Article

Biotic interactions between Collembola, soil-born pathogenic fungi, and plant growth

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Abstract: The activity of some soil organisms can significantly influence the growth of plants. One of the more common are Collembola, which play an important role in suppressing soil-borne pathogens such as *Fusarium* spp. Here, the species *Folsomia candida* was taken for laboratory studies. One of the main research hypotheses was to assess whether springtails influence the growth of wheat and pea plants by increasing the rate of decomposition and providing nutrients to plants. The purpose was also to assess whether Collembola will reduce the occurrence of fungal diseases, presumably by feeding on fungi. The factors tested were 1) wheat grown individually or in the mixture with pea 2) Collembola number; 3) the presence of the plant pathogenic fungus *Fusarium culmorum*. The experiment was carried out in 4 replicates for each treatment in 2 series. The soil used for the test was a mixture of field soil, sand, and peat. The following analyzes were performed: measuring of plant growth, decomposition rate, assessment of plant infection, assessment of *F. culmorum* in springtails bodies. The inoculation of the fungi was found to not disturb plant growth. However, the fungus was present in the root neck of plants incubated with the fungus. Collembola decreased the number of fungus colonies isolated from plants. The decomposition was accelerated by springtails. However, this was not linked with the improved plant growth. Additionally, *F. culmorum* was isolated from the bodies of Collembola, indicating its ability to feed on this fungus.

Keywords: springtails; *Folsomia candida;* wheat; pea; *Fusarium culmorum*; interactions

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1. Introduction

Collembola, as representatives of the mesofauna, are closely related to the soil environment [1]. Their activity in the soil indirectly affects plants. They are mediators of positive changes in soil structure and porosity and contribute to the decomposition of organic matter and an increase in the humus content. The soil mesofauna, by stimulating humification and mineralization, provide plants with nutrients, that is, potassium, sulphur, phosphorus, iron and, in particular nitrogen. Collembola could also alter water infiltration to lower levels of the soil profile and therefore increase the ability to penetrate the soil by the roots [2]. Springtails regulate the activity of microorganisms, including mycorrhizal fungi that live in symbiosis with plant roots. When feeding on fungal hyphae, they cause it to spread in soil layers and grow faster, ultimately dissolving more nutrients for the plant [3]. The feeding of mycorrhizal fungi can cause the growth of soil bacteria, which bind to atmospheric nitrogen and make it available to plants [4]. Therefore, the contribution of springtails is the decomposition process in rather indirect ways, by altering the microorganisms [5].

Many species of springtails feed on pathogenic forms of fungi, thus reducing plant disease infestation [6]. Comprehensive explanations of this topic have been compiled by Innocenti and Sabatini [7] review work. In the food preferences study, it was found that some Collembola species (*Onychiurus armatus*, *O. tuberculatus,* and *Folsomia candida*) effectively feed on plant pathogenic fungi [8]. In the pot experiment [9], it was found that plants

previously infected with *Fusarium culmorum* grown in the presence of springtails (*F. candida*) had a significantly lower disease rate, as well as higher biomass than plants grown in the absence of springtails. Some studies confirm that springtails feed on fungi in the environment. For example, in the work of Berg et al. [10] studies of enzyme activity showed the highest activity of enzymes responsible for digesting fungal hyphae in springtails bodies. On the other hand, using the isotope method, it was found that most Collembola species in the forest had different food preferences (they fed on plant and animal food) [11].

