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Influence of elevated CO_2 concentrations on the growth of *Armillaria ostoyae* (Romagn.) Herink rhizomorphs *in vitro*

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Abstract. A comparative experiment was carried out in growth chambers to determine the effects of elevated CO_2 concentrations (either 760 ppm or 1,140 ppm) versus ambient CO_2 conditions on the growth of Armillaria ostoyae (Romagn.) Herink rhizomorphs, which is the infectious organ of a fungal pathogen affecting many forest trees. We found that one out of three isolates in the experiment differed significantly in rhizomorph production, which was measured as rhizomorph dry mass/100 days of growth. Rhizomorph production was also affected by the tree species used as a food source in the inoculum preparation, with beech wood being significantly different from oak and hazel. Under higher CO_2 regimes the production of rhizomorphs was consistently lower for all three isolates compared to ambient CO_2 concentrations. For one isolate (no. 11) the growth differences were significant between 380 ppm and both elevated CO_2 concentrations (760 ppm and 1,140 ppm), while for the other two (no. 30 and 32) significance was observed only between 380 ppm and 760 ppm. No statistically significant differences have been noted between 760 ppm and 1,140 ppm CO_2 for these two isolates. It was concluded that elevated concentrations of CO_2 inhibited A. ostoyae rhizomorph growth and therefore have the potential to lessen the pathogenicity of the fungus.

Keywords: Armillaria ostoyae, CO_2, rhizomorph growth

1. Introduction

Rhizomorphs are infectious organs of honey fungi, including the most destructive pathogen of this genus affecting most of forest tree species in Poland – *Armillaria ostoyae* (Romagn.) Herink. Next to the contacts of mycelium and spores with tree roots, rhizomorphs add up to propagation of the so-called 'white rot' root disease caused by honey fungi in forest stands (Żółciak 1999, 2005). For this reason, the morphology and functions of rhizomorphs, as well as rhizomorphogenesis, have long been the subject of numerous studies (Hartig 1873; Manka 1953; Jacques-Felix 1967, 1968; Redfern 1973; Rykowski 1984; Redfern, Filip 1991; Łakomy 2004; Guillaumin, Botton 2005; Guillaumin, Legrand 2005; Lung-Escarmant et al. 2005). Amongst other things, the influence of several substances, such as ethanol and other alcohols, growth substances (o-aminobenzoic acid, p-palminobenzoic acid, indole-3-acetic acid) (Pentland 1965, 1967; Garraway, Weinhold 1967, 1968 a, b; Garraway 1970; Sortkjaer, Allermann 1972a, b, c) and also inorganic nutrients (Morrison 1975, Rykowski 1984, Przybył 1998), on the formation and growth of rhizomorph has been studied. Furthermore, the effects of soil moisture and temperature on the rhizomorphogenesis have been demonstrated. Appropriate humidity conditions boost proper functioning of the apical meristem and thus stimulate the growth of rhizomorph (Rykowski 1984). The temperature affects not only the initiation and development but also the number and extent of branching of rhizomorph (Redfern 1973). The response of rhizomorphs to the presence of oxygen and carbon dioxide in the soil environment was also reported (Hintikka, Korhonen 1970; Hintikka 1974; Morrison 1976). According to Morrison (1976), rhizomorphs prefer the anaerobic environment and the direction of their growth in a given soil profile depends on fluctuations in oxygen and carbon dioxide pressure. Hintikka (1974) showed the stimulatory effect

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of CO_2 on the growth of rhizomorphs, which was explained by their expansion towards the roots that diffuse CO_2 into the soil. Olszyk et al. (2001) observed initial fungal colonies in forest soil and noted their enhanced formation and growth under the influence of elevated concentrations of atmospheric CO_2. The ability of wood-decay fungi, including honey fungi, to assimilate CO_2 was also experimentally demonstrated; however, the assimilation intensity was low: 1 g of the fungal tissue structure contained about 0.017 mg of assimilated carbon (Schinner, Concin 1981).

In the coming decades, the increase in atmospheric CO_2 (already observed in the past 200 years) will go on faster and faster to reach around 490–1,250 ppm at the end of this century – depending on the adopted variant of fossil fuel consumption and implemented models of economic development (Climate Change 2001). The study results concerning the effects of elevated CO_2 on the rhizomorphogenesis and rhizomorph production of *A. ostoyae*, as well as those regarding the infection potential of this fungus, have been hardly available. The results obtained by Lech and Żółciak (2006, 2017) have been published – however, these seem not explicit enough. The results of the first study (2006) showed the growth stimulation of rhizomorphs under elevated CO_2 concentration (750 ppm), but pine seedlings were not yet infected or killed by the fungus examined. The results of the second study (2017) showed that the increase in CO_2 concentration to 1,000 ppm slowed down the disease process, as well as the mortality of 2-year-old pine seedlings and 3-year-old spruce seedlings was decreased 16 months after artificial inoculation with *A. ostoyae*.

