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BB: research idea, writing the manuscript; GB: field work, laboratory work, analyses; IN: laboratory work; AR: molecular analyses; DF: design of the molecular analyses, molecular data analysis, writing the manuscript

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ORIGINAL RESEARCH PAPER

What influences the composition of fungi in wheat grains?

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Abstract
Wheat grains are inhabited by different fungi, including plant pathogens and fungi – mycotoxin producers. The composition of seed mycobiota can be influenced by different factors, including agronomic practices, but the results are still contradictory. The aim of this study was to evaluate the mycobiota of wheat grains depending on agroecological conditions. Wheat grains were obtained from a two-factorial field trial: A – tillage system (A1 – ploughing at a depth of 22–24 cm; A2 – harrowing at a depth of up to 10 cm); B – crop rotation (B1 – continuous wheat; B2 – oilseed rape and wheat; B3 – crop rotation). The mycobiota of grain were determined by mycological and molecular methods. The most abundant and widespread of the mycobiota were *Pyrenophora tritici-repentis*, *Alternaria* spp., *Arthrinium* spp., and *Fusarium avenaceum*. Higher amounts of precipitation increased the infection of grains with *Fusarium* fungi. Seven species of *Fusarium* were identified in the grain samples: *F. avenaceum*, *F. poae*, *F. graminearum*, *F. culmorum*, *F. acuminatum*, *F. sporotrichioides*, and *F. tricinctum*. The soil tillage method and crop rotation did not influence the total incidence of *Fusarium* spp., but the abundance of a particular species differed depending on agronomic practice. The research suggests that continuous wheat sowing under conditions of reduced soil tillage can increase the level of risk of grain infection with *F. graminearum* and, consequently, the accumulation of mycotoxins.

Keywords
Fusarium; *Gibberella*; *Microdochium*; soil tillage; crop rotation

Introduction

Wheat is one of the most important and economically beneficial crops in Latvia. Consequently, investigations of the risk factors that can influence wheat production have become increasingly crucial for the economy of the country. Wheat grains are inhabited by different fungi, yet the role of many of them in the development and health of wheat plants is not clear [1]. Numerous fungi colonize different parts of the wheat plant, including the ears and grains, without causing any disease [2]. However, seed mycobiota can significantly influence the cultivation of wheat. Many wheat pathogens (*Pyrenophora tritici-repentis*, *Parastagonospora nodorum*, etc.) survive in the grains. The most serious problem is grain contamination by the causal agents of wheat head blight, mainly fungi from the *Fusarium*/*Gibberella* genera. The taxonomy of the *Fusarium* genus has drastically changed during recent years, and no unified view has so far been reached. Part of the species has been recognized as *Gibberella* because of its ability to produce ascospores, but the other part still bears the name *Fusarium*. There are different opinions about the correct solution for this issue [3]. In this study, the name *Fusarium* is used for the purpose of simplicity.

The composition of wheat grain mycobiota can be influenced by different factors, including agronomic practices and meteorological conditions, for example, high amounts of precipitation promote infection by *Fusarium*. The results obtained regarding the impact of agronomic practices are still contradictory. In general, the level of infection of *Fusarium* head blight depends on relationships between soil tillage, crop rotation, and meteorological conditions. Crop rotation has been recognized as the most important tool for reducing *Fusarium* head blight. Research findings indicate that by not rotating wheat every year, increases the severity of the disease, which is caused by *Fusarium* spp. and *Microdochium* spp., regardless of the tillage practice [4]. On the other hand, investigations have confirmed that the frequency of the isolation of *Fusarium* spp., particularly *F. graminearum*, depends significantly more on the year rather than on sites within a year. This points to the importance of annual meteorological conditions [4]. Parikka and colleagues [5] suggested that although future climate changes may increase the total pathogenicity of *Fusarium* spp., the species composition will likely depend on different weather scenarios. For example, greater amounts of precipitation and higher temperatures may increase the occurrence of *F. graminearum*, whereas rainfall near the beginning of harvest may promote the development of *F. avenaceum*. Different species of fungi, including *Fusarium* spp., have different levels of pathogenicity, fungicide sensitivity, and toxicity. A detailed knowledge about the spectrum of pathogens and the mycobiota in general are therefore necessary to understand the circumstances affecting the infection of the wheat crop.

