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Review

Insight into Yeast–Mycotoxin Relations

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Abstract: Fungal mycotoxins are secondary metabolites that can be present in green forage, hay, or silage. Consumption of contaminated plants or agricultural products can cause various animal and human diseases, which is why problems associated with mycotoxins have received particular attention. In addition, public pressure to produce healthy food and feed is also increasing. As the results of several surveys indicate that yeasts can decrease toxic effects by binding or converting secondary metabolites or control growth of harmful fungi, this article provides an overview of the yeast species that can have great potential in detoxification. The most important antagonistic yeast species against toxigenic fungi are described and the mode of their inhibitory mechanisms is also discussed. We provide an insight into toxin binding and biotransformation capacities of yeasts and examples of their use in silo. Issues requiring further study are also mentioned.

Keywords: food and feed safety; yeast; fungal mycotoxin; secondary metabolites; bio-detoxification; antagonism; silage

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1. Introduction

Mycotoxins are secondary metabolites produced by several genera of fungi, such as *Fusarium*, *Aspergillus*, and *Penicillium* [1–6]. These fungi are able to produce various chemically different toxins [1–4]. The most potent toxins are Aflatoxins (AFs), ochratoxins (OTs), fumonisins (FBs), zearalenone (ZEA), or trichothecenes [1,2]. Aflatoxins are difuranocoumarin derivatives, produced mainly by *Aspergillus* species and have four different types (B1, B2, G1, and G2) [1,2,4]. Ochratoxins are weak organic acids consisting of a dihydroisocumarin moiety joined by a peptide bond to 1-phenylalanine, secreted by *Aspergillus* sp. and *Penicillium* sp. [1,2]. OTs come in three forms (A, B, C). Fumonisins are thought be synthetized by condensation of alanine into an acetate-derived precursor and produced by *Fusarium* species [1,2,6]. ZEA is biosynthesized through a polyketide pathway by *Fusarium* species [1]. Trichothecenes constitute a large family of mycotoxins. They are produced by various fungal species like *Fusarium* or *Trichoderma* and others. The trichothecenes have a common 12,13-epoxytrichotechene skeleton and an olefinic bond with various side chains. They are classified as macrocyclic and non-macrocyclic. Deoxynivalenol (DON) and T2 toxin belong to the best studied trichotechenes. Besides the toxins mentioned above, further compounds like patulin, fusaric acid, gliotoxin, roquefortine, enniatin, and so on are also be produced by these toxigenic fungi [1,2].

One species can simultaneously produce several toxic compounds [6,7]. However, we have to mention that filamentous fungi do not always produce toxins [8,9]. The toxin production of these fungi strongly depends on environmental circumstances, such as weather conditions [3,10–14]. Higher water activity and about 28–30 °C temperature

mostly support growth and toxin production of these fungi [3,14]. That is, occurrence of mycotoxins is more frequent in areas with a hot and humid climate. In addition, in vitro experiments show that stress factors can also contribute to fungal toxin production [15–17].

Various molecular techniques and bioinformatic methods allowed us to reveal the mechanism and genes of the toxin production. Products of ZEA genes are required for synthesis of the zearalenone, while biosynthesis of the trichothecene and fumonisins correlates with gene expression of the TRI and FUM genes. These toxin genes are arranged on the chromosome in clusters, highly conserved in the different species, as revealed by the comparisons of the fungal genome sequences [18–25].

The rapidly developing analytical methods allowed us to detect these fungal toxins [3,26]. These analyses pointed to the fact that the different toxins can be found not only in raw feed or food materials, but also in food samples, because they can remain stable during food processing [27–32]. In addition, co-occurrence of certain toxins can also happen [3,10,32–34].

The toxin producing fungal species and their toxins can cause great yield losses in agriculture and can also lead to animal or human diseases, because the toxins can enter both the animal and human body [12,13,35–37]. They can cause a broad spectrum of health damage, such as nail or pulmonary infections or cancer [30,38–41]. The toxigenic fungi and their metabolites are especially dangerous for immune-compromised persons [42–46]. Consequently, one of our current tasks is to decrease occurrence of fungi and concentration of toxins in food and feed. This is also necessary, because the allowed toxin levels are regulated [13,47,48].

To prevent or decrease cell division of fungi and mycotoxin contamination, we need integrated agricultural practices, which include correct pre-harvest and soil management, proper harvest time and techniques, or ensuring appropriate storage parameters and post-harvest procedures. Besides, control of the toxin-producing fungi is very important, if not the most important factor for decreasing or preventing toxin contamination. Generally, fungicidal chemicals are the most frequently used methods to prevent growth of harmful fungi. As these fungicides can cause environmental pollution and health problems, public demand is increasing to reduce chemicals and produce more healthy food and feed. That is why application of antifungal microorganisms as biocontrol agents to inhibit growth of the destructive and harmful fungi seems to be a promising and environment-friendly alternative solution along with or instead of the commonly used methods.

The purpose of this review is to give an insight into those possibilities where yeast species can be used as alternatives to synthetic chemicals in plant protection or bio-detoxification of the different agricultural products.

