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Studies on the symbiotic properties of mycorrhizal fungi of Scots pine (*Pinus sylvestris* L.) as affected by age of the fungal culture

Abstract

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The main purpose of the study was to examine the mycorrhizal ability of 10 different strains and species of mycorrhizal fungi stored on synthetic media over 2 to 17 years. The symbiotic potential of fungi used in the experiment was not related with their age in pure cultures. Best results were obtained with the oldest culture of *Rhizopogon luteolus*. However all the remained fungi revealed to a varying extent a lowered mycorrhizal ability to infect the host tissue with age. Individual features of each strains appear to play the most important role for the preservation of the symbiotic potential of mycorrhizal fungi during storage. The origin of the great variability among mycorrhizal symbionts of Scots pine as regards their ability to infect host tissues is discussed.

Additional key words: *Amanita muscaria*, *Suillus bovinus*, *S. luteus*, *S. hirtellus*, *S. granulatus*, *Rhizopogon luteolus*, *Paxillus involutus*.

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INTRODUCTION

The great importance of mycorrhizal associations for growth and development of forest trees is well documented (Marks and Kozłowski 1973). Research on mycorrhizal symbiosis has increased dramatically during the last decade, particularly in applied sciences. However certain important physiological and biochemical problems (eg. mechanisms causing formation and the disappearance of mycorrhizal associations, role of growth regulators in mycorrhizae) are not receiving the attention they merit (HacsKaylo 1983). Several methods were developed for this kind of physiological and structural experiments on ectomycorrhizae (Melin 1922, HacsKaylo 1953, Marx and Zak 1965, Fortin et al. 1983). Use of the pure culture synthesis technique belongs to the most popular ones and was reviewed and evaluated in several papers (Shemakhanova 1967, Pachlewska 1968). Pure isolates of mycorrhizal fungi, maintained on synthetic or semisynthetic media with glucose as the main source of carbon are used for inoculating roots of sterile seedlings in these

methods. Nutritional requirements of ectomycorrhizal fungi in pure culture are well documented in many studies and summarized in detail by Molina and Palmer (1982). However caution must be exercised in evaluating growth or physiological activity of mycorrhizal fungi maintained for long periods in axenic conditions. After several years of repeated subculturing on agar or liquid media and storage at low temperature (5°C) these fungi can change their nutritional requirements and some growth habits and sometimes lose their virulence or symbiotic potential or even die. The isolate of mycorrhizal fungus *Suillus bovinus* after a few years of storage in pure cultures on synthetic media stopped or greatly reduced the production of polyphenolic pigments (Rudawska — unpublished data). Certain isolates of *Rhizopogon luteolus* stimulate growth of *Pinus radiata* more than others; one isolate improved seedlings growth nearly twice as much as the other isolates (Theodorou and Bowen 1970). Laiho (1979) found, that certain isolates of *Paxillus involutus* lost their capacity to form ectomycorrhizae in the course of experiments in aseptic conditions. Marx (1979, 1981) and Marx et al. (1970) found significant variability of different isolates of *Pisolithus tinctorius* in growth rate as well as in the ability to form ectomycorrhizae with *Pinus taeda* as dependent on age, host origin and location of the fungus culture. These authors and others (Theodorou and Bowen 1970, Melin 1936, Trappe 1977, Shemakhanova 1967, Göbl 1975) have emphasized the need to use a fresh mycelium (recently obtained in a pure culture) and to test several isolates to choose a superior fungus for the experiments.

The objectives of this study were to examine mycorrhizal ability of different strains and species of mycorrhizal fungi of varying ages in axenic cultures with Scots pine.

MATERIALS AND METHODS

Ten species and strains of mycorrhizal fungi were used (Table 1). They were grown in test tube slants on a medium described by Rudawska (1980) and stored at 5°C in darkness. Isolates were subcultured into a new medium every 6 months. To

Table 1

Strains of ectomycorrhizal fungi used for inoculation of *P. sylvestris* seedlings in pure culture on agar (arranged in descending order of their mycorrhizal potential)

Ectomycorrhizal fungus	Years in pure culture	Isolate obtained by
<i>Rhizopogon luteolus</i>	17	R. Pachlewski
<i>Paxillus involutus</i> II	2	Author
<i>Suillus bovinus</i> II	2	Author
<i>Suillus luteus</i> II	5	Author
<i>Suillus luteus</i> I	12	R. Pachlewski
<i>Suillus bovinus</i> I	12	R. Pachlewski
<i>Paxillus involutus</i> I	2	Author
<i>Suillus hirtellus</i>	?	?
<i>Suillus granulatus</i>	12	R. Pachlewski
<i>Amanita muscaria</i>	5	Author

prepare an inoculum for ectomycorrhizal synthesis the isolates were grown for 3 weeks in a liquid shakeculture on the same medium as for storage. After that time the mycelium was ready for the inoculation of seedlings.