The aim of this investigation was to evaluate the mycobiota of wheat grain depending on agro-ecological conditions.

Material and methods

Wheat grains were obtained at the beginning of fall 2008 from a two-factorial field trial carried out at the Peterlauki study and research farm of the Latvia University of Agriculture. Winter wheat variety 'Zentos' was used in this trial. The following factors were studied: A – tillage system (A1 – ploughing at a depth of 22–24 cm; A2 – harrowing at a depth of up to 10 cm); B – crop rotation (B1 – continuous wheat; B2 – oilseed rape and wheat; B3 – crop rotation). Data obtained between 2012–2016 were analyzed in the present study.

Symptoms of ear scab (caused by *Fusarium* spp.) or other wheat ear diseases were not observed during the investigation period. After harvest, grains were collected and dried and a composite 500-g sample was taken from each plot. Afterwards, 100 visually healthy grains were randomly chosen from each sample for mycological analyses. Grains were sterilized with 1% sodium hypochlorite for 3 min, rinsed three times in sterile distilled water, and placed onto potato dextrose agar (PDA), which was enriched with streptomycin (100 ppm L^{-1}) and penicillin (100 ppm L^{-1}) to avoid bacterial infection. Plates were incubated at +20°C in darkness for 7 days. The isolates obtained were divided into morphologically similar groups (color and texture of mycelium, pigmentation of medium, and morphological characteristics of the spores), and the samples from each group were prepared for molecular genetic analyses.

The identification of fungal isolates at the genus level was performed through the isolation of genomic DNA from ~10 μg of fungal material, sequencing of the ribosomal internal transcribed spacer (ITS) region of the RNA gene, and subsequent BLAST analysis of acquired sequences against the National Center for Biotechnology Information (NCBI) nucleotide database. The identification of *Fusarium* spp. fungal isolates at the species level was performed through a similar "sequencing–BLAST analysis" approach; only in this case, was sequencing of the transcription elongation factor (TEF) region carried out.

The DNA extraction was performed by the homogenization of fungal samples for 2×60 s using the FastPrep-24 (MP Biomedicals, USA) instrument in combination with Lysing Matrix D (MP Biomedicals, USA), the treatment of the acquired lysate supernatant phase with phenol and chloroform, and purification with the NucleoMag 96 Plant kit (Macherey-Nagel, Germany).

Amplification of the ITS and TEF regions by polymerasechain reaction (PCR) was carried out using Phire Plant Direct PCR Master Mix (Thermo Fisher Scientific, USA) supplemented with 0.3 μM of ITS4 (5′-TCCTCCGCTTATTGATATGC-3′) and ITS5 (5′-GGAAGTAAAAGTCGTAACAAGG-3′) primers [6] or 0.3 μM of EF1T-Fw (5′-ATGGGTAAGGAGGACAAGAC-3′) and EF2T-Rs (5′-GGAAGTACCAGTGATCATGTT-3′) [7], respectively, and 1 μL of fungal DNA. The thermal conditions within the GeneAmp PCR System 9700 (Applied Biosystems, USA) were as follows: initial denaturation at 98°C – 5 min, followed by 40 cycles of 98°C – 5 s, 52°C (ITS) / 55°C (TEF) – 5 s, and 72°C – 20 s, and concluding with final elongation at 72°C – 1 min.

The success of the amplification was verified through the inspection of PCR products by agarose gel electrophoresis.

Positive reaction mixtures underwent enzymatic treatment by Exonuclease I (0.5 μL) (Thermo Fisher Scientific, USA) and Shrimp Alkaline Phosphatase (2 μL) (Thermo Fisher Scientific, USA) (incubated for 40 min at 37°C and inactivated at 95°C for 20 min) to remove the excess dNTPs and primers. Further, 1 μL of cleaned fragment solution was transferred to a BigDye Terminator v3.1 Cycle Sequencing reaction mixture, which was prepared according to the manufacturer's instructions (Applied Biosystems, USA). Both DNA strands of each PCR product were sequenced using ITS4 and ITS5 or EF1T-Fw and EF2T-Rs as primers, and sequencing products were analyzed on a 3130xl Genetic Analyzer (Applied Biosystems, USA).

