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Stimulation of *Armillaria* rhizomorph growth by oak root fungi

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Thirty one different genera of fungi were isolated from the wood of roots of 50-year-old oak (*Quercus robur*). The most frequently isolated fungi were: *Mycelium radicis atrovirens alpha* (*MRAA*), *Clonostachys* sp. and *Penicillium daleae*. *Beauveria bassiana*, *Clonostachys* sp., *Cryptosporiopsis radicicola*, *Geotrichum candidum*, *Mortierella vinacea*, *MRAA*, *P. daleae*, *P. janczewskii*, *P. spinulosum*, *Sporothrix schenckii* and *Tolypocladium niveum* significantly enhanced *Armillaria mellea* rhizomorph initiation and growth from oak branch segments *in vitro*. The biggest stimulation effect was noticed when the dematiaceous hyphomycetes, e.g. *MRAA*, *P. dimorphospora* and *S. schenckii* were studied.

Key words: *Armillaria mellea*, *Armillaria ostoyae*, *Quercus robur*, microfungi, roots.

INTRODUCTION

Armillaria species cause root disease and butt rot of many economically important forest tree species throughout the world (Wargo and Shaw 1985). In the Northern hemisphere *Armillaria ostoyae* (Romagn.) Herink is the most often associated with *Armillaria* root disease in conifers, and *A. mellea* (Vahl: Fr.) Kummer with disease of broadleaved trees rather than conifers (Kile et al. 1991; Guillaumin et al. 1993; Ota et al. 1998).

In Poland *Armillaria* butt and root rot occurs on 156 608 ha of broadleaved and coniferous forests, mainly in the south and north-east (Anonymous 1998). *Armillaria ostoyae* is the principal species recorded. It causes severe losses particularly in young Scots pines (20 415 ha of 10–20 year-old stands) planted often in/after mixed stands. *Armillaria mellea* occurs more rarely. There are only single records on its occurrence (Żółciak 1999 a, b), but intensive studies on the distribution of different *Armillaria* species in Poland are carried out.

Armillaria infects trees either by rhizomorph penetration of healthy roots or through physical contact of a suscept root with a diseased root. Rhizomorphs are important in dissemination and survival of the pathogen. During infection rhizomorphs penetrate the bark and form mycelial fans, which spread within the inner bark and cambium of the host root.

The common occurrence of *Armillaria* basidiomes at the bottom of trunks, and rhizomorphs on roots and butts of diseased oaks in mixed Scots pine (*Pinus sylvestris*) – oak (*Quercus robur*) stands shows that diseased oak may serve as a food base for *Armillaria*, from where rhizomorphs grow and attack healthy trees continuously.

Fungi and their metabolites may inhibit or stimulate *Armillaria* growth and rhizomorph formation in the field. *Trichoderma* spp. and a few members of *Basidiomycotina* may inhibit the rhizomorph production or prevent colonization of woody material (Hagle and Shaw 1991). Other fungi, e.g. *Mycelium radicis atrovirens* Melin (Mańka 1953), *Aureobasidium pullulans* (de Bary) Arnaud (Pentland 1965, 1967), *Macrophoma*, *Gliocephalis*, *Diplodia*, *Sordaria* (Watanabe 1986), *Zygorhynchus moelleri* Vuill. (Kwaśna and Łakomy 1998), and a few members of *Deuteromycotina* (Watanabe 1986) may induce rhizomorph formation.

The purpose of the study was to determine the effect of the most commonly occurring fungi in oak (*Q. robur*) roots on the initiation and growth of *A. ostoyae* and *A. mellea* rhizomorphs *in vitro*. *Armillaria ostoyae* and *A. mellea* were chosen for studies due to their host specialization. Generally, in Europe, *A. mellea* can infect vigorous oak trees, and *A. ostoyae* can colonize oaks, when growing within diseased conifer stands, particularly when their resistance is reduced by suppression (Guillaumin and Lung 1985; Rishbeth 1985 b; Roll-Hansen 1985; Davidson and Rishbeth 1988).