Fungal diseases are one of the major problems in agriculture. Currently, there are no effective biological methods that could limit them. Many groups of invertebrates, particularly Collembola, feed on fungi [12], but there is currently no practical possibility of use in reducing fungal diseases. The important pathogens, dangerous to many crops, are soilborne fungi such as *Phytophthora*, *Rhizoctonia,* or *Fusarium,* which produce spores, sclerotia, and mycelium, constituting primary inoculum in the surface soil layer. When considering these pathogens, the more abundant the pathogen population, the greater the risk of plant infection. Therefore, in such diseases, fungus feeding invertebrates such as Collembola could potentially decrease fungus populations [7]. The study of the food preferences of springtails has shown that they feed on hyphae and spores of pathogenic fungi. At the same time, it is known that the food preferences of most species are quite broad and they can eat different groups of fungi (e.g., mycorrhizal), as well as plant tissue or bacteria. In this pot experiment, our intention was to investigate the plant, fungus and Collembola interactions.

Our experiment is the development of the studies performed by Sabatini and Innocenti [6], Innocenti et al. [13] and Endlweber and Scheu [14]. In contrast to that work, we used a different method of assessment of plant infection and determined the presence of fungi in springtail bodies. It was hypothesized that a) plant growth will be inhibited by *Fusarium culmorum*, b) springtails improve plant growth by increasing the rate of decomposition and providing nutrients to plants, c) plants will have better growth in cultivation with legumes than in monoculture, and d) springtails will reduce the occurrence of fungal diseases, presumably by the feeding on fungus.

2. Materials and Methods

2.1. Experimental Design

The experiment was carried out in two series in June and September 2020. The following factors were tested:

1. Plant diversity: wheat, wheat and pea;
2. Collembola number per test vessel: 100 individuals, 50 individuals, 0 individuals;
3. The presence of the plant pathogenic fungus: present, absent;

To test the effect of the factors, 9 treatments were determined. The experiment was carried out in 4 replicates for each treatment (40 test vessels) in 2 series. The test vessels were 29 cm high, 9.5 cm x 9.5 cm wide, 11.5 cm in diameter, and a capacity of 2600 cm^3, each filled with 600 g of soil. There were drainage holes in the bottom of the container and the bottom of the container (about 5 cm) was covered with aluminium foil to ensure the darkening of the roots. The number of plants in the repeat was 6. That means that in treatments 2, 3, 7, 8, and 9 there were 6 winter wheat plants per test vessel and in treatments 2, 5, and 6 – 3 plants of winter wheat plants and 3 pea plants per test vessel (Table 1).

Table 1. Description of the treatments used in the experiment.

	Plant	Collembola	Fungus
1	Wheat	-	-
2	Wheat, Pea	-	-

3	Wheat	50	-
4	Wheat	100	-
5	Wheat, Pea	50	-
6	Wheat, Pea	100	-
7	Wheat	-	+
8	Wheat	50	+
9	Wheat	100	+

2.2. Soil Preparation

The soil used for the test was a mixture of field soil, sand, and peat in a ratio of 1: 1: 0.5. The physical-chemical parameters of the soil are shown in Table 2. The prepared mixture was characterized by a medium rich in organic matter with a high content of calcium and magnesium, slightly alkaline. The mixture was sieved and sterilized by autoclaving.

Table 2. Soil properties used in the experiment.

Parameter	Unit	Agricultural soil	A mixture of soil, sand, and peat
pH w H_2O		5,1	6,6
Salinity	g NaCl/dm^3	<0,2(n)	<0,2(n)
N-NO_3		<10(5)	<10(4)
P		17	19
K		30	14
Ca	mg/dm^3	109	429
Na		<6(4)	<6(5)
Mg		17	47
Chlorides		10	10
C- org	% dry mass	0,62	0,69
Organic matter		1,07	1,19

2.3. Organisms and Incubation

The test fungus species was *Fusarium culmorum* (Wm.G. Sm.) Sacc. PCR analysis with species-specific primers confirmed that the tested isolate belongs to the *F. culmorum* (Supplementary material 1). The analysis was performed in duplicate (P1 and P2). The positive control (PM) was the isolate Fc24 from the collection of UTP in Bydgoszcz, Poland.