The relative density and incidence of fungi genera/species was calculated. Relative density shows the percentage of a particular species/genera out of all the isolates obtained, whereas incidence demonstrates the percentage of the isolates of each species/genera in 100 grains [8].

The importance of the relationship among different factors was demonstrated as reduction in the incidence of *F. graminearum* expressed in relation to the worst case scenario, i.e., harrowing at a depth of up to 10 cm and sowing continuous wheat = 100% [9].

For the statistical analyses of the incidence of fungi, a three-way analysis of variance (ANOVA) was performed, including crop rotation, soil tillage, and year. Pairwise comparisons between factor levels were done using the Bonferroni test; the level of significance was set at $\alpha = 0.05$.

The meteorological data were collected from a meteorological station located close to the trial site, and the amounts of precipitation as well as average temperatures were calculated in accordance with wheat development stages. The average temperatures from wheat heading until ripening were similar in all years under investigation (17–19°C). The observed differences were not essential for infection with *Fusarium* spp.; however, the amount of precipitation varied significantly (Fig. 4).

Results

Altogether, 60 wheat grain samples, 12 from each year during the period of investigation 2012–2016, were analyzed. In total, 3567 fungal isolates were obtained and identified at the genus or species level, and 21 genera/species were found.

The occurrence of different fungi was characterized by the relative density (RD) indicator. Fungi from different ecological groups were found in the wheat grains. The most abundant and widespread (RD > 10%) of these were: *Pyrenophora tritici-repentis*, *Alternaria* spp., *Arthrinium* spp., and *F. avenaceum*. The majority of isolates, which belonged to the *Fusarium*/*Gibberella* complex or to *Microdochium nivale*/*majus*, were included in the group of moderate occurrence (RD = 2.55–9.28%); the rest of the fungi were found only in some cases (Fig. 1).

The causal agents of wheat leaf and ear diseases (*P. tritici-repentis*, *P. nodorum*, and *Bipolaris sorokiniana*) were isolated in 21.31% of cases, while *Alternaria* spp. together with *Cladosporium* spp. were isolated in 15.84% of cases, of which only 0.53% were *Cladosporium* spp.

Many isolates belonged to pathogens – the causal agents of wheat head blight. The RD of *Fusarium* spp. was 30.42%, whilst that of *M. nivale*/*majus* was 8.41%.

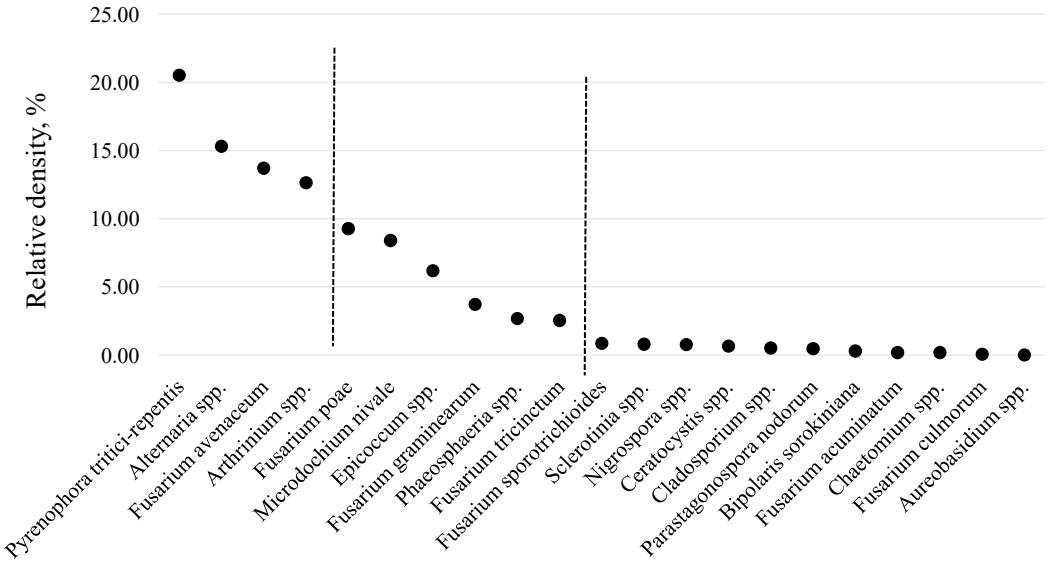

Fig. 1 Relative density of different fungi in wheat grains.