MATERIALS AND METHODS

Isolates. The fungi were isolated from the root wood of the common oak (*Q. robur*) trees found in mixed stand with Scots pine (*P. sylvestris*) affected by *A. ostoyae*. The roots were collected from 5, randomly selected, apparently healthy 50-year-old co-dominant oaks within a 30 × 50 m area in the Huta Pusta Forest District (western Poland, 17°10′ E, 52°50 N) division 131 d. Three roots of approximately 30 cm length and 5–10 mm in diameter were excavated from the A – soil horizon around each of the 5 trees. The roots were kept at 4°C until they were washed under running water and 2–3 randomly selected segments of 10 mm length were excised per root. Segments were serially washed 10 times for 3 minutes in sterile, distilled water. The bark was removed aseptically with a scalpel and wood from each segment was aseptically cut into 1 mm thick discs (sub-segments). The sub-segment wood was placed onto the surface of 2% malt extract agar (20 g Difco(R) malt extract, 15 g agar, 0.1 g streptomycin sulphate, 1 l distilled water) and selective nutrition agar (SNA) (0.2 g glucose, 0.2 g sucrose, 1 g KH_2PO_4, 1 g KNO_3, 0.5 g $MgSO_4 \times 7H_2O$, 0.5 g KCl, 15 g agar, 0.1 g streptomycin sulphate, 1 l distilled water), (N i r e n b e r g 1976). A total of 180 sub-segments (36 per tree) were put onto each medium in 30 Petri dishes (90 mm × 15 mm) and incubated at 22°C for 10–12 days in daylight. The plates were examined microscopically and sporulating fungi (mostly on SNA) were identified. Non-sporulating colonies arising from the sub-segments were transferred to potato dextrose agar (39 g Difco(R) PDA, 1 l distilled water) slants and incubated at room temperature under diffused daylight until sporulation occurred. Some dematiaceous hyphomycetes were induced to sporulate under UV light (310–420 nm for 12 h a day) at 20°C, or on 2% malt extract agar kept at 5°C in high humidity for 12–15 months. The frequency of colonization by particular fungal species was defined as the percentage of isolation of the fungus from sub-segments on both media. The isolated fungi are hereafter referred as the 'test' fungi.

The *A. ostoyae* isolates (94 125, 94 126) were obtained from basidiomes fruiting in severely diseased 6-year-old Scots pine at Jamy Forest District (Poland 18°50′ E, 53°38 N). These two isolates were selected because in experiment on rhizomorph production by different genotypes of *A. ostoyae*, 94 125 produced the lowest and 94 126 the highest number of rhizomorphs in culture. The *A. mellea* isolates (94 056, 94 080) were obtained from basidiomes fruiting on the *Q. petraea* Liebl., and *Juglans regia* L. in Ursa and Soprow (Hungary), respectively. Polish isolates of *A. mellea* were unavailable at the time of the study.

G r o w t h i n o a k s e g m e n t s. Freshly cut live branches segments (2 cm in diameter) of 20-year-old *Q. robur* were cut into 1-cm long discs, and 5-cm long lengths, washed with 70% ethanol and autoclaved twice at 121°C for 60 min. The 1 cm long discs were immersed into cultures of *A. ostoyae* or *A. mellea* growing on 8% malt agar (as above with 8% Difco® malt extract) and incubated in the dark for 30 days at 22°C. The 5 cm long oak segments were inoculated with 'test' fungi by immersing the segment in a jar containing a fungal culture growing on PDA at the bottom. Jars were filled with wet, sterilized sand, closed and left for 2 months in the dark at 22°C. When the 1cm long discs were covered with thin mats of white-cream to light brown *Armillaria* mycelium (after 30 days of incubation) they were used to inoculate the 5 cm long segments infested by the root fungi. Discs and segments were joined by nailing them together with 2 cm long nails. The control treatment consisted of a sterile branch segments attached to *Armillaria* infested discs. Joined discs and segments were put into wet, sterilize sand in jars and incubated in the dark at 22°C. After 2 months, when the *Armillaria* species in the control segments were well established, all segments (control and 'test' fungi/*Armillaria* spp. infested) were carefully removed from jars and inserted into plastic bags containing 0.7 kg of a substrate consisting of forest soil, sand, peat and humus (1:1:1:1). After 2 months at 22°C, the number of rhizomorphs, their length, number of living initials, and dry weight were assessed. Each 'test' fungus/*Armillaria* species treatment and the control treatment were replicated four times.

G r o w t h i n c u l t u r e. Two inocula (3 mm diameter plugs cut from the margin of 2-week-old colonies on 2% malt agar); one of a 'test' fungus, and the other of *A. ostoyae* or *A. mellea* were placed on 2% malt agar in the centre of a Petri dish at 2 cm distance. Each 'test' fungus, and *A. ostoyae* and *A. mellea* also were grown separately as controls. Cultures were incubated for 28 days at 23°C. Each two-fungal culture and the control treatment were replicated four times. The fungal interactions were estimated using the scoring system developed by M a ń k a et al. (1991). A final score of a two-fungi culture included the number of points allocated for the surrounding of a colony, the inhibition zone between two colonies, and the change in colony size.