Ectomycorrhizal aseptic synthesis was made in 300×40 mm test tubes by the method described by Pachlewska (1968). Aseptic seedlings were obtained from seeds of Scots pine soaked for 30 min. in 30 percent H_2O_2 and rinsed aseptically with 1 liter of sterile distilled water, then germinated on water agar in Erlenmayer flasks. When radicles were approximately 1 to 2 cm long, germinants were aseptically transferred into the tubes. The whole radicle was inserted into the agar substrate quite near the tube wall so that the ectomycorrhiza formation could be seen directly through the glass. Inoculation of seedlings with mycorrhizal fungi was performed after two weeks, using two pieces of the mycelium (about 1 cm in diameter) from a shake culture. The tubes were kept at room temperature and received approximately 75% of full sunlight. Supplemental light for a 16h photoperiod was provided. The experiment was conducted over 7 month since 15 March till end of September.

Observations of the development of seedlings, fungal cultures and mycorrhizae formation was done with a stereomicroscope through the glass of the test tube under a $\times 4$, $\times 6$, $\times 10$ and $\times 25$ magnification. After harvest, each root system was visually assessed for mycorrhiza and representative ectomycorrhizae were freehand sectioned and estimated for the fungal mantle and Hartig-net presence at $125 \times$. The mycelium and seedlings state was estimated using the criteria of Pachlewska (1968):

Seedlings

1. Very good state — long, thick needles, dark green, strong growth of apical shoot,
2. Good state — long, green needles, good growth of apical shoot,
3. Rather good state — shorter, thinner needles, light green, poor growth of apical shoot,
4. Poor state — short, thin needles, very often become yellow, poor growth of apical shoot.

Mycelium cultures

- | | |
|-----------------------|-----------------------|
| 1. Very good state, | 4. Rather poor state, |
| 2. Good state, | 5. Poor state, |
| 3. Rather good state, | 6. Very poor state. |

RESULTS

Results of the experiments are presented in Table 2 and on Figs. 1-3. All isolates of ectomycorrhizal fungi used in the described experiment formed ectomycorrhizae with *Pinus sylvestris*, however to a different degree. The most abundant and rapidly increasing were mycorrhizae formed on seedlings inoculated with *Rhizopogon luteolus*.

Results of an experiment on mycorrhizal synthesis of *Pinus sylvestris* L. in pure cultures on agar

No of test tube	Species of fungus	Results of mycorrhizal synthesis	Time of appearance the first mycorrhizae (in months)	Total numbers of mycorrhizae per seedling	Morphological characters of mycorrhizae		Development of seedlings		Numbers of first laterals	Development of mycelium		
					single straight	dichotomously branched	general	height cm		above agar	within agar	
												numbers
1.	<i>Amanita muscaria</i>	+	6	7	6	1	3	8	86	—	4	
2.		—	—	—	—	—	3	9	76	—	6	
3.		—	—	—	—	—	2	9	73	—	3	
4.		+	7	15	11	4	1	8	118	6	5	
5.		—	—	—	—	—	1	9	90	3	3	
6.		—	—	—	—	—	1	6	37	6	3	
7.		+	7	3	3	—	2	7	59	6	6	
8.		—	—	—	—	—	1	8	56	—	—	
1.	<i>Suillus bovinus</i> I.	—	—	—	—	—	4	6.5	64	—	—	
2.		+	5	12	11	1	2	6	69	4	—	
3.		—	—	—	—	—	3	5.5	60	4	—	
4.		—	—	—	—	—	2	5.5	39	3	—	
5.		—	—	—	—	—	2	7	25	—	—	
6.		+	6	1	1	—	2	5.5	55	3	—	
7.		—	—	—	—	—	1	8.5	53	3	—	
8.		—	—	—	—	—	2	6	46	6	—	
9.		+	6	2	2	—	1	7.5	77	4	—	
1.	<i>Suillus bovinus</i> II.	—	—	—	—	—	2	10	79	—	3	
2.		+	4	5	5	—	2	7	62	5	—	
3.		+	4	11	11	—	3	7.5	80	5	—	
4.		—	—	—	—	—	6	6.5	33	—	—	
5.		—	—	—	—	—	4	5	44	—	—	
7.		—	—	—	—	—	3	5.5	87	—	—	
9.		+	5	8	8	—	3	6	60	4	—	
1.		<i>Suillus luteus</i> I.	—	—	—	—	—	3	6.5	63	—	—
2.			+	4	9	8	1	2	6.5	98	5	—
3.	+		5	3	2	1	3	5.5	87	5	5	
4.	+		5	4	1	3	3	6.5	82	5	—	
5.	+		5	6	6	—	2	7	125	5	—	
6.	—		—	—	—	—	3	7.5	76	6	—	
7.	+		6	2	2	—	3	6	36	6	—	
8.	—		—	—	—	—	2	7	88	—	—	

