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Effect of the Mycorrhizosphere on Soil Micromycete Biodiversity and Community Structure and Its Relation to the Rhizosphere and Hyphosphere Effects

E. Yu. Voronina[1]

Moscow State University, Biological Faculty, Moscow, 119992 Russia

Abstract—The impact of ectomycorrhiza on soil micromycete biodiversity and community versus the effect of the rhizosphere and hyphosphere was studied under natural conditions. Root-free soil was used as the control. The mycorrhizosphere effect manifested itself in changes in the structure of the complexes of the dominant and frequent micromycete species or in complete elimination of certain species, as well as in the influence of the mycorrhizal root zone on soil micromycete diversity. The changes in the structure of the soil micromycete community occurring in the mycorrhizosphere, as well as significant changes in their species composition in the mycorrhizosphere and other habitats, are indicative of the specificity of this niche and its differences from both the habitats influenced by only one of the two symbionts (plant–rhizosphere or mycobiont–hyphosphere) and free soil.

Keywords: ectomycorrhiza, mycorrhizosphere, rhizosphere, hyphosphere, soil micromycetes, biodiversity.

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Mycorrhizal symbioses are very common in nature and are present in practically all plant communities [1]. Apart from such functions as improvement of mineral nutrition, protection of the root system from pathogens, etc., the mycorrhizae-forming symbiotrophic fungi affect the host plant species, determining many aspects of the functioning of a phytocenosis by redistributing and modifying the nutrients in soil and intensifying the turnover of biogenic elements [2]. All the main forest-forming species in the forest communities of the boreal zone form ectomycorrhizae, predominantly with basidiomycetous symbionts [3]. In forest soils, symbiotrophic basidiomycetes constitute a considerable part of the biomass and are involved in a broad spectrum of interactions with various soil organisms [4–9]. Despite the fact that the mycorrhizosphere, the mycorrhizal root influence zone, is being actively studied, the studies are predominantly conducted in microcosms, which differ from natural conditions and are usually focused on the bacterial component [8–13]. As far as soil micromycetes are concerned, the effect of the mycorrhizosphere was mainly studied in relation to their number [14, 15], whereas the influence of the mycorrhizosphere on the species composition and the community structure has been as yet insufficiently studied and the data obtained are often contradictory. Moreover, no works exist in which the mycorrhizosphere is compared with the habitats directly influenced by only one of the symbionts (rhizosphere and hyphosphere). The antagonistic effect of ectomycorrhizal symbionts on the root pathogens from the genera *Phytophthora*, *Pythium, Fusarium*, and *Cylindrocarpon*, which dominate on mycorrhiza-free roots but drastically decrease in number in the mycorrhizosphere, as well as the stimulation of the development of nonpathogenic micromycetes, pathogen antagonists, in the mycorrhizosphere, is most often noted [14–18]. The question of the specificity of the micromycete species to the ectomycorrhiza of woody plants remains open. According to R. Summerbell, none of the species isolated from the mycorrhizosphere of *Pseudotsuga menziesii* has a high degree of specificity to the mycorrhizal mantle, so that the species complex present in the mycorrhizosphere is in many respects similar to the rhizosphere community [19–21]. At the same time, there exist opposite data; some researchers suggest that special micromycete communities, which differ from both the nonmycorrhizal root rhizosphere communities and free soil, develop on the mycorrhizal tip surface; these communities differ depending on the mycobiont species [14, 15, 22].

The goal of the present work was to study the influence of the ectomycorrhizal mycorrhizosphere of spruce and birch on the species composition and structure of the soil micromycete community under natural conditions and to compare the mycorrhizosphere effect to the hyphosphere (the influence of the free mycelium of symbiotrophic fungi) and the rhizosphere effects (the influence of the root system of tree species).

[1] Corresponding author; e-mail: mvsadnik@list.ru.