ANOVA and analysis of variance of ranks with the Kruskal-Wallis test were used for evaluation of the effects of 'test' fungi on *A. mellea* and *A. ostoyae* rhizomorph production, respectively. Multiple comparison analysis was used to evaluate differences between treatments (S i g m a S t a t. 1995).

RESULTS

F u n g i. 136 isolates of fungi belonging to 31 genera were isolated from 360 *Q. robur* root sub-segments plated on 2% malt agar and selective nutrition agar (SNA) (Table 1). The media did not seem to effect the number or species of fungi isolated, (65 isolates on 2% malt agar, and 71 on SNA) nor did they influence the vegetative growth of specific fungi. Selective nutrition agar (SNA), however, stimulated the sporulation of a few species, e.g. *Clonostachys* sp., *Cryptosporiopsis radicicola* and *Phialocephala dimorphospora*.

The most frequently isolated species was a non-sporulating dematiaceous hyphomycete – *Mycelium radicis atrovirens alpha* (*MRAA*) type 1 and 2, which accounted for more than 46 of the total number of isolates. *MRAA* – type 1 included fungi with grayish – brownish – black mycelium, partly encrusted and coiled hyphae, which often formed the thick funicles. *MRRA* – type 2 included fungi with distinctly black mycelium, rarely encrusted and coiled, single (never in funicles) hyphae, and distinct right-angled hyphal branching (M e l i n 1921, 1923). Only the single isolate of dematiaceous hyphomycete produced phialoconidia in dark, after 15 months at 5°C, and this was identified as *P. dimorphospora*. None of the *MRAA* types produced brown soluble pigment suggesting *M. r. atrovirens beta* (M e l i n 1923; L e v i - s o h n 1960).

The second most abundant fungus was *Clonostachys* sp., which accounted for 16.9% of all isolates. This fungus produced white, cream or pink, slow growing colonies, with many encrusted hyphae in the aerial mycelium and

Table 1
Fungi isolated from root segments of *Quercus robur*

Species of fungus	Frequency (%) in fungal assemblage
Mycelium radicis atrovirens alpha (1)	34.6
Clonostachys sp.	16.9
Mycelium radicis atrovirens alpha (2)	11.8
Penicillium daleae Zaleski	6.6
Penicillium janczewskii Zaleski	3.7
Tolypocladium niveum (Rostrup) Bissett	3.7
Sporothrix schenckii Hektoen et Perkins	2.2
Cryptosporiopsis radicicola Kowalski et Bartnik	1.5
Geotrichum candidaum Link	1.5
Mortierella vinacea Dixon-Stewart	1.5
Penicillium citrinum Thom	1.5
Penicillium herquei Bainier et Sartory	1.5
Beauveria bassiana (Balsamo) Vuill.	0.7
Penicillium spinulosum Thom	0.7
Phialocephala dimorphospora Kendrick	0.7
Total number of isolates (including rare species)	136

Rare species isolated only from one root segment: *Botrytis cinerea* Pers., *Chrysosporium merdarium* (Link) J. Carm., *Exophiala jeanselmei* (Langeron) McGinnis et Padhybe, *Exophiala* sp., *Heterobasidion annosum* (Fr.) Bref., *Mortierella gracilis* Linn., *M. microspora* Wolf. var. *macrocystis* (Gams) Linn., *Mortierella schulzeri* (Sacc.) de Hoog, *Trichoderma koningii* Oudem., sterile dematiaceous hyphomycetes-8 species.

dimorphic conidiophores. Primary conidiophores were solitary, verticillate to more-level verticillate, with compressed branches and phialides forming a slender penicillus, with stipes usually longer than penicillus, but sometimes short and bearing long branches. Secondary conidiophores were solitary or loosely aggregated, with stipe not considerably longer than the penicillus. Penicilli were bi- to quaterverticillate with compressed branches forming imbricate chains of conidia, which, on SNA after 3 months incubation at 5°C, cohered in round colourless to white, watery, globose slimy masses. Conidia were oblong, slightly curved with one end broadly rounded, and measured $4.5-8 \times 2-4$ µm. The morphology was similar irrespective of the colony colour. *Penicillium* species accounted for 15% of all isolates. The most common were *P. daleae*, *P. janczewskii* and *P. citrinum*. The remaining 22% were other fungi belonging to 26 different genera.

