible for the observed features and trends of mycorrhiza formation in plants with different strategies. In the most general form, these trends may be explained in the context of two groups of hypotheses emphasizing either the role of morphophysiological properties of plants themselves or the role of environmental conditions to which plants with a certain life strategy are best adapted.

Thus, the type of ecological strategy in the Grime–Ramenskii's C–S–R system is connected not only with certain values of morphophysiological parameters of individual plants (Grime, 1979; Grime et al., 1988; Mirkin et al., 1999; P'yankov and Ivanov, 2000) and specific chemical composition of their leaves (P'yankov et al., 2001) but also with a certain strength of association between plants and arbuscular fungi. The strongest association is characteristic of herbaceous plants with the competitive strategy. In stress tolerators, the abundance of fungal mycelium in the roots is lower than in competitors, and the group of plants with the ruderal strategy includes a relatively large proportion of species showing no interaction with arbuscular fungi.

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