MATERIALS AND METHODS

The work was carried out at the Department of Mycology and Algology, Biological Faculty, Moscow State University. Field studies and sampling were carried out on the territory of the forest preserve of the Skadovskii Zvenigorod Biological Station (Moscow oblast, Odintsovo raion). This territory is characterized by acidic sod–podzolic soils; plant associations are mainly represented by spruce forests of different types. Ten sampling plots 100 m^2 each were established for long-term observation in the forest areas represented by a grass-free spruce forest with an admixture of birches and pines. Preliminary study of the biota of agaricoid symbiotrophic basidiomycetes and their spatial distribution was carried out there. As a result of many years' mapping of the basidiomes (fruit bodies) of the ectomycorrhizal species, the outlines of their colonies were reconstructed for the subsequent soil sampling. Soil sampling for the assessment of the mycorrhizosphere effect on the species composition and the soil micromycete community structure was carried out according to two schemes: (1) to compare the mycorrhizosphere effect to the rhizosphere one—from soil cores 30 × 30 × 50 cm in the spruce or birch root systems, the root-free litter or soil from the same depth served as the control—and (2) to compare the effects of the mycorrhizosphere and of the free mycelium of symbiotrophs of different species (hyphosphere)—from the superficial layers of soil within colonies of 14 dominant species (*Amanita citrina* var. *citrina* (Pers.) Pers., *A. muscaria* var. *muscaria* (L.) Lam., *A. rubescens* var. *rubescens* Pers., *Cortinarius betuletorum* M.M. Moser ex M.M. Moser, *C. flexipes* (Pers.) Fr., *Hebeloma crustuliniforme* (Bull.) Quél., *Laccaria laccata* (Scop.) Cooke, *Lactarius aurantiacus* (Pers.) Gray, *L. camphoratus* (Bull.) Fr., *L. flexuosus* var. *flexuosus* (Pers.) Gray, *Leccinum scabrum* (Bull.) Gray, *Rhodocollybia butyracea* f. *butyracea* (Bull.) Lennox, *Russula xerampelina* (Schaeff.) Fr., and *Tricholoma fulvum* (Bull.) Sacc.)—the soil outside the colonies served as the control. The sampling was carried out in August and September from 2002 through 2004; a total of 234 samples were obtained. Every sample was treated in ten replicates, the micromycetes were isolated from them using Waxman's method for plating the serial soil dilutions on nutrient media, the species were identified, and their occurrence and relative abundance were calculated. In order to determine the similarity of the species composition of soil micromycetes between the habitats studied, Sörensen's index (qualitative) and Sörensen–Chekanovskii's index (quantitative) were used; in order to reveal biodiversity, Shannon's index was used. Wilcoxon's nonparametric test was used for the similarity indices to reveal the statistical significance of differences between the mean values and Student's *t*-test for Shannon's index [23].

RESULTS AND DISCUSSION

During the period of investigation, 132 species of soil-inhabiting micromycetes belonging to 45 genera were revealed in the samples of free soil, rhizosphere, and mycorrhizosphere of the tree species studied, as well as in the hyphosphere of symbiotrophic basidiomycetes. The overwhelming majority of the species (110) belonged to anamorphic fungi. A comparatively high species richness was noted for the genera *Penicillium* (43), *Aspergillus* (10), and *Trichoderma* (7); other genera were represented by four or fewer species.

According to the occurrence (O) values, the micromycete species revealed were subdivided into dominant (D) and frequent (F), forming a complex, and rare (R). The O value intervals for identifying the complex-forming species were determined by constructing the rank curves and pinpointing the points of their sharp breaks. The application of fixed intervals for the occurrence values seemed to be incorrect, because, at the same O value of a species in different habitats or in different seasons of study, the difference between it and the neighboring values could be variably substantial.

In order to reveal the soil micromycete species dominating in soil communities on the explored territory irrespective of the habitats studied (the rhizosphere, mycorrhizosphere, and hyphosphere of symbiotrophic basidiomycetes), the species constituting the general soil complex were identified. The complex composition varied from season to season, but such species as *Aureobasidium pullulans* (de Bary) G. Arnaud (the O in different seasons from 38.3 to 60.0%), *Beauveria bassiana* (Bals.-Criv.) Vuill.[2] (34.8–66.7%), *Geomyces pannorum* var. *pannorum* (Link) Sigler et J.W. Carmich. (80.0–90.0%), and *Umbelopsis ramanniana* (Oudem.) W. Gams (65.2–86.7%) remained dominant or frequent throughout the period of study.