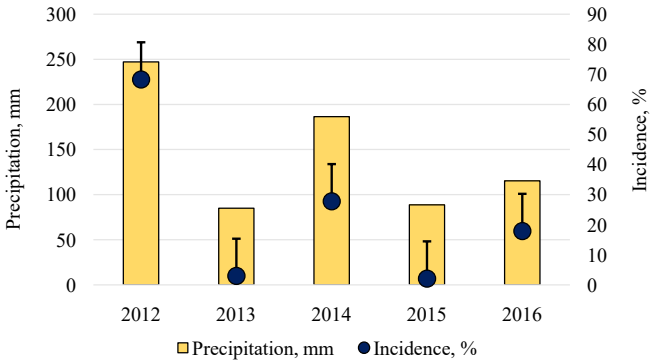

Fig. 2 Incidence of *Fusarium* spp. depending on the amount of precipitation from heading until ripening.

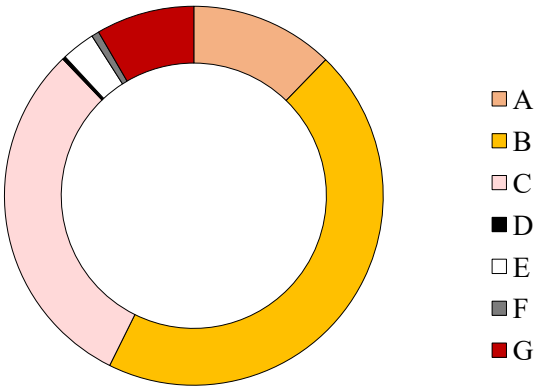

Fig. 3 Spectrum of *Fusarium* species: A – *F. graminearum*; B – *F. avenaceum*; C – *F. poae*; D – *F. culmorum*; E – *F. sporotrichioides*; F – *F. acuminatum*; G – *F. tricinctum*.

The meteorological conditions each year significantly influenced the incidence of grain infected with *Fusarium* spp. ($p < 0.0001$) (Fig. 2). The highest incidence (the number of species isolated from 100 wheat grains) of fungi belonging to the genus *Fusarium* were observed in years with greatest amounts of precipitation during heading until ripening.

Seven species of *Fusarium* were identified in the grain samples. *Fusarium avenaceum* was the most dominant species – 45.1% of all *Fusarium* isolates belonged to this species. The occurrence of *F. poae* was also high, whereas *F. graminearum* was determined in 12.3% of cases; *F. culmorum* and *F. acuminatum* were found only occasionally (Fig. 3).

The method of soil tillage and crop rotation did not influence the total incidence of *Fusarium* spp., but the level of a particular species differed depending on the agronomic practice. The average incidence of *F. graminearum* during the whole investigation period was only 2%, although this species was only found in 2012, 2015, and 2016. Ploughing slightly decreased the incidence of *F. graminearum*; likewise, crop rotation also affected the spread of this species. However, these differences were not statistically significant. The relative incidence data demonstrated the efficacy of combined agronomic practices; reduced soil tillage and continuous wheat sowing were the worst case, whereas ploughing and crop rotation were the best (Fig. 4).

The average incidence of *F. avenaceum* was 8%. This species was dominant in 2012 and 2014 but in other years, only some isolates were detected. Although statistically significant differences were not detected, crop rotation decreased the level of *F. avenaceum*; in contrast, in the ploughed plots, it increased the incidence of the pathogen. In addition,

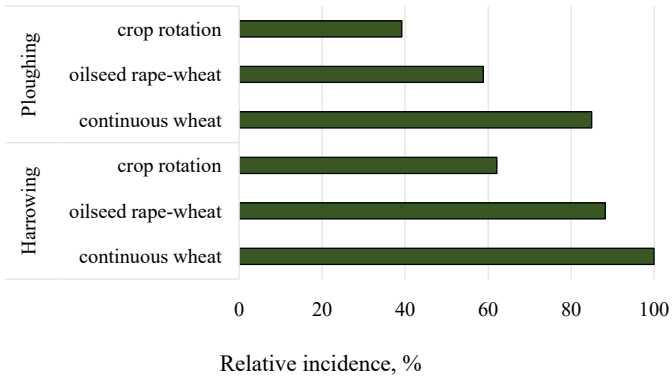

Fig. 4 Effect of soil tillage and crop rotation on the relative incidence of *Fusarium graminearum*. Reduction is expressed in relation to the worst case, i.e., continuous wheat sowing, harrowing up to a depth of 10 cm (average in 2012, 2014, and 2016).