Rhizomorph formation by *Armillaria* influenced by 'test' fungi. The 'test' fungi did have an effect on rhizomorph characteristics of *A. mellea*. *Beauveria bassiana*, *Clonostachys* sp., *C. radicicola*, *Geotrichum candidum*, *Mortierella vinacea*, *MRAA*, *P. daleae*, *P. janczewskii*, *P. spinulosum*, *Sporothrix schenckii*, and *Tolypocladium niveum* significantly ($P \leqslant 0.05$, $P \leqslant 0.01$) enhanced number of rhizomorphs, number of rhizomorph initials, rhizomorph length and weight of *A. mellea* 94 080 when they were growing from oak branch segments (Table 2). *Mortierella vinacea*,

Table 2

The effect of fungi isolated form *Quercus robur* on rhizomorph production of *Armillaria ostoyae* and *A. mellea*

Treatment	Armillaria species (isolate)	Number of rhizomorphs	Number of rhizomorph initials	Rhizomorph length (mm)	Rhizomorph weight (mg)
Control (*Armillaria* spp. alone)	*A. ostoyae* 94 125	0	0	0	0
	A. ostoyae 94 126	0	0	0	0
	A. mellea 94 056	4.25	5.25	58.75	5.25
	A. mellea 94 080	3.0	3.0	32.25	3.50
Beauveria bassiana	*A. ostoyae* 94 125	0	0	0	0
	A. ostoyae 94 126	0	0	0	0
	A. mellea 94 056	3.75	3.75	25.0*	1.75
	A. mellea 94 080	9.75*	12.25*	174.0*	21.0*
Clonostachys sp.	*A. ostoyae* 94 125	0	0	0	0
	A. ostoyae 94 126	0	0	0	0
	A. mellea 94 056	7.25	7.75	57.50	3.50
	A. mellea 94 080	11.0*	13.50*	196.25*	18.0*
Cryptosporiopsis radicicola	*A. ostoyae* 94 125	0	0	0	0
	A. ostoyae 94 126	0	0	0	0
	A. mellea 94 056	2.0	2.75	53.75	5.0
	A. mellea 94 080	12.0*	14.25*	265.0**	22.50**
Geotrichum candidaum	*A. ostoyae* 94 125	0	0	0	0
	A. ostoyae 94 126	0	0	0	0
	A. mellea 94 056	1.75	1.75	30.0	3.50
	A. mellea 94 080	12.5*	19.25**	255.0**	34.75**
Mortierella vinacea	*A. ostoyae* 94 125	1.0	11.25	0.75	
	A. ostoyae 94 126	0	0	0	0
	A. mellea 94 056	10.0*	12.0*	155.0**	15.5*
	A. mellea 94 080	16.0**	19.0**	183.75**	27.5**
Mycelium radicis atrovirens (1)	*A. ostoyae* 94 125	0.25	0.25	21.25	3.75
	A. ostoyae 94 126	0.50	0.50	6.25	1.25
	A. mellea 94 056	6.0	6.50	97.50*	6.25
	A. mellea 94 080	2.50	3.50	83.75*	5.25
Mycelium radicis atrovirens (2)	*A. ostoyae* 94 125	2.25*	2.50	21.25	2.50
	A. ostoyae 94 126	0	0	0	0
	A. mellea 94 056	17.25**	19.00**	252.50**	17.25**
	A. mellea 94 080	7.75	9.75*	195.0**	20.0**
Penicillium citrinum	*A. ostoyae* 94 125	0.25	0.25	8.75	0.50
	A. ostoyae 94 126	1.75	1.75	40.0	5.0
	A. mellea 94 056	3.50	4.50	70.0	11.75
	A. mellea 94 080	5.25	5.75	95.0*	8.25
Penicillium daleae	*A. ostoyae* 94 125	0	0	0	0
	A. ostoyae 94 126	2.75	3.0	31.25*	4.52
	A. mellea 94 056	10.0*	11.50*	157.50*	9.0
	A. mellea 94 080	10.75*	12.50*	187.50*	13.75*