2.	<i>Suillus luteus</i> II.	+	5	3	3	-	4	5.5	43	-	3
3.		-	-	-	-	-	1	7	54	-	-
4.		+	4	4	4	-	3	7	88	5	-
5.		+	5	3	3	-	2	6.5	67	2	3
1.	<i>Rhizopogon luteolus</i>	+	4	1	1	-	2	7	108	6	-
2.		+	2	4	4	-	1	7	96	3	-
3.		+	2	6	3	3	3	7	55	4	-
4.		+	4	3	3	-	3	6.5	75	4	-
5.		+	3	12	11	1	3	7	64	2	-
6.		+	5	4	4	-	3	6.5	60	6	-
8.		+	5	3	3	-	3	7	68	5	-
9.		+	6	6	5	1	2	6.5	83	3	-
1.	<i>Suillus hirtellus</i>	-	-	-	-	-	1	7.5	82	-	5
2.		+	7	2	2	-	2	8	89	5	-
3.		-	-	-	-	-	-	-	15	-	-
4.		+	7	3	3	-	2	6.5	64	-	2
5.		-	-	-	-	-	4	5	55	6	-
6.		-	-	-	-	-	3	6	61	-	-
9.		-	-	-	-	-	3	6	80	-	-
1.	<i>Paxillus involutus</i> I. (K)	-	-	-	-	-	2	7.5	43	2	-
2.		-	-	-	-	-	3	7	46	-	2
3.		-	-	-	-	-	3	6	24	-	1
5.		-	-	-	-	-	3	8.5	105	-	-
6.		-	-	-	-	-	3	7	142	-	2
7.		+	5	3	3	-	2	7	103	4	2
8.		-	-	-	-	-	2	8	127	-	-
9.		-	-	-	-	-	1	8.5	68	-	-
1.	<i>Paxillus involutus</i> II. (G)	-	-	-	-	-	2	7.5	88	2	4
2.		+	4	7	5	2	2	6.5	59	2	4
3.		-	-	-	-	-	4	6.5	9	4	3
4.		+	4	7	7	-	2	6	106	2	5
5.		+	4	7	3	4	2	7.5	90	6	2
6.		+	5	2	2	-	2	6	63	1	5
7.		-	-	-	-	-	2	8	66	-	1
9.		-	-	-	-	-	2	7	60	-	1
1.	<i>Suillus granulatus</i>	-	-	-	-	-	1	7	85	-	-
2.		-	-	-	-	-	3	7	65	-	4
3.		-	-	-	-	-	2	7	64	-	2
4.		+	6	1	1	-	2	7.5	73	-	2
5.		-	-	-	-	-	3	6.5	7	-	2
6.		-	-	-	-	-	3	6.5	94	-	-
7.		-	-	-	-	-	2	5	35	-	2
8.		-	-	-	-	-	2	7	73	-	-

The first mycorrhizae appeared after 2 months since inoculation and then formed on all 10 test seedlings. Good results were also obtained with strains of *Suillus luteus* and medium with *Amanita muscaria*. Relatively low activity to mycorrhiza formation was revealed by *Suillus granulatus*.