Not too many experimental studies have been so far devoted to the impacts of climate change on other fungal pathogens of forest trees. Those that have been undertaken were focused on the effect of increased concentrations of CO_2 on threat patterns in oak and beech populations due to *Phytophthora* species (Fleischman et al. 2010; Tkaczyk et al. 2014; Oszako et al. 2016), as well as those in poplar populations due to *Melampsora medusa* Thümen – the causal agent of poplar rust (Percy et al. 2002). Then again, the results obtained were inconclusive, as both the disease stimulation as well as no effects of elevated CO_2 on the course of the disease process were observed.

Scarcity of studies with regard to the impact of predicted climate change on forest fungal tree pathogens, as well as incompleteness and ambiguity of the results obtained, have been noted in subject literature reviews (Manning, von Tiedemann 1995; Chakraborty et al. 2000; Garrett et al. 2006). The authors emphasise that further research is the only way to fill knowledge gaps in this field. This argument was the reason behind undertaking the present study. The null hypothesis assumed that elevated CO_2 would have stimulating effect on the growth of *A. ostoyae* rhizomorphs.

2. Material and Methods

In order to verify the null hypothesis, the experiment was carried out under artificial, controlled environment. The development of *A. ostoyae* rhizomorphs was initiated using inoculum placed in glass cylindrical containers (opened at both ends). These were filled with medium-sized grains quartz sand and sterilised before the placement of the inoculum inside. The containers with inoculum were placed in the climatic chambers and exposed to the atmosphere with the following CO_2 concentrations for the next 6–7 months: 380 (control, nearly ambient CO_2), 760 and 1,140 ppm (2- and 3-fold of control CO_2 concentration, respectively). Other than that, the conditions for all the experimental variants were maintained the same for the duration of the experiment, that is, constant relative humidity (80%) and temperature (22ºC). In order to ensure the adequate moisture of inoculum substrate (sand), irrigation with deionised water was applied twice a week. The experiment was conducted with the use of the climatic chambers Mytron WB 750.

Three *A. ostoyae* isolates were used for inoculum production. The isolates were obtained from 3 different spruce stands, growing in the Forest Districts: Ujsoły located in the Żywiec Beskid Mts. and Wisła – in the Silesian Beskid Mts. The fungal material for research was collected and the species was classified based on the morphological features of fruiting bodies (Żółciak 1999) as well as pure cultures were identified by means of intersterility tests (Korhonen, 1978) . Beech, oak and hazel wood were used as food base for *A. ostoyae*. The inoculum was prepared consistent with the methodology by Rykowski (1984) and Redfern and Filip (1991). Tree branches, 5–7 cm long and 1.5–2 cm in diameter, were inoculated with *A. ostoyae* isolates, after washing and autoclaving for 40 minutes at 108°C under 0.05-MPa pressure and re-sterilizing on the next day (following the above procedure). The incubation lasted approximately 3 months.

The dry mass of rhizomorphs was determined using Sartorius analytic A200S balance (accurateness 0.0001 g) approximately 6–7 months after placing the containers with the inocula into the climatic chambers and was adopted as criterion of rhizomorph development. In order to perform the comparisons and statistical analyses, dry mass results were expressed per 100 days of rhizomorph growth. Owing to the large number of observations and rhizomorph brittleness, evaluations of other biometric parameters, such as the length or the number of active peaks, were neglected.

In total, the study comprised 177 observations. The number of observations ranged from 28 to 86 for individual main factors, and that for interactions ranged from 10 to 30 (Table 1). The experiment might be described with the following model:

$$SM = Isolate + CO_2 + Tree\ species\ used\ for\ inoculum\ production + interaction\ (Isolate \times CO_2)$$

Where:
SM is the rhizomorph dry mass per 100 days of growth,
Isolate is the *A. ostoyae* isolate used for artificial inoculation,
CO_2 is the CO_2 concentration tested,
Tree species used for inoculum production is the wood of a given tree species used as inoculum food base.