F. poae was a widespread pathogen; its average incidence was 5.5%. Crop rotation did not affect the incidence of *F. poae* but ploughing slightly increased the level of this species.

Other species were detected only occasionally, and the number of isolates was too small to evaluate the factors influencing the incidence of any particular species.

Discussion

During the 5 years of investigation, fungi from different ecological groups – 21 genera/species altogether – were identified in the wheat grains. *Pyrenophora tritici-repentis* was frequently isolated, which was to be expected because this fungus is the causal agent of one of the most important wheat diseases in Latvia and Lithuania [10].

The occurrence of *Alternaria* spp. reached 78%, which is similar to the results reported in different regions by many researchers [2,11–14]. The fungi from the genus *Alternaria* are common members of the mycobiota of wheat grain, but the importance of this fungal group depends on various conditions and the species of pathogens. Polish researchers [15] have determined a similar level of grain infection with *Alternaria* and *Cladosporium*, but the results of our investigations were completely different; the occurrence of *Cladosporium* spp. was only 15%.

Arthrinium spp. were found in almost all samples of wheat grain during the research period, which is contrary to other findings in which this fungus was isolated only in some cases [16,17]. In Canada, however, a high occurrence of *Arthrinium* spp. has been reported [18], which concurs with the findings of Abdullah and Atroshi [19], who described this fungus as a common species in wheat grain. Up until now, the role of *Arthrinium* spp. in the wheat cropping system has been unclear. Vujanovic and colleagues [2] reported that this fungus was atypical for wheat. Other researchers have described *Arthrinium* spp. as weak pathogens that cause seedling blight in wheat [20]. More detailed investigations are necessary to understand the relationships between wheat and fungi from the genus *Arthrinium*.

Epicoccum spp. are common saprotrophs on wheat grains. Large numbers of these fungi (occurrence 50%) were detected in the present study, which agrees with several other findings in the literature [2,21].

Microdochium nivale/*majus* are described as important causal agents of wheat head blight throughout the world, especially in Europe [22]. It has been reported that these fungi have occurred in >90% of grain samples in Denmark over the years [23]. Previously, only *M. nivale* was recognized as a wheat pathogen, but the latest findings have also revealed the pathogenicity of *M. majus* [24]. The occurrence of both fungi was also high in our investigation, reaching on average 40% in the 5 years. These data permit the hypothesis that *M. nivale*/*majus* have become more important in recent years.

The present research suggests that *Fusarium* spp. constitute the most important group of fungi isolated from wheat grain; more than 50% of the grain samples were infected with *Fusarium* spp. It is essential to emphasize that the fungi were isolated from visually healthy ears and grains. *Fusarium* infection can occur without any visible symptoms, which is the reason why further investigations of grain infections are so important. Seven species of *Fusarium*/*Gibberella* were identified by sequencing the TEF region and subsequent BLAST analysis of acquired sequences against the NCBI nucleotide database.

The spectrum of *Fusarium* species depends on the wheat growing region, the year, the agronomic practice, the site of a trial, and other circumstances. However, all researchers cited in this paper have stressed the importance of precipitation during wheat flowering and ripening in so far as it promotes the spread of infection. Our investigations clearly confirmed this argument. The incidence of *Fusarium* spp. increased in years with

higher amounts of precipitation in the above-mentioned period of wheat development. The impact of temperature was not evaluated because the average temperatures in the crucial period of ear infection were similar throughout all investigation years and did not exceed 17–19°C.

The present investigation showed that *F. avenaceum* was the dominant species, which agrees with several other findings [25–27]. Similarly, a high occurrence of *F. poae* was detected in our research, which also supports the data in the literature [22,28]. *Fusarium graminearum* has been recognized as the most important pathogen because of its aggressiveness and pathogenicity as both a causal agent of *Fusarium* head blight and as a mycotoxin producer, which was frequently found in Poland, but was detected less often in our trials [29,30].