Monoconidial cultures of *F. culmorum* were placed on potato dextrose agar (PDA) and incubated at 25°C and a photoperiod of 12 h. The inoculum was prepared by mixing 3 plates with *F. culmorum* colonies on a PCA medium with 100 ml of physiological saline. The density of the suspension of the propagules was counted using hemocytometer (and the desirable densities were obtained by diluting the stock with sterile water. 100 ml of final suspension containing 10^5 conidia/mL were added to the soil surface. To the remaining treatments 100 ml of water was added. This volume of liquid was needed to obtain 50% WHC of the test soil.

The winter wheat variety (*Triticum aestivum* L.) was Natula, while the pea variety (*Pisum sativum* L.) – Cysterski. The seeds were sterilized in 10% sodium hypochlorite and rinsed with distilled water. Seed germination and early plant development were performed in Petri dishes on moist cotton. In total, 12 seeds were placed on each Petri dish (7 cm diagonal) in combinations corresponding to the experimental design. After 15 days, the winter wheat plants had the development stage (BBCH) 12 (leaf development) and pea 2 (shoots development). Then the additional plants were eliminated (there should be

6 in one replication). The cotton plants were placed on the surface of the soil in the test vessels.

The Collembola species used for the test was the soil-dwelling parthenogenetic *Folsomia candida* Willem, which is recommended as a model organism. The Collembola were derived from the culture of Wrocław University of Environmental and Life Sciences. They were bred on the plaster of paris and charcoal. For the test, 12-day organisms were used. The number of Collembola per one test vessel (100 or 50) corresponds to the number of 10,000 r 5000 individuals per m^2, which means it is possible to see Collembola in agricultural fields. *F. candida* is able to reproduce after 2-4 weeks from hatching [15]. Therefore, at the end of the test, there should be juveniles and adults in the test vessels.

The first step of incubation was the watering of the soil in the test vessels with inoculum or water. After 3 days, the plants and Collembola were added to the test vessels in combinations and numbers according to the experimental scheme. The incubation period was 28 days. The test vessels were placed in a randomized block design in a phytotron room at 25°C±2°C under a 12 day/night photoperiod. The plants in the test vessels were watered every two days according to the water loss expressed by weight. Both series of experiments were carried out under the same conditions, including soil, inoculum volume, plant development phases, and springtails age, as well as light and temperature conditions. Collembola were not fed during the experiment.

2.3. Analyzes After Incubation

Plants. At the end of the experiment, the plants were harvested and the above and below-ground parts were measured. The stage of wheat development was in the BBCH faze 28-29 (end of tilling) and the stage of development of the pea was 6 (flowering).

Decomposition rate. The activity of the organisms was determined by measuring the decomposition rate. For this, the litter bags method [16] was used. Organza bags of sizes 3 × 5 cm in diameter were used, allowing access to soil organisms. The bags were filled with 0.9 g of dry plant biomass, which was the mixture of parent grasses (*Festuca rubra* L., *Lolium perenne* L., *Poa pratensis* L., *Festuca ovina* L., *Festuca arundinacea* Schreb., *Agrostis capillaris* L.). A bag was placed in the surface soil layer at each test vessel at the beginning of the experiment and incubated for 28 days. After the incubation period, the plant biomass was separated from soil residues, dried, and weighed. The decomposition rate was determined according to the formula [17]: $Ln(X_0/X_t) = k_t$, where X_0 – initial biomass, X_t – weight loss in time t; t – incubation time. The decomposition rate was measured only in the second series of the experiment.

Evaluation of plant infection. The evaluation of plant infection was determined immediately after the removal of the plants from the soil. For this, the plant root necks were used, which are the most target plant parts. Fragments of the root necks were washed out in distilled water and inoculated on a PCA medium. Six plates were made in each combination and eight plant fragments were placed on one plate. After one week of incubation, the number of *Fusarium culmorum* colonies in each dish was evaluated. The species was identified under the microscope based on morphological features [18] (Supplementary material 2).