In the course of the investigation, it was revealed that all three habitats (the nonmycorrhizal and mycorrhizal root rhizosphere and the hyphosphere of the symbiotrophic basidiomycetes) influenced the distribution of soil micromycetes and induced changes in both their abundance [24] and the taxonomic structure of their community. This manifested itself both at the level of frequent and dominant species and the species that were not part of the complex. Complete elimination from any habitats in question was observed at the rare species level, which may give evidence of the preference of such habitats as rhizosphere, mycorrhizosphere, hyphosphere, or free soil. The greatest number of species (15) were revealed only in free soil (control): *Acremonium kiliense* Grütz, *Alternaria tenuissima* (Kunze) Wiltshire, *Aspergillus clavatus*

[2] Here and hereinafter, in the case of absence of an observation of the teleomorphic stage in the culture, the name is given for the anamorph according to the data from the Index Fungorum database (http://www.indexfungorum.org/Names/Names.asp).

Desm., *A. nidulans* (Eidam) G. Winter, *A. terreus* Thom, *A. versicolor* (Vuill.) Tirab., *Chrysosporium merdarium* (Ehrenb.) J.W. Carmich., *Fusarium* sp., *Metarhizium anisopliae* (Metschn.) Sorokin, *Microascus cinereus* Curzi, *Papulaspora* sp., *Penicillium nalgiovense* Laxa, *Phialophora fastigiata* (Lagerb. et Melin) Conant, *Phoma levellei* Boerema et G.J. Bollen, and *Stachybotrys chartarum* (Ehrenb.) S. Hughes. Ten species were present only in the mycorrhizosphere and were eliminated from other habitats: *Aphanocladium album* (Preuss) W. Gams, *Chaetomium cochlioides* Palliser, *Cladosporium sphaerospermum* Penz., *Mucor mucedo* Fresen., *Penicillium chermesinum* Biourge, *P. corylophilum* Dierckx, *P. solitum* var. *crustosum* (Thom) Bridge, *P. variabile* Sopp, *Stemphylium botryosum* Sacc., and *Trichoderma asperellum* Samuels, Lieckf. et Nirenberg. Five species occurred only in the nonmycorrhizal root rhizosphere: *Aspergillus ochraceus* G. Wilh., *Mucor racemosus* Fresen., *Penicillium rugulosum* Thom, *P. vermiculatum* P.A. Dang., and *Periconia igniaria* E.W. Mason et M.B. Ellis; only one species—*Ramichloridium schulzeri* (Sacc.) de Hoog—was revealed solely in the hyphosphere.

The manifestation of the mycorrhizosphere effect and the influence of the other types of habitats on the complex-forming species, which are more significant in the soil micromycete community, appear to be more interesting. It was shown that the main type of the mycorrhizosphere effect on the species composition of soil micromycetes was the rearrangement of the soil mycobiota complexes consisting in a sharp change in the occurrence ranks rather than in complete elimination of one or another species in this zone (the general data are presented in Table 1). Thus, the dominant and frequent micromycete species may be subdivided into nonspecific (the species included in the composition of the general complexes, retained in the rank of complex-formers in all the habitats studied), the species confined only to one of the habitats, and those that occurred in more than one habitat but were invariably eliminated from other habitats. *Penicillium funiculosum, P. ochrochloron*, and *P. paxilli* occurred only in the free soil complex; *Alternaria alternata, Trichoderma koningii,* and *Zygorhynchus moelleri*, was found only in the rhizosphere complex; *Paecilomyces farinosus, Penicillium brevicompactum, Trichoderma asperellum*, and *T. virens*, were restricted to the mycorrhizosphere complex; and *Aspergillus niger, Lecanicillium* sp., *Penicillium daleae*, and *P. viridicatum*, occurred in the hyphosphere complex. We can also identify the species that occurred only in the root system (rhizosphere and mycorrhizosphere)—*Penicillium raistrickii*—or in the zone of influence of mycorrhizal mycelium (mycorrhizosphere and hyphosphere)—*Mucor hiemalis*—and those eliminated from the habitats indicated (*Umbelopsis isabellina* and *Geomyces vinaceus*, respectively).