Penicillium herquei	*A. ostoyae* 94 125	0.25	0.25	2.75	0.25
	A. ostoyae 94 126	1.25	1.25	37.0	3.25
	A. mellea 94 056	3.0	4.50	54.50	17.50
	A. mellea 94 080	0	0	0	0
Penicillium janczewskii	*A. ostoyae* 94 125	0	0	0	0
	A. ostoyae 94 126	1.75	1.75	23.50*	1.25
	A. mellea 94 056	2.0	2.0	23.0	1.75
	A. mellea 94 080	9.0	10.75**	268.75**	22.75*
Penicillium spinulosum	*A. ostoyae* 94 125	1.0	1.0	6.0	1.25
	A. ostoyae 94 126	0	0	0	0
	A. mellea 94 056	14.75**	18.25**	241.25**	19.25**
	A. mellea 94 080	11.50**	13.75**	162.5**	13.25**
Phialocephala dimorphospora	*A. ostoyae* 94 125	0.50	0.75	7.50	0.75
	A. ostoyae 94 126	0.25	0.25	7.50	0.75
	A. mellea 94 056	8.25	10.0	164.50*	11.25
	A. mellea 94 080	4.50	5.25	108.25*	8.25
Sporothrix schenckii	*A. ostoyae* 94 125	0.25	0.25	2.50	0.50
	A. ostoyae 94 126	0.50	0.50	5.0	0.25
	A. mellea 94 056	11.25*	11.75*	150.00*	12.75*
	A. mellea 94 080	12.0*	13.25**	195.0**	17.50**
Tolypocladium niveum	*A. ostoyae* 94 125	1.75	1.75	37.50*	5.0
	A. ostoyae 94 126	1.0	1.0	7.50	1.0
	A. mellea 94 056	4.25	4.25	75.0	10.0
	A. mellea 94 080	21.25*	28.0**	380.0**	43.0**

Explanations: Values are means, n = 4; * Significantly different from control at $P \leqslant 0.05$; ** Significantly different from control at $P \leqslant 0.01$.

MRAA 2, *P. daleae*, *P. spinulosum* and *S. schenckii* significantly ($P \leqslant 0.05$, $P \leqslant 0.01$) enhanced three and four rhizomorph characteristics of *A. mellea* 94 056. In control both isolates of *A. mellea* produced in average 3.6 rhizomorphs with 4.1 rhizomorph initials, 45.5 mm length and 4.3 mg weight. In all treatments with 'test' fungi both isolates of *A. mellea* produced in average 8.4 rhizomorphs with 9.7 rhizomorph initials, 145.2 mm length and 14.1 mg weight. Results indicate that there were statistically significant differences between effects of 'test' fungi. Multiple comparison analysis based on 'test' fungi showed the statistically significant differences ($P \leqslant 0.05$) for *P. spinulosum* vs. *P. herquei*, *T. niveum* vs. *P. herquei*, and *M. vinacea* vs. *P. herquei* for rhizomorph number and number of rhizomorph initials; *MRAA* (2) vs. *P. herquei* for rhizomorph numbers only; *T. niveum* vs. *MRAA* (1) for rhizomorph weight. Multiple comparison analysis based on *A. mellea* isolate showed that there were statistically significant differences ($P \leqslant 0.05$) between *A. mellea* 94 056 and 94 080 for *C. radicicola*, *G. candidum* and *T. niveum* for all the rhizomorph characteristics; *P. janczewskii* for rhizomorph number, number of rhizomorph initials and rhizomorph length; *B. bassiana* for number of rhizomorph initials, rhizomorph length and weight; *Clonostachys* sp. for

Table 3

Effects of fungi isolated form *Quercus robur* roots on the growth of *Armillaria ostoyae* and *A. mellea* on 2 malt extract agar

Species of fungi	Surrounding of the colony				Inhibition zone (mm)				Change in the colony size			
	A. ostoyae		*A. mellea*		*A. ostoyae*		*A. mellea*		*A. ostoyae*		*A. mellea*	
	94 125	94 126	94 056	94 080	94 125	94 126	94 056	94 080	94 125	94 126	94 056	94 080
Beauveria bassiana	0	0	0	0	2	0	0	0	0	0	0	−1
Clonostachys sp.	0	0	0	−3	0	3	2	2	0	0	0	0
Cryptosporiopsis radicicola	+1	+1	+1	−2	0	0	0	0	+1	0	0	−1
Geotrichum candidum	+4	+4	+4	+1	0	0	0	0	+3	+3	+2	0
Mortierella vinacea	+4	+2	+1	−3	0	0	0	0	0	0	0	−3
Mycelium radicis atrovirens alpha (isolate 1)	0	0	0	−4	0	2	2	0	0	0	0	−2
Mycelium radicis atrovirens alpha (isolate 2)	+1	0	+1	−3	0	0	0	0	0	−1*	0	−2*
Penicillium citrinum	+1	+2	0	−2	0	0	0	0	0	0	0	0
Penicillium daleae	+1	0	0	−2	2	3	2	0	0	0	0	−1
Penicillium herquei	+2	+2	+2	+3	2	2	2	0	0	0	0	+2
Penicillium janczewskii	+1	+1	0	0	2	0	2	5	0	0	0	0
Penicillium spinulosum	+3	+2	0	−1	1	2	2	0	+2	0	0	0
Phialocephala dimorphospora	+1	+1	0	−4	0	0	0	0	0	0	0	−3
Sporothrix schenckii	+4	+2	+1	−1	1	0	1	0	+3	0	0	−1
Tolypocladium niverum	+1	+1	0	−2	0	0	0	0	0	0	0	+1**