Assessment of Fusarium culmorum in springtails bodies. After the incubation period, Collembola were extracted from the soil in certain soil vessels using the Tullgren funnels. The extraction period was 48 h and the Collembola was kept in distilled water. Springtails were sterilized in 100% ethyl alcohol and transferred to PDA plates in a set of 6 plates of each combination. On each plate, springtails were placed in 6 groups of several individuals. After one week of incubation, the number and size of *F. culmorum* and other fungi were assessed on each plate. The photographic documentation is attached in Supplementary material 3. There was also a series of plates with springtails, which were sterilized to isolate the fungi on the skin of the springtails. However, the results were difficult to analyze due to contamination with other microorganisms. We established that Collembola can transfer fungi hyphae to their skin, as was observed under a microscope.

2.4. Data Analysis

The results obtained were compared using the mixed model (*proc mixed*) at the significance level of p=0.05. In the case of two series of experiences, the series was a repeated factor. Furthermore, the HSD Tukey test was performed to indicate significant differences. Analyzes were performed in Microsoft Excel and SAS University Edition. The link between experimental factors and the dependent variables was determined using constructed analysis with linear method (RDA) in Canoco software version 5.0. The significance of the axes was analysed using the permutation test.

3. Results

3.1. Effect on Plant Growth Parameters and Number of Fungal Colonies

Plant growth. We evaluated the effects of three factors that could affect plant growth: the number of plant species (1 – wheat or 2 - wheat and pea), the number of Collembola (0, 50, or 100 individuals), and the presence of fungus (2 variants). It was found that a number of plant species significantly affected both the plant height and the number of shoots (p=0.01, p=0.02, respectively). The plants were significantly higher when grown in monoculture than in coordinated cultivation with pea (Table 3; Figure 1). Similarly, significantly more shoots developed in plants grown in wheat grown in monoculture. The other factors (Collembola and fungus) had no significant effect on plant growth. This means that inoculation with pathogenic fungi did not disturb plant development.

Table 3. The height of the plant and number of shoots to the number of plant species (two variants), the number of individuals from Collembola (3 variants), and the presence of *Fusarium* (2 variants) (mixed model).

Effect	Plant height			Number of shoots		
	DF	F	*p*	Df	F	*p*
Number of plant species	1	6.12	0.01	1	5.47	0.02
Number of Collembola	2	0.23	0.80	2	0.13	0.88
Presence of fungus	1	0.01	0.90	1	2.48	0.12

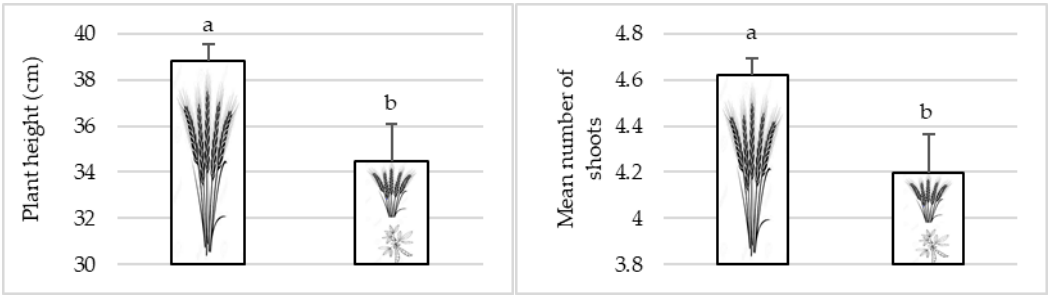

Figure 1. Plant height, and the mean number of shoots of winter wheat grown individually and in the mixture with p.ea

Fungus infection. The number of *Fusarium* colonies was significantly affected both by the presence of *Fusarium* and by the number of Collembola (p=0.0001, p=0.02) (Table 4). The number of fungus colonies was significantly higher in the test vessels, where the fungus was inoculated, confirming effective fungus infection in the tissues of plants (Figure 2). It was also found that fungus could accidentally occur in test vessels without fungus inoculation. Taking into account the effect of the number of Collembola, it was found that the mean number of fungus colonies was significantly lower in the pots incubated with Collembola (both 50 and 100 individuals) compared to the test vessels without Collembola

(Figure 2). This result could indicate that Collembola could effectively decrease the development of the fungus in the soil and therefore inhibit the plant infection.