The results obtained were statistically analysed by means of analysis of variance ANOVA with the main effects: *A. ostoyae* isolate (No. 11, 30 and 32), CO_2 concentration (near-ambient, approximately 380 ppm; elevated, 760 and 1,140 ppm) and tree species used for inoculum production (beech, oak and hazel), as well as interaction effect (*A. ostoyae* isolate) × (CO_2 concentration). In order to meet ANOVA assumptions (normality of variable distribution and equality of variances for the tested variant combinations), data was subjected to logarithmic transformation. Tukey's highest significanf difference HSD test was used to compare the means obtained in experimental variants (rhizomorph dry mass/100 days of growth), taking into account adjustments due to different numbers of observations in the variants of the experiment. The analyses were carried out using Statgraphics Centurion XV software.

3. Results

Statistical characteristics of the results with respect to rhizomorph dry matter/100 days of growth are presented in Table 1. Out of the three pathogen isolates used in the experiment, the largest dry mass of rhizomorphs was produced by the isolate No. 11 (0.02186 g), whereas other two isolates (No. 30 and 32) showed clearly lower values for this parameter (0.01229 and 0.00909 g, respectively). The greatest dry weight values were observed in rhizomorphs growing under control (near-ambient) concentration of CO_2 (0.02923 g). At higher CO_2 concentrations (760 and 1,140 ppm), rhizomorph dry mass was lower (0.00549 and 0.00852 g, respectively). All three isolates showed the highest dry mass of rhizomorphs/100 days of growth under 380 ppm of CO_2. At higher CO_2 concentrations, rhizomorph dry mass values were lower, and the lowest dry mass values were observed in all the isolates growing under 760 ppm of CO_2. Under 380 ppm of CO_2, the isolate No. 11 showed the highest mean rhizomorph dry weight (0.05240 g), then the isolate No. 30 (0.02174 g; almost 2.5-fold lower as compared to No.11) and the isolate No. 32 (0.01355 g; nearly 4-fold lower as compared to No.11). Rhizomorphs growing under 760 ppm of CO_2 showed the highest mean dry mass value in the case of the isolate No.30 (0.00740 g), then No. 32 (0.00558 g; 50% of No. 30), whereas dry mass of the isolate No. 11 was the lowest (0.00349 g). In the case of the highest CO_2 concentration tested (1,140 ppm), the highest mean dry weight of rhizomorphs was observed in the isolate No. 11 (0.00968 g); it was lower in the isolate No. 32 (0.00815 g) and the lowest in the isolate No. 30 (0.00774 g) (Table 1).

ANOVA results are presented in Figures 1 and 2 and Table 2. The analysis showed statistically significant differences in the production of *A. ostoyae* rhizomorphs per 100 days of growth, for all three main effects: *Isolate*, *Tree species used for the production of inoculum* and CO_2, as well as in the case of interaction *Isolate* × CO_2 (Table 2). As shown by the results of Tukey's test, the isolate No. 11 as well as the rhizomorphs initiated from inoculum growing on beech wood showed significantly different means of rhizomorph dry weight. The growth of rhizomorphs significantly differed depending on the CO_2 concentration, reaching the highest values under 380 ppm of CO_2 and the lowest under 760 ppm of CO_2. The differences between dry mass values obtained for rhizomorphs of the isolates No. 30 and No. 32 were not statistically significant, as were the differences between the mean rhizomorph dry mass values observed when oak wood and hazel wood were used for inoculum production (Fig. 1).

With regard to the interaction *Isolate* × CO_2, Tukey's test showed the significance of differences between the means of rhizomorph dry mass/100 days of growth. For the isolate No. 11, these differences were significant between 380 ppm of CO_2 and both elevated concentrations (760 and 1,140 ppm), whereas for the isolates No. 30 and No. 32, the significant differences were observed only between 380 and 760 ppm. In the case of the isolates No. 11 and No. 30, no significant differences in rhizomorph dry mass were found between 760 and 1,140 ppm of CO_2, and in the case of isolate No. 32, no significant differences in rhizomorph dry mass were found between 380 and 1,140 ppm (Figure 2).