Mean, n = 4

Explanations:

„+" – root fungus surrounds (surrounding of the colony) or inhibits (change of the colony size) *Armillaria* colony

„−" – *Armillaria* surrounds (surrounding of the colony) or inhibits (change of the colony size) the root fungus colony

* – increase in diameter of *Armillaria* colony

** – increase in diameter of *T. niveum* colony rhizomorph length and weight; and *M. vinacea* for rhizomorph weight. Rhizomorphs of *A. mellea* were produced from one or several points, mostly at the end of wood segments.

Preliminary statistical analysis showed that the data for the *A. ostoyae* rhizomorph characteristics was not 'normal' and therefore could not be analyzed by ANOVA. An analysis of variance of ranks using the Kruskal-Wallis test showed that there was no significant difference between the 'test' fungi treatments and the control. In control *A. ostoyae* did not produce rhizomorphs, but only a fine mycelium under the bark. In all treatments both isolates of *A. ostoyae* produced in average 0.6 rhizomorphs with 0.6 rhizomorph initials, 9.2 mm length and 1.1 mg weight. This insignificant stimulation was caused by *M. vinacea*, *MRAA*, *P. citrinum*, *P. daleae*, *P. herquei*, *P. spinulosum*, *P. dimorphospora*, *S. schenckii* and *T. niveum*.

Armillaria growth in culture. In two-fungi cultures on 2% malt extract agar the majority of 'test' fungi did not stimulate but rather inhibited the growth of all four isolates of *Armillaria* (Table 3). The inhibition resulted from (i) surrounding of *Armillaria* colonies (mostly of *A. ostoyae* and *A. mellea* 94 056; only *B. bassiana*, *Clonostachys* sp. and *MRAA* (1) usually grew irrespective of the presence of *Armillaria*), (ii) production of inhibition zone (1-5 mm wide between *Armillaria* and *Clonostachys* sp., *MRAA* (1), a few *Penicillium* spp. and *S. schenckii*, (iii) decrease of *Armillaria* colony surrounded by a 'test' fungus (only the faster growing *A. mellea* 94 080 inhibited the growth of *B. bassiana*, *C. radicicola*, *M. vinacea*, *MRAA* (1), *P. daleae*, *P. dimorphospora* and *S. schenckii*). *MRRA*, *P. dimorphospora* and *S. schenckii* stimulated the growth of rhizomorphs in both *Armillaria* species. Both isolates of *A. mellea* grew faster and more profusely compared to *A. ostoyae*.

DISCUSSION

The most common microfungi found in wood of *Q. robur* roots (when 2% malt agar and SNA medium were used for isolation) were non-sporulating dematiaceous hyphomycetes belonging to *M. r. atrovirens alpha* (*MRAA*). *MRAA* is considered here as a complex of two morphologically and ecologically similar taxa (Melin 1921, 1923; Wang and Wilcox 1985). The fungus had been usually associated with ecto- endo- and pseudomycorrhizae of conifers. For many years it had never been observed in the root/soil habitat of broadleaved trees (Linhell 1939; Krzemieniewska and Badura 1954; Robertson 1954; Harley and Waid 1955; Mańka and Truszkowska 1958; Mańka 1960; Gochenaur and Backus 1967; Mańka et al. 1968; Morrall and Vanterpool 1968; Novak and Whittingham 1968; Gochenaur and Woodwell 1974; Morrall 1974; Richard and Fortin 1974; Wicklow et al. 1974; Gochenaur 1978, 1984; Kowalski 1982; Wang and Wilcox 1985; Schild et al. 1988; Summerbell 1989; Kwaśna

1997 a, b; S a m p o et al. 1997). S u m m e r b e l l (1989) and K w a ś n a (1996 a; b) showed, however, that *MRAA* is a common, non specific, root – associated fungus in the boreal sites. Even though apparently healthy, newly formed and older, mycorrhizal and non-mycorrhizal roots frequently yield *MRAA*, it is even more commonly associated with weakened, senescent and degraded tree roots (R o b e r t s o n 1954; L i v i n g s t o n e and B l a s c h k e 1984; H o l d e n r i e d e r and S i e b e r 1992) and stump roots (K w a ś n a 1996 a, b). The fungus is strongly associated with tissues of root interior, and it is far less predominant in root – free soil (K w a ś n a 1995; 1996 a, b; 1997 a, b, c). Although *MRAA* is often isolated from the bark of oak roots (K w a ś n a, unpublish.) it is the most commonly found in the wood of oak roots.