Table 4. A number of *Fusarium* colonies to the number of Collembola (3 variants) and the presence of *Fusarium* (2 variants) (*proc mixed*).

Effect	DF	F	*p*
Number of Collembola	2	4.28	0.02
Presence of fungus	1	18.49	0.0001

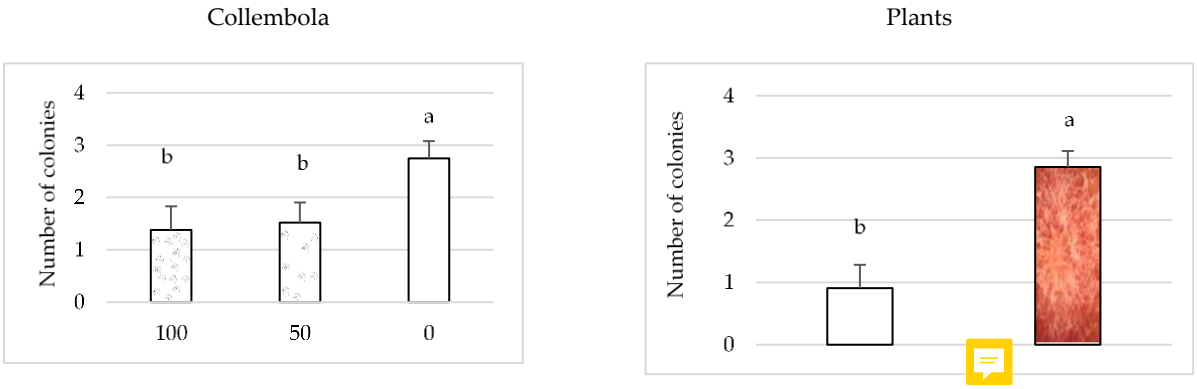

Figure 2. A number of *Fusarium* colonies isolated from plants in three variants of Collembola number (100, 50, and 0 individuals) (proc mixed). The different lowercase letters indicate significant differences between treatments, $p \leq 0.05$.

3.1. Collembolan Feeding on Fungus and Decomposition Rates

Fungus colonies isolated from Collembola. The presence in the body of springtails was presented as the mean number of colonies from each treatment (Figure 3). The number of colonies was significantly higher in test vessels incubated with fungi, than to control (treatments without the presence of fungus) (p=0.002). This could indicate that Collembola can feed on this fungus species.

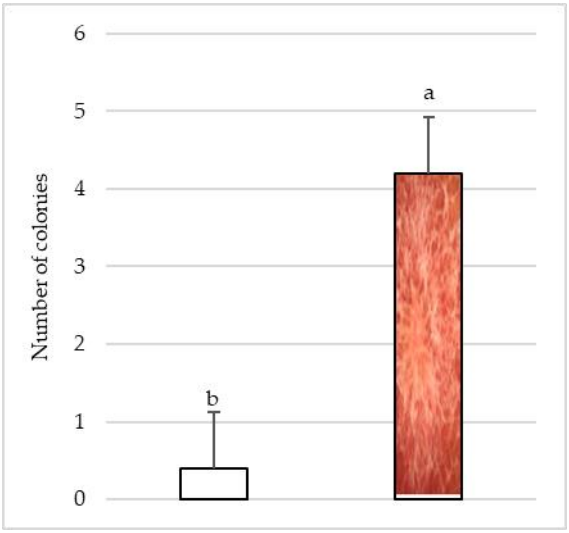

Figure 3. A number of *Fusarium* colonies isolated from Collembola in pots incubated with and without the fungus.