4. Discussion

The results of the study and statistical analyzes carried out did not confirm the null hypothesis. Elevated CO_2 concentrations (760 and 1,140 ppm) did not stimulate the growth of *A. ostoyae* rhizomorphs; on the contrary, rhizomorph growth was somewhat inhibited under these conditions. In all three pathogen isolates tested, the largest dry mass of rhizomorphs was recorded under near-ambient CO_2 concentration (380 ppm). For one isolate, the differences between ambient and both elevated CO_2 concentrations tested were statistically significant, and for the remaining two, the differences were significant between near-ambient CO_2 and one of the elevated CO_2 concentrations (760 ppm). These results correspond to those of the earlier study by Lech and Żółciak (2017), who showed the slowed-down course of the disease process as well as reduced mortality of pine and spruce seedlings

Table 1. Mean values of rhizomorphs dry mass per 100 days of growth and confidence limits for means for main effects (isolation of *A. ostoyae*, level of air CO_2 and tree species used for inoculum production) as well as for interaction: *isolate x level* CO_2

Sources of variation		Number of observations	Mean SM / 100 days [g]	95% confidence intervals for means	
				lower	upper
Experiment total		177	0.01441	0.01363	0.01988
Isolate no.	11	86	0.02186	0.01906	0.02465
	30	44	0.01229	0.00777	0.01681
	32	47	0.00909	0.00480	0.01338
CO_2 [ppm]	380	66	0.02923	0.02568	0.03277
	760	52	0.00549	0.00137	0.00961
	1140	59	0.00852	0.00473	0.01232
Tree species used for inoculum production	Bk	28	0.01449	0.00879	0.02019
	Db	74	0.01430	0.01122	0.01738
	Lesz	75	0.01445	0.01143	0.01746
Interaction (Isolate^x CO_2)	11^x380	30	0.05240	0.04767	0.05713
	11^x760	27	0.00349	-0.00150	0.00847
	11^x1140	29	0.00968	0.00487	0.01449
	30^x380	19	0.02174	0.01547	0.02800
	30^x760	10	0.00740	-0.00107	0.01587
	30^x1140	15	0.00774	0.00076	0.01471
	32^x380	17	0.01355	0.00695	0.02015
	32^x760	15	0.00558	-0.00141	0.01257
	32^x1140	15	0.00815	0.00117	0.01513

Table 2. Analysis of variance for rhizomorphs dry mass and adopted model of experiment. Statistically significant differences were marked with bold fonts.

Sources of variance	Sum of squares	Degree of freedom	Mean square	F	P
A: Isolate	46.51	2	23.25	15.19	**<0.001**
B: CO_2	134.42	2	67.21	43.90	**<0.001**
C: Tree species used for inoculum production	13.83	2	6.91	4.52	**0.012**
Interaction (AB)	23.26	4	5.81	3.80	**0.006**
Residuals	254.15	166	1.53		
Total	505.02	176			