The similarity between the habitats in the micromycete species composition was assessed using Sörensen's and Sörensen–Chekanovskii's indices. When the species diversity in free soil was compared to the nonmycorrhizal and mycorrhizal root rhizosphere, the similarity indices were low. The sample volume allowed use of the statistical apparatus, and Wilcoxon's nonparametric test was used for assessing the significance of the differences in the mean values. Generally, the indices took low values (the highest C_S value was 0.59; the C_N value was 0.46), and the maximal similarity in both cases was observed between nonmycorrhizal root and free soil, which is confirmed statistically (Table 2). The sharpest interhabitat difference in the soil micromycete composition was revealed between the nonmycorrhizal root rhizosphere and free soil; as for the comparison between mycorrhizosphere and rhizosphere, their similarity was relatively low. Thus, in the series of the rhizosphere–mycorrhizosphere–free soil habitats, the mycorrhizal root zone of influence differs from the nonmycorrhizal root rhizosphere to a greater degree than from free soil, which determines the necessity of considering the mycorrhizosphere as an independent habitat unequal to the rhizosphere in terms of both the number and composition of soil microorganisms [24].

The use of the similarity indices for comparing the habitats inside the colonies of symbiotrophic basidiomycetes yielded mosaic results: for the colonies of different species, the index values varied quite substantially. Generally, both the qualitative (C_S) and quantitative (C_N) similarity index values varied within wide limits—from 0.13 to 0.62 and from 0.03 to 0.59, respectively—and did not always vary in synchrony (Table 3). The highest interhabitat similarity between free soil and the hyphosphere was observed in the C_S values for the colonies of four species (*Amanita muscaria* var. *muscaria*, *A. rubescens* var. *rubescens*, *Cortinarius betuletorum*, and *Hebeloma crustuliniforme*); in the C_N values, for six species (*Amanitia citrina* var. *citrina*, *A. muscaria* var. *muscaria*, *Cortinarius betuletorum, Hebeloma crustuliniforme, Laccaria laccata*, and *Rhodocollybia butyracea* f. *butyracea*). For two species (*Cortinarius betuletorum* and *Hebeloma crustuliniforme*), it was observed when both similarity measures were used. In most cases, the mycorrhizosphere differed substantially from free soil in the species composition of soil micromycetes: a higher similarity between this habitat and the control compared to the free soil–hyphosphere pair was noted in the values of both indices only for the colonies of *Russula xerampelina* and in the C_S values for *Lactarius camphoratus.* Despite the fact that the hyphosphere and mycorrhizosphere are influenced by the same factor, the mycelium of the mycorrhizal symbiont fungus, the similarity between these habitats was not substantially higher than between each of them and free soil and was only noted for two species (*Leccinum scabrum* and *Tricholoma fulvum*) and only in terms of the C_N values (Table 3). An approximately equal similarity between all the habitats studied, including a similar values of

Table 1. Changes in the structure of soil micromycete complexes influenced by the rhizosphere, mycorrhizosphere, and hyphosphere compared to free soil

Species	Species rank in the habitats studied			
	C	**R**	**M**	**H**
Nonspecific:				
***Beauveria bassiana* (Bals.-Criv.) Vuill.**	F	F	F	D
***Geomyces pannorum* var. *pannorum* (Link) Sigler et J.W. Carmich**	D	D	D	D
***Penicillium citrinum* Thom**	D	F	D	F
***P. janczewskii* K.M. Zalessky**	D	D	D	D
***P. simplicissimum* (Oudem.) Thom**	F	D	F	D
***P. velutinum* J.F.H. Beyma**	D	D	D	D
***Pochonia bulbillosa* (W. Gams et Malla) Zare et W. Gams**	D	D	D	F
***Umbelopsis ramanniana* (Oudem.) W. Gams**	D	F	F	D
Confined to one of the habitats				
Alternaria alternata (Fr.) Keissl.	Ra	F	Ra	Ra
Aspergillus niger var. *niger* Tiegh.	Ra	Ra	–	F
Lecanicillium sp.	Ra	–	–	F
Paecilomyces farinosus (Holmsk.) A.H.S. Br. et G. Sm.	Ra	Ra	F	Ra
Penicillium brevicompactum Dierckx	Ra	Ra	F	–
P. daleae K.M. Zalessky	–	–	–	F
P. funiculosum Thom	F	Ra	–	Ra
P. ochrochloron Biourge	F	–	Ra	Ra
P. paxilli Bainier	F	Ra	Ra	—
P. viridicatum var. *viridicatum* (Westling) Frisvad et Filt.	–	–	–	D
Trichoderma asperellum Samuels, Lieckf. et Nirenberg	–	–	F	–
T. koningii Oudem.	Ra	F	Ra	Ra
T. virens (J.H. Mill, Giddens et A.A. Foster) Arx	–	Ra	F	Ra
Zygorhynchus moelleri Vuill.	Ra	F	Ra	Ra
Eliminated from certain habitats				
***Aureobasidium pullulans* (de Bary) G. Arnaud**	D	Ra	F	F
Geomyces vinaceus Dal Vesco	F	F	Ra	Ra
Mucor hiemalis Wehmer	Ra	Ra	F	F
***Penicillium canescens* Sopp**	F	–	F	D
***P. chrysogenum* var. *chrysogenum* Thom**	D	Ra	D	F
P. frequentans Westling	Ra	F	Ra	F
***P. purpurogenum* Stoll**	Ra	F	Ra	F
P. raistrickii G. Sm.	Ra	F	F	Ra
***P. spinulosum* Thom**	Ra	D	D	D
***P. thomii* Maire**	F	Ra	D	Ra
***Tolypocladium inflatum* W. Gams**	F	F	F	Ra
***Trichoderma polysporum* (Link) Rifai**	D	–	F	F