The different lowercase letters indicate significant differences between treatments, $p \leq 0.05$.

Decomposition. The decomposition process was significantly affected by the abundance (p=0.007) (Table 5; Figure 4). The decomposition rate was significantly higher in the moderate number of Collembola (50 individuals) compared to the test vessels without Collembola. We can suppose that the decomposition was mainly the effect of Collembola (due to the absence of other organisms in sterilised soil). Therefore, in this case, the decomposition rate is also the measure of Collembola feeding activity.

Table 5. Decomposition rate concerning the number of plant species (two variants), the number of Collembola individuals (3 variants), and the present fungus (2 variants) (mixed model).

Effect	DF	F	p
Number of plant species	2	0.2	0.82
Number of Collembola	2	6.44	0.007
Presence of fungus	1	0.82	0.37

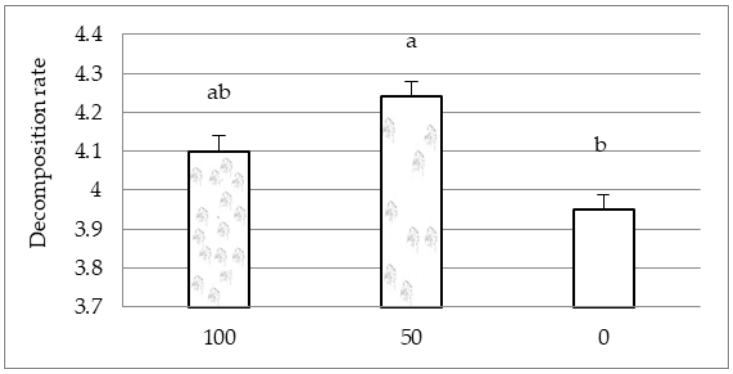

Figure 4. The decomposition rate in three variants of Collembola number (100, 50, and 0 individuals).The different lowercase letters indicate significant differences between treatments, $p \leq 0.05$.

3.1. Link Between the Plant Growth Parameters, Decomposition Rate, and Number of Fungus Colonies

The traits values – dependent variables (decomposition rate, plant height, stem number, and number of *Fusarium* colonies) are correlated with experimental factors (number of plant species, inoculated/not inoculated with *Fusarium*, number of Collembola) (Figure 5). The eigenvalues of the first two canonical axes are 0.40 and 0.11, respectively (Supplementary material 4). The total variance explained by the two axes is 51.61 % (p=0.002). The most significant effects on the graph are 1. The decrease in the height of the plant and stem number in the treatment with two plants and 2. The higher number of *Fusarium* colonies in treatments inoculated with the fungus.