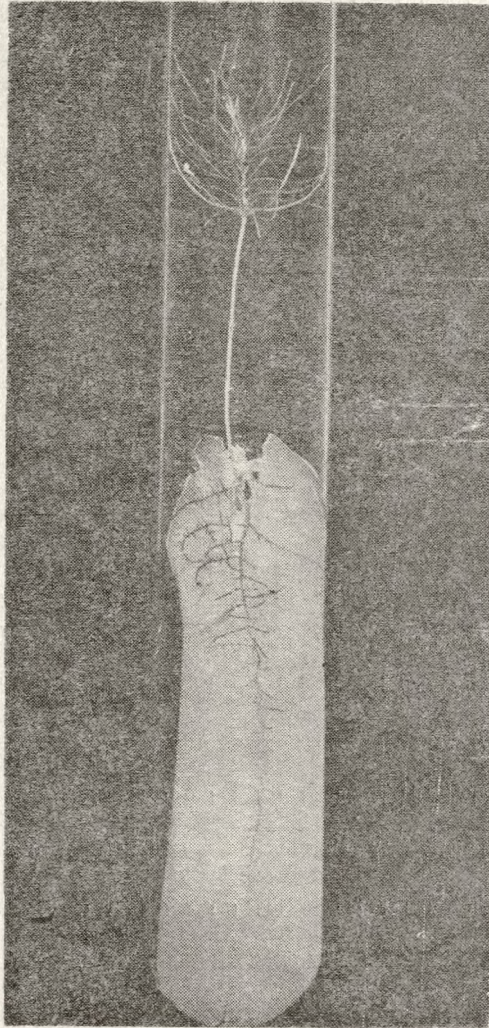


Fig. 1. Synthesis set on agar (*Pinus sylvestris* and *Amanita muscaria*)

Particularly interesting were mycorrhizae formed between *Pinus sylvestris* and *Suillus hirtellus*. This fungus does not belong to the mycorrhizal symbionts of *Pinus sylvestris* and is not present in the soil of a Scots pine stand. The phenomenon of mycorrhizae formation between this fungus and *Pinus sylvestris* is evidence for lack of host specificity in this fungus.

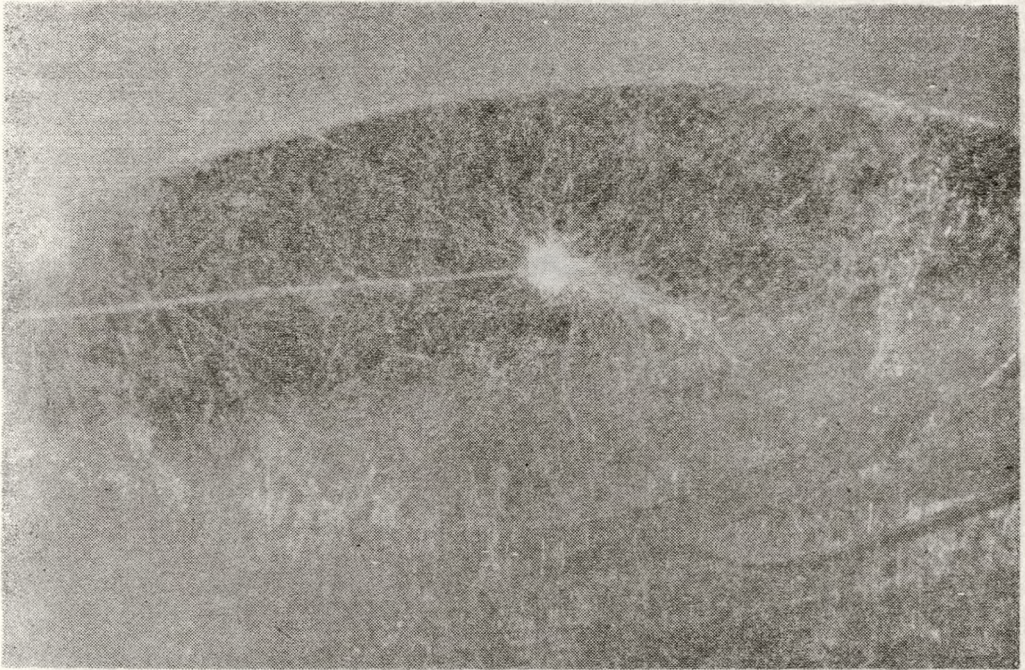


Fig. 2. Ectomycorrhiza of *P. sylvestris* with *Suillus bovinus* in vivo — above the substrate ($\times 15$)