Clonostachys sp., the anamorph of *Bionectria* (S c h r o e r s et al. 1999) was detected in oak healthy roots for the first time. It is a rare fungus, presumably with very specific nutritional preferences. Earlier, it had been found only on bark of dying and recently dead woody plants, less frequently on fruits, in South America and Australasia (S a m u e l s 1988). It was not previously observed in temperate climate.

The occurrence of *Cryptosporiopsis radicicola* in oak roots was confirmed only recently. It was one of the most frequently isolated species from roots of declining *Q. robur* in southern Poland. The fungus appears to be specific to roots although sometimes it reaches the tissues at the root collar (B a r t n i k 1989; K o w a l s k i 1991; K o w a l s k i and B a r t n i k 1995). Its high frequency in roots of declining oaks suggests that it may be important for the health of oak. Adaptation of *C. radicicola* to roots contrasts with other *Cryptosporiopsis* species which occur mainly on aerial plant parts, especially on branches and trunks (B u t i n 1981; K o w a l s k i and K e h r 1992; S u t t o n 1992; D u g a n et al. 1993).

Rhizomorphs are discrete, aggregations of hyphae that can vary in their complexity (T o w n s e n d 1954). *Armillaria* rhizomorphs are highly developed structures with meristems, medullary and cortical cells (M o t t a 1969). They are important in the infection, spread and persistance of *Armillaria* root disease. Abiotic factors that affect rhizomorph growth have been reviewed by R e d f e r n and F i l i p (1991). D u m a s (1992) found several bacteria species from forest soil capable of inhibiting *A. gallica* Marxmüller and Romagn. rhizomorph growth in culture. There is little known, however, about an effect of fungi on *Armillaria* rhizomorph growth or the microfungi/*Armillaria* interactions. The only reports on the effect of soil/root fungi are these of M a ń k a (1953) and K w a ś n a and Ł a k o m y (1998). They reported that *MRAA* from spruce roots, and *Z. moelleri* from birch roots, might increase *A. ostoyae* rhizomorph formation *in vitro*. The stimulatory effect of *A. pullulans, Diplodia, Gliocephalis, Macrophoma* sp. and *Sordaria* on *Armillaria* rhizomorph production had been shown by P e n t l a n d (1965, 1967) and W a t a n a b e (1986). The majority of fungi tested by them, however, are not being usually found in the forest soil/root habitat in Poland (K w a ś n a unpubl.), and their effect on rhizomorph production cannot be taken into consideration in epidemiology of *Armillaria* disease.

This study has shown that there are several oak-root fungi that can stimulate *Armillaria* rhizomorph production. The stimulation of rhizomorph formation resulted in an increase of number of rhizomorphs, number of rhizomorph initials, rhizmororph length and dry weight.

The stimulation effect was statistically proven in case of *A. mellea*. The much smaller effect observed in *A. ostoyae* could be explained by duration of the experiment, which should have taken longer. It seems that both *A. ostoyae* isolates required longer than 16 weeks time for rhizomorph formation. In study of Ł a k o m y (1996) *A. ostoyae* produced rhizomorphs after 25 weeks, and in study of K w a ś n a and Ł a k o m y (1998) after 8 months of growth in oak segments. The inhibition of rhizomorph formation by certain strains of *A. ostoyae* was observed also in studies of G u i l l a u m i n and R y k o w s k i (1980), R i s h b e t h (1985 a, b) and S i e p m a n n (1985). The degree of stimulation of 'test' fungi varied among isolates of *Armillaria*.