Different agronomic practices were evaluated to understand their impact on grain contamination with *Fusarium* spp., but the results were contradictory. The importance of crop rotation was highlighted by Wenda-Piesik et al. [27], where an increasing proportion of *Fusarium* spp. was detected in wheat grains after the precropping of wheat and maize. In contrast, Tillmann et al. [31] recognized only maize as a precrop that promotes the development of *Fusarium* head blight, whilst the importance of wheat as a precrop was not confirmed in their study.

In Sweden, ploughing has been recognized as an important tool to control *Fusarium* head blight [26]. On the other hand, Blandino et al. [9] determined that the successful control of *Fusarium* head blight could be achieved only by combining different factors; a single factor, such as the management of plant residues, was not effective.

In our research, we did not find any statistically significant influence of the soil tillage system or crop rotation scheme on either the total number of *Fusarium* spp. or the composition of the species. The numbers of *F. avenaceum* and *F. poae* were not influenced by soil tillage or crop rotation in our study.

Many researchers have demonstrated the significance of crop rotation for minimizing the risk of *F. graminearum* infection. However, this effect could be mitigated by many different factors, e.g., meteorological conditions, the presence of other fungi, and other agrotechnical measures [32]. In our investigation, statistically significant differences in the incidence of this fungus based on agronomic factors were not determined but a slight effect of agronomic practices was observed.

In our research, the method suggested by Blandino et al. was used to illustrate the importance of the combination of agronomic factors [9]. The highest incidence of *F. graminearum* was found in continuous wheat sowings under reduced soil tillage; in all other variants, this indicator was lower. A similar level of *F. graminearum* was found in two different schemes: reduced soil tillage + oilseed rape as a precrop, and ploughing + wheat as a precrop. The lowest incidence was observed when ploughing was combined with crop rotation.

According to our results, the grain mycobiota partially depend on agronomic practices, but meteorological conditions mitigate this impact. However, continuous wheat sowing under conditions of reduced soil tillage can increase the level of risk of grain infection with *F. graminearum* and, consequently, the accumulation of mycotoxins.

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Co wpływa na skład gatunkowy grzybów zasiedlających ziarniaki pszenicy?

Streszczenie

Ziarniniaki pszenicy zasiedlane są przez różne grzyby, w tym patogeny roślin oraz gatunki produkujące mykotoksyny. Skład gatunkowy grzybów kolonizujących nasiona może być modyfikowany przez różne czynniki, między innymi zabiegi agrotechniczne. Celem badań była ocena zbiorowiska grzybów występujących na ziarniakach pszenicy w zależności od warunków agroekologicznych. Ziarniaki pochodziły z roślin uprawianych w teście polowym uwzględniającym dwa czynniki : A – system uprawy roli (A1 – orka na głębokości 22–24 cm; A2 – bronowanie na głębokości do 10 cm); B – zmianowanie (B1 – pszenica w monokulturze; B2 – rzepak i pszenica; B3 – różne rośliny). Grzyby zasiedlające ziarniaki pszenicy zostały oznaczone na podstawie metod klasycznych i molekularnych. Do najliczniej i powszechnie występujących gatunków grzybów należały *Pyrenophora tritici-repentis*, *Alternaria* spp., *Arthrinium* spp., and *Fusarium avenaceum*. Zwiększone opady deszczu przyczyniały się do silniejszego zakażania ziarniaków przez *Fusarium* spp. W badanych próbach zidentyfikowano 7 gatunków tego rodzaju: *F. avenaceum*, *F. poae*, *F. graminearum*, *F. culmorum*, *F. acuminatum*, *F. sporotrichioides* i *F. tricinctum*. Rodzaje zastosowanego systemu uprawy roli oraz zmianowania nie wpłynęły na ogólną liczbę *Fusarium* spp., ale przyczyniły się do zróżnicowania liczebności poszczególnych gatunków. Wyniki badań sugerują, że przedłużająca się uprawa pszenicy w monokulturze i w warunkach zredukowanej uprawy roli może prowadzić do zwiększenia ryzyka infekcji ziarniaków przez *F. graminearum*, a w konsekwencji większej akumulacji toksyn w ziarniakach.