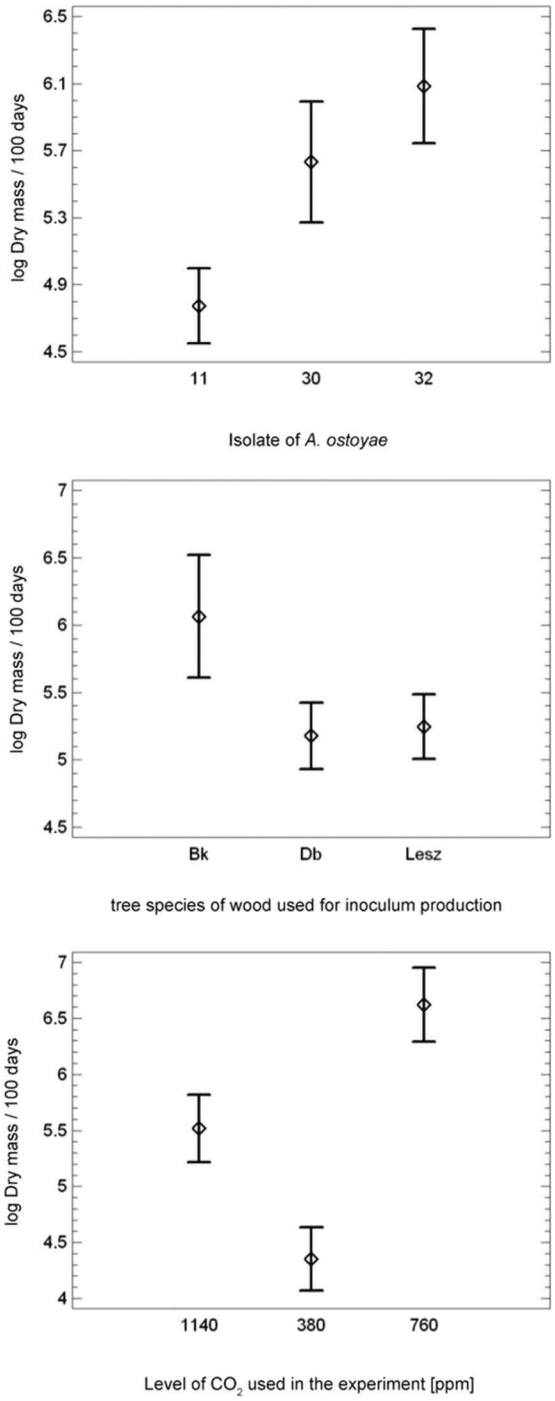

Figure 1. Means of rhizomorphs dry mass (after logarithmic transformation) and 95% confidence intervals for main effects of experiment: isolate of *A. ostoyae*, tree species of wood used for inoculum production and level of CO_2 used in the experiment

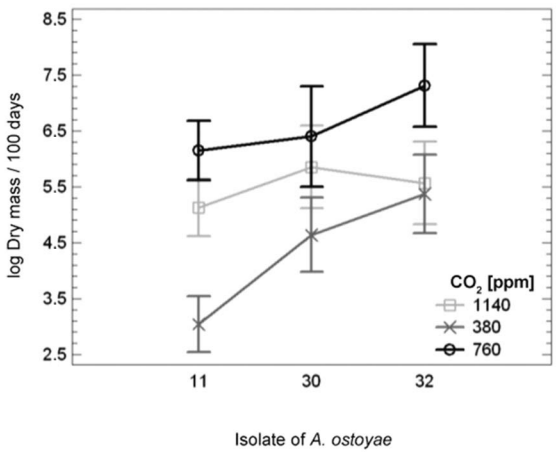

Figure 2. Means of rhizomorphs dry mass (after logarithmic transformation) and 95% confidence intervals for interaction: isolates of A. ostoyae (no. 11, 30 and 32) and level of CO_2 used in the experiment (380 ppm, 760 ppm and 1,140 ppm)

subjected to artificial inoculation with *A. ostoyae* and grown under elevated CO_2 (up to 1,000 ppm). In the latter study, as a possible explanation of lower seedling mortality, the compensatory hypothesis was presented (Herms, Mattson 1992), assuming the targeted allocation of increased plant resources to actively defend against stress factors. This does not exclude, however, that in addition to the compensatory effect of increased CO_2 concentration on plants, raised CO_2 concentrations also inhibit rhizomorph growth and thus reduce the infection potential of the pathogen. Both of these phenomena may, therefore, contribute to slowing down the course of the disease process and decreasing seedling dieback.

The results of the study are fundamentally different from the results of another earlier study by Lech and Żółciak (2006), which showed a greater production of rhizomorphs from inoculum placed in the containers with pine seedlings grown under 750 ppm of CO_2. Then, no contact rhizomorphs–tree roots and no infection of pine seedlings were observed; therefore, it was concluded that enhanced rhizomorph growth resulted from stimulating effect of raised CO_2 concentration. The ability of honey fungi to assimilate carbon dioxide (Schinner, Concin 1981) could support this explanation. At present, it seems that the reason behind rhizomorph growth enhancement could be higher air humidity in the climatic chambers with increased concentration of CO_2. During the previous study (Lech, Żółciak 2006), the examined seedlings were grown in Mytron WB 750 chambers, using the B-647 controller (MKS Instruments) and a special hermetic container to maintain the assumed, increased concentration of CO_2. The container was not equipped to regulate the relative humidity level, and this could have caused the increase/persistence of long-standing high moisture after watering the substrate, on which the seedlings were grown and *A. ostoyae* inoculum was

placed. The high moisture content of the substrate, as shown experimentally, is a factor favouring the growth of honey fungi rhizomorphs (Redfern 1973, Rykowski 1984).

5. Conclusions

The results of the study allow to draw the following conclusions:

• Raised CO_2 concentrations (760 and 1,140 ppm) inhibited the growth and development of *A. ostoyae* rhizomorphs initiated from inocula placed in quartz sand.

• The projected increase in CO_2 concentration in the atmosphere should not cause the future increase in the amount of *A. ostoyae* infectious material.

Conflict of interest

The authors declare the lack of potential conflicts.

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Authors' contribution

P.L. – research concept, literature review, methodology, measurements, preparation of test results, statistical analysis, manuscript writing/editing; AŻ. – collection/identification of fungal material in the field, preparation of inoculum, methodology, literature review, manuscript writing/editing.

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