Note: Habitat: C, control soil; R, rhizosphere; M, mycorrhizosphere; H, hyphosphere; the species ranks: D, dominant; F, frequent species; Ra, rare species; – species is absent. The species included in the general complexes of the soil studied are outlined in boldface.

Table 2. Similarity of the species composition of soil micromycetes in the habitats studied

Index	Compared categories (the index mean value)		p	Statistical significance of differences
C_S	C-M (0.59)	C-R (0.47)	0.005062	C-M > C-R
	C-M (0.59)	M-R (0.51)	0.059337	ID
	C-R (0.47)	M-R (0.51)	0.074463	ID
C_N	C-M (0.46)	C-R (0.37)	0.028418	C-M > C-R
	C-M (0.46)	M-R (0.35)	0.046854	C-M > M-R
	C-R (0.37)	M-R (0.35)	0.386271	ID

Note: C_S, Sörensen's index; C_N, Sörensen–Chekanovskii's index; p, the significance level; ID, the difference is insignificant as assessed by Wilcoxon's test; C, control; M, mycorrhizosphere; R, rhizosphere.

both indices (*Lactarius aurantiacus*), was noted for a number of species. Generally speaking, it may be concluded that the mycorrhizosphere differs from both free soil and the hyphosphere, although both zones had a similar impact on a number of microorganisms [24].

The influence of habitats on soil micromycete biodiversity assessed with the use of Shannon's diversity index was of a statistically significant character in most cases. The highest soil micromycete biodiversity was noted in free soil (the index value of 3.57); the lowest one, in the rhizosphere (3.16), which is likely to be associated with the competition in this habitat for root exudates and other resources provided by the plant root system [18]. The mycorrhizosphere differed significantly from the other two habitats; its species diversity was lower than in free soil but exceeded the rhizosphere values (3.34).

When we considered the influence of the free mycelium of different types of symbiotrophs and made a comparison between the mycorrhizosphere and the hyphosphere effects, the species specifics of the direction of influence of the colonies of symbiotrophic basidiomycetes was revealed. Four main types of influence on soil micromycete diversity may be singled out (see figure):

(1) the absence of statistically significant influence of the colony zones (hyphosphere, mycorrhizosphere) on the species diversity of soil micromycetes (*Leccinum scabrum*);

(2) a statistically significant micromycete biodiversity decrease in the mycorrhizosphere compared to free soil in the absence of a marked hyphosphere effect (*Amanita rubescens* var. *rubescens*) or a sharper biodiversity decrease in the mycorrhizosphere compared to the hyphosphere (*Cortinarius flexipes, Hebeloma crustuliniforme*);