DISCUSSION

Various disease studies have shown, that repeated passage of a pathogen through susceptible plant hosts enhances virulence of fungal pathogens (Day 1969). Host passage apparently affects the ability of the fungus to produce sufficient quantities of adaptive enzymes in response to stimulation from the enzyme substrates produced by the host plant. So as Marx (1981) underlined the extended periods of vegetative growth on artificial media in the absence of essential substrates and without frequent reassociation with susceptible plant tissue may change the adaptive enzyme systems and decrease the ability of the fungus to infect host tissue.

Similar situation as in the pathogen-host relation can occur in mycorrhizal symbiosis. Ectomycorrhizal fungi also utilize specific enzymes, growth regulators and perhaps some still unknown metabolites of the host plant (M-factor), to infect the host roots. It is very probable that they may lose their ability to form ectomycorrhizae after extended culture on agar or liquid media. Marx (1981) supposes that frequent passage of ectomycorrhizal fungi through susceptible tree host can revitalize older cultures that have lost symbiotic capacities after extended periods of time on synthetic media.

The main purpose of this study was to examine the mycorrhizal ability of 10 different strains and species of mycorrhizal fungi held in store on synthetic media over 2 to 17 years. It is very surprising that the best results, i.e. mycorrhiza formation in all synthetic sets, were obtained with the oldest culture of *Rhizopogon luteolus* kept





Fig. 3. Ectomycorrhizae of *P. sylvestris* with *Rhizopogon luteolus* in vivo ($\times 15$)

in storage about 17 years. Age of this pure culture was apparently not related with its symbiotic potential. The first mycorrhizal tips among all isolates used in this study were also observed following synthesis with *Rhizopogon luteolus* and appeared 2 months after inoculation. This results are in agreement with the HacsKaylo (1981) report presented at the 5th North American Conference on *Mycorrhizae* in Quebec in 1981 who found that even 16 years old cultures kept on synthetic media maintain original vitality and *Suillus punctipes* even increased its growth rate many times. According to HacsKaylo mycorrhizal ability of all these fungi remained very high. Probably, favourable conditions during culture storage were a very important factor of such good survival of these fungal cultures. Marx and Daniel (1976) also indicate the necessity to fulfil some special conditions during culture storage of mycorrhizal fungi. They have shown that cold storage of mycelial discs in sterile water is an early, rapid and inexpensive way to maintain fungal collections. In the presented study apart from *Rhizopogon luteolus* all remaining fungi revealed a more or less lowered mycorrhizal ability to infect host tissue with age, which was manifested by greatly delayed time of appearance of the first mycorrhizal tips (Table 1). All mycorrhizal isolates used in the course of this study formed first mycorrhizae later than in a very similarly done experiment of Pachlewski and Pachlewska (1974) performed mostly with the same species and in a few cases even with the same isolates. This means that during storage these fungal cultures partly lost their mycorrhizal vitality. Marx (1981) in an experiment with *Pisolithus tinctorius* found that age of mycelium

in pure culture was not responsible for the lack of symbiotic potential. Sometimes much older isolates formed more abundant *Pisolithus* ectomycorrhizae than others. Marx (1981) underlined however that the condition during culture storage is an important factor. The 17 year old pine isolate of *P. tinctorius* formed very few ectomycorrhizae on pine in one study (1981) whereas earlier this isolate formed abundant symbioses (Marx et al. 1970). From the data presented and from several recent experiments (Marx 1981, Laiho 1970, HacsKaylo 1981) it can be concluded that though the conditions during culture storage as well as age of mycelium culture are important factors determining mycorrhizal ability, individual features of each strains seem to play the most important role in the preservation of symbiotic potential of mycorrhizal fungi during storage. This can be connected with the great variability revealed in mycorrhizal fungi in relation to auxin and cytokinin production (Tomaszewski 1974) as well in some enzyme activity (Tomaszewski, Wojciechowska 1974). Tomaszewski (1974) even assumed the existence of a correlation between the capability for auxin and cytokinin production and the mycorrhizal activity of symbiotic fungi. It would be interesting to determine and compare the auxin and cytokinin production of mycorrhizal fungi over many years of culture storage.