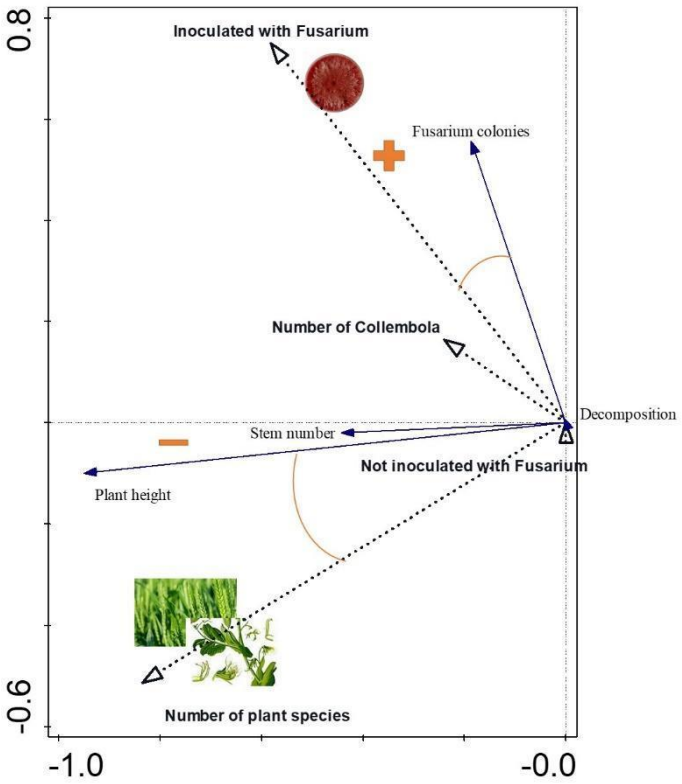

Figure 5. RDA biplot representing the dependent variables correlated with the experimental factors.
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3. Discussion

The main findings of this work are:

1. The inoculation with fungi did not disturb plant growth. However, the fungus was present in the root neck of plants incubated with the fungus.
2. Collembola decreased the number of fungus colonies isolated from plants.
3. The decomposition was accelerated by Collembola. However, this was not linked with the improved plant growth.
4. *Fusarium culmorum* was isolated from the bodies of Collembola, indicating the ability to feed on this fungus.

On this basis, it can be assumed that Collembola that occur in large numbers may limit the height of plants, which does not confirm the assumed hypothesis. Perhaps when springtails are too abundant, they begin to feed on plant tissue, limiting its growth. However, it should be noted that 100 springtails per volume of soil in an experimental container corresponds to the average number of springtails in agricultural soils. A similar trend was found by Harris and Boerner [19]. The experiment carried out by these authors with the use of geranium (*Geranium robertianum* L.) showed that the total and aboveground growth of this plant was greater with a low abundance of *Folsomia candida* than with or without higher abundance. Therefore, they found that plant growth could be stimulated with low Collembola abundance and inhibited with high.

The average number of spreads of winter wheat was the highest in wheat grown without springtails and the lowest in wheat grown with peas and springtails. These results show a similar trend to plant height. In a study by Endlweber [20], in two weed species (*Cirsium arvense* and *Epilobium adnatum*), the presence of springtails (*Protaphorura fimata*) changed the morphology of the roots (their elongation and branching), but had no effect on their biomass. In the own research, no root tissue was observed, but it would be an interesting aspect for future experiments. When comparing the height of the wheat in two treatments, with and without peas, it is found that the wheat reaches higher height

when grown separately. This may be due to the strong competition between the peas and the other plant. Pea has a strongly developed root system, which dominates the root system of wheat, which has it the least developed of all cereals [21]. Peas could effectively take up nutrients, an additional advantage is the ability to fix atmospheric nitrogen by legumes [22]. Similar results were obtained by Endlweber and Scheu [14], examining the influence of springtails on grasses and legumes. His experience has also shown that Collembola increases the competitive power of legumes against grasses. Also, research by Endlweber [20] showed interspecific competition in the case of breeding two species of weeds in one treatment, which was manifested by weaker growth.

In studies of other authors [23–25], the activity of soil fauna was positively correlated with greater plant biodiversity. In the case of the own research, it was found that the decomposition processes took place more effectively when the plants were grown separately. The presence or absence of a legume plant did not affect the decomposition processes. A large number of springtails (100 individuals per container) inhibited the decomposition processes, while these processes were most effective in a moderate number (50) of springtails. However, these results were not statistically significant. Perhaps the impact of springtails on decomposition would be more pronounced with longer incubation times (28 days in our experiment). In other mesocosm studies [26], it was shown that the presence of springtails has a positive effect on the decomposition rate, especially in the case of increasing their species diversity. The decomposition rate may be influenced by many factors, such as the quantity and quality of biomass or the mesh size in litter bags [1,27).

Supplementary Materials: material 1: The results of PCR analysis; Supplementary material 2: Fungus colonies isolated from plants in series 2; Supplementary material 3: Fungus colonies isolated from Collembola in series 2; Supplementary material 4: Summary of RDA analysis.

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