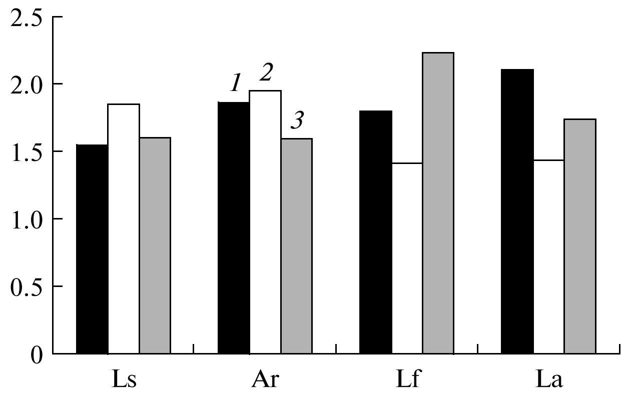
(3) a statistically significant micromycete biodiversity decrease in the hyphosphere and mycorrhizosphere compared to free soil (a unidirectional action of both effects) with a significantly more marked inhibitory influence of the hyphosphere; the most common type (*Amanita citrina* var. *citrina*, *Laccaria laccata, Lactarius aurantiacus, L. camphoratus*, etc.); and

(4) a statistically significant micromycete biodiversity increase in the mycorrhizosphere with the oppo-

Table 3. Similarity of the species composition of soil micromycetes in the zones of the symbiotrophic basidiomycete colonies

Symbiotrophic basidiomycete species	C_S				C_N		
	C-H	C-M	H-M		C-H	C-M	H-M
Amanita citrina var. *citrina*	0.49	0.24	0.46		0.33	0.14	0.24
A. muscaria var. *muscaria*	0.61	0.13	0.25		0.48	0.08	0.17
A. rubescens var. *rubescens*	0.54	0.45	0.33		0.44	0.44	0.49
Cortinarius betuletorum	0.45	0.36	0.33		0.42	0.08	0.03
C. flexipes	0.61	0.6	0.5		0.4	0.36	0.37
Hebeloma crustuliniforme	0.6	0.25	0.21		0.38	0.09	0.07
Laccaria laccata	0.37	0.38	0.44		0.32	0.2	0.25
Lactarius aurantiacus	0.36	0.38	0.42		0.1	0.14	0.14
L. camphoratus	0.44	0.5	0.37		0.29	0.28	0.2
L. flexuosus var. *flexuosus*	0.52	0.62	0.57		0.32	0.33	0.24
Leccinum scabrum	0.38	0.35	0.38		0.16	0.1	0.27
Rhodocollybia butyracea f. *butyracea*	0.38	0.29	0.38		0.44	0.15	0.18
Russula xerampelina	0.43	0.57	0.33		0.41	0.52	0.42
Tricholoma fulvum	0.52	0.36	0.48		0.34	0.35	0.59

Note: C_S, Sörensen's index; C_N, Sörensen–Chekanovskii's index; C, control; H, hyphosphere.



Examples of the main types of influence of the zones of symbiotrophic basidiomycete colonies on soil micromycete biodiversity (Shannon's index, selected data). Abscissa: symbiotrophic basidiomycete species; ordinate: Shannon's index values. *Ls*, *Leccinum scabrum*; *Ar*, *A. rubescens* var. *rubescens*; *La*, *Lactarius aurantiacus*; *Lf*, *L. flexuosus* var. *flexuosus*. Control (*1*), hyphosphere (*2*), and mycorrhizosphere (*3*).

site action of the hyphosphere effect (*Lactarius flexuosus* var. *flexuosus*, *Tricholoma fulvum*).

The data obtained give evidence of the diversity of the types of influence of the mycorrhizosphere (even for the species of symbiotrophic basidiomycetes belonging to one genus) on the species diversity of the communities of soil micromycetes. For example, the mycorrhizosphere effect of the representatives of the genus *Lactarius* may consist in either a statistically significant decrease in soil micromycete diversity versus soil control (*L. aurantiacus*) or its significant increase (*L. flexuosus* var. *flexuosus*).

Thus, it may be concluded that mycorrhizosphere exerts a multifactorial influence on the species composition and structure of the community of soil micromycetes. The mycorrhizosphere effect manifests itself in a change in the structure of the complexes of dominant and frequent micromycete species or complete elimination of certain species, as well as in the influence of the mycorrhizal root zone on soil micromycete biodiversity. The structural changes in the community of soil micromycetes occurring in mycorrhizosphere, as well as significant differences in their species composition in mycorrhizosphere and the other habitats compared, allow us to consider this zone to be specific and different both from the habitats influenced only by one of the two symbionts (plant–rhizosphere or mycobiont–hyphosphere) and from free soil.

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