The abundant network of rhizomorph produced in forest soil, sand, peat and humus substrate by *A. mellea*, but not by *A. ostoyae*, contrasts with results of R i s h b e t h (1985 a), who found that *A. mellea* produced much shorter rhizomorphs from woody inocula immersed for 2 years in soil, compared to *A. ostoyae*. The tree species used for the production of woody inocula were not described by R i s h b e t h (1985 a). Differences in abilities of *A. mellea* and *A. ostoyae* to form rhizomorphs might be due to (i) the experimental method used, and to (ii) the geographical origin and variation between *Armillaria* isolates. Pure and sterile sand used in experiment in first two months could have distinctly inhibited the rhizomorph formation (G a r r e t t 1956; R e d f e r n 1973; R y k o w s k i 1984), which was enhanced when samples were transferred into substrate rich in nutrients.

The stimulation of rhizomorph formation in oak sections *in vitro* could be caused by violatile and non-violatile metabolites secreted by 'test' fungi. This thesis is supported by findings of W a r g o and H a r r i n g t o n (1991) and K w a ś n a and Ł a k o m y (1998) who showed that *Armillaria* rhizomorph production may be stimulated by abundant volatiles produced by *Ceratocystis virescens* (Davids) C. Moreau, and tryptophol, which is a major secondary, non-volatile metabolite produced by *Z. moelleri*. A few 'test' fungi, e.g. *MRAA*, *P. janczewskii* and *P. spinulosum* have been shown to produce xylan- and cellulose-degrading enzymes (B ä ä t h and S ö d e r s t r ö m 1980; D o m s c h et al. 1980). These, through the degradation of wood, may additionally favour colonization of wood by *Armillaria*.

The biggest stimulation of *Armillaria* growth and rhizomorph formation in wood sections and on malt agar was noticed when the effects of dematiaceous hyphomycetes, e.g. *MRRA*, *P. dimorphospora* and *S. schenckii* were tested. Melanins occurring in cell walls of these fungi are known to bind a wide variety of compounds including heavy metals and organic compounds (L a r s s o n 1998; B u t l e r et al. 2001), and to inactivate antifungal agents in a habitat, what could make the *Armillaria* rhizomorph formation easier. This study introduces also a note of uncertainty to the idea that *Armillaria* may 'steal' precursors for melanin synthesis from accompanying fungi.

The type of interaction between *Armillaria* and a 'test' fungus in wood segment was only rarely related with similar type of interaction in two-culture test on agar medium. The majority of 'stimulants' of *Armillaria* rhizomorph formation in oak segments did not stimulate pathogen's growth on malt agar. They usually inhibited (through surrounding) *A. ostoyae* and the slower growing *A. mellea* 94 056 colonies on malt agar. Only dematiaceous hyphomycetes, e.g. *MRAA, P. dimorphospora* and *S. schenckii* caused usually the simultaneous increase of *Armillaria* colonies growth on malt agar, and rhizomorph formation on agar and in wood. In contrast, *G. candidum* entirely surrounded and inhibited *A. mellea* 94 056 growths on malt agar and reduced the formation of its rhizomorphs in wood. *Goetrichum candidum* did not also inhibit *A. mellea* 94 080 growths on malt agar what was related with a stimulation of fungus rhizomorph production in wood (Table 2, 3). This means that two-culture test may not always reflect the real interactions between fungi in wood *in vitro* and *in vivo*.

The study presents only the effect of 15 hyphomycetous fungal species. There are, however, thousands of fungal species in root/soil habitat, and it is presumed that microbial interactions are far more complex. There is no doubt, however, that the observation of rhizomorph reactions to different media, substrates and habitats, as well as connection of an extent of *Armillaria* infection with occurrence of the specific fungal communities (P r z e z b ó r s k i and K w a ś n a 1989) suggest the fact of rhizomorph stimulation by chemical or microbiological factors.

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Stymulacja wzrostu ryzomorf *Armillaria* przez grzyby z korzeni dębu

Streszczenie

Z drewna korzeni 50-letniego dębu szypułkowego (*Quercus robur*) wizolowano 31 gatunków mikrogrzybów. Najczęściej występowały *Mycelium radicis atrovirens alpha, Clonostachys* sp. i *Penicillium daleae. Beauveria bassiana, Clonostachys* sp., *Cryptosporiopsis radicicola, Geotrichum candidum, Mortierella vinacea, Mycelium radicis atrovirens alpha, P. daleae, P. janczewskii, P. spinulosum, Sporothrix schenckii* i *Tolypocladium niveum* stymulowały istotnie powstawanie i wzrost ryzomorf *Armillaria mellea* w drewnie dębowym *in vitro*. Największy efekt stymulujący obserwowano w testach z grzybami ciemnozabarwionymi: *MRAA, Phialocephala dimorphospora* i *Sporothrix schenckii*.