It can be concluded from this study that ectomycorrhizal symbionts of *Pinus sylvestris* maintained for a long time on artificial media can change their mycorrhizal ability during culture storage and should always be carefully tested before use in basic or applied research.

SUMMARY

The paper describes tests with growth of mycorrhizae of pine in pure cultures on agar substrate. The main purpose of the study was to examine the mycorrhizal ability of 10 different strains and species of mycorrhizal fungi stored on synthetic media over 2 to 17 years. Mycorrhizae formation with all tested fungi was rather poor and unrelated to age of fungal culture. Relatively most abundant and rapidly increasing were mycorrhizae formed on seedlings inoculated with the oldest (17 year) culture of *Rhizopogon luteolus*. The first mycorrhiza in this case appeared after 2 month since inoculation and formed on all 10 test seedlings. All the remained fungi revealed to a varying extent a lowered mycorrhizal ability to infect the host tissue with age. The first mycorrhizae formed late since inoculation (4-7 months). Usually only 1 to 4 pine seedlings of the 10 seedlings tested had ectomycorrhizae and the incidence was very low.

Individual features of each strains appear to play the most important role for the preservation of the symbiotic potential of mycorrhizal fungi during storage.

It can be concluded from this study that ectomycorrhizal symbionts of *Pinus sylvestris* maintained for a long time on artificial media can change their mycorrhizal ability during culture storage and should always be carefully tested before use in basic or applied research.

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Badania symbiotycznych własności mikoryzowych grzybów sosny (Pinus sylvestris L.) w zależności od wieku kultury grzybowej

Streszczenie

Celem badań było przetestowanie zdolności do tworzenia mikoryzy z sosną przez 10 różnych gatunków i szczepów grzybów mikoryzowych utrzymywanych w czystej kulturze przez 2 do 17 lat. Do badań zastosowano metodę czystych kultur syntetyzujących na agarze. Formowanie się mikoryz sosny z badanymi grzybami było bardzo zróżnicowane i nie pozostawało w związku z wiekiem kultur grzybowych użytych do syntezy mikoryzowej. Stosunkowo najszybciej i najobficiej powstawały mikoryzy z najstarszą (17 lat) kulturą grzyba *Rhizopogon luteolus*. Pierwsze mikoryzy pojawiły się w tym zestawie po 2 miesiącach od inokulacji i potem utworzyły się we wszystkich zestawach syntetyzujących. Wszystkie pozostałe grzyby użyte w tym doświadczeniu wykazały znacznie obniżoną zdolność do tworzenia mikoryz, które pojawiały się późno (4 - 7 miesięcy od inokulacji), mało obficie i nie we wszystkich zestawach. Z doświadczenia wynika, że o zachowaniu lub utracie symbiotycznych własności poszczególnych grzybów mikoryzowych decydują raczej ich indywidualne własności niż czas przechowywania w czystej kulturze. Konieczne wydaje się każdorazowe sprawdzenie symbiotycznych własności kultur grzybowych przed ich użyciem do badań.

МАРИЯ РУДАВСКА

Исследование симбиотических свойств микоризных грибов сосны (Pinus sylvestris L.) в зависимости от возраста культуры грибов

Резюме

Целью исследований являлось тестирование способности к образованию микоризы с сосной 10 различными видами и штаммами микоризных грибов выращиваемых в чистой культуре в течение от 2 до 17 лет. Для исследований применяли метод чистых, синтетизирующих на агаре культур. Формирование микоризы сосны с исследуемыми грибами было очень дифференцированное и не оставалось в связи с возрастом культур грибов применяемых для микоризного синтеза. Относительно быстро и наиболее обильно образовалась микориза с наиболее старой (17 лет) культурой гриба *Rhizopogon luteolus*. Первые микоризы появлялись в этом составе 2 месяца спустя после инокуляции, а затем они образовались во всех синтетизирующих составах. Все остальные примененные в этом опыте грибы проявляли значительно пониженную способность образования микоризы, которая появлялась по истечении нескольких месяцев (4 - 7), с небольшой обильностью и не во всех синтетизирующих составах. Результаты опыта указывают на то, что в сохранении или потере симбиотических способностей отдельных микоризных грибов решающую роль играют скорее их индивидуальные свойства нежели период их сохранения в чистой культуре. Необходимой кажется каждый раз перед применением грибных культур в исследованиях проверка их симбиотических свойств.