2. Yeasts and Yeast-like Fungi Can Have Growth Inhibitory Effects against Toxin Producing Fungi

Various microbes live together in nature, from the rhizosphere to the phyllosphere. A large group of them belong to the yeasts, which are eukaryotic unicellular microorganisms. This group is quite heterogeneous and has diverse biological activities. Consequently, they have great potential from the food and beverage industry to agriculture or preservation of the agricultural products.

Numerous studies have investigated the interactions between yeasts and other microbes. Their data suggest that the microbial interaction is a complex process, which can be either stimulation or growth inhibition, which, in addition, is based on different mechanisms [49–55]. When a yeast species is able to inhibit the growth of an adjacent microorganism, a clear zone can be seen around the yeast cells on the laboratory medium (Figure 1).

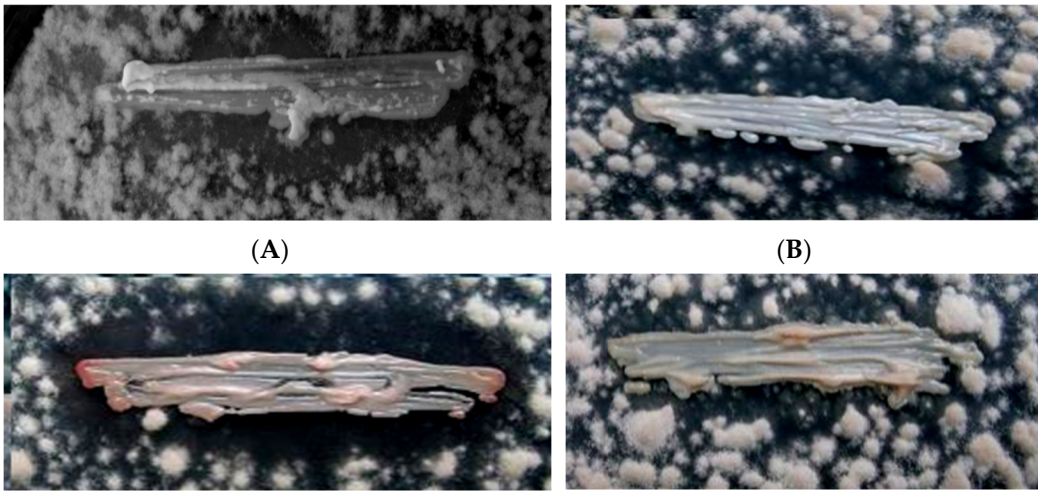

Figure 1. Growth inhibition of *Botrytis cinerea* by yeasts (yeasts were streaked onto the middle region of the *Botrytis cinerea* lawn and were cultured on PDA medium, at room temperature, and photographed after 7 days). (**A**): *Pichia kudriavzevii* (11-460), (**B**): *Wickerhamomyces anomalus* (11-502), (**C**): *Metschnikowia fructicola* (11-579), (**D**): *Saccharomyces cerevisiae* (11-481). (11-460, 11-502, 11-579, 11-481: collection number of the strains in the collection of Department of Genetics and Applied Microbiology) (photos were taken by Enikő Horváth).

The appearance of the inhibitory zone strongly depends on the partner microorganism and the culture factors like composition of the medium, pH, or temperature [54–61]. That is, the same yeast species can inhibit certain microbes, while others are not inhibited under the same environmental conditions. Alternatively, growth of a given species is inhibited at a lower pH, while not at a higher pH [54,55]. The results of Giobbe are in line with this, because she found that *Pichia fermentans* was effective on the surface of apples, while its inhibitory capacity disappeared on peaches [62]. Further in vitro experiments on fruits proved that *Candida tropicalis* significantly decreased anthracnose disease of postharvest bananas, while *Metschnikowia* sp. inhibited rotting of pears or apples caused by *Botrytis* or other fungal species [52,63,64]. The *Pichia* species could inhibit growth of *Aspergillus flavus* or *Monilinia* [62,65]. Further yeast or yeast-like species that have shown growth inhibitory effects either on laboratory media or on the surface of fruits are listed in Table 1.

Table 1. Antagonistic yeast species.

Yeast Species Having Growth Inhibitory Capacity	Inhibited Microorganism	Reference
Aureobasidium pullulans	*Fusarium cerealis*	[66]
	Fusarium graminearum	[66]
	Fusarium sporotrichioides	[66]
	Penicillium verrucosum	[66]
	Fusarium culmorum	[67]
	Botrytis cinerea	[49,68]
	Penicillium expansum	[49,68]
	Aspergillus niger	[49]
	Monilinia laxa	[61,68,69]
Candida krusei	*Fusarium guttiforme*	[70]

Table 1. *Cont.*

Yeast Species Having Growth Inhibitory Capacity	Inhibited Microorganism	Reference
Candida intermedia	*Aspergillus carbonarius*	[71]
	Aspergillus flavus	[72]
Candida sake	*Fusarium avenaceum*	[66]
	Fusarium cerealis	[66]
C. saitoana	*Aspergillus ochraceus*	[66]
	Fusarium species	[66]
	Penicillium verrucosum	[66]
Candida parapsilosis	*Fusarium proliferatum*	[73]
Candida famata	*Penicillium digitatum*	[74]
Candida friedrichii	*Aspergillus flavus*	[72]
	Aspergillus carbonarius	[71]
Candida stellimalicola	*Penicillium italicum*	[75]
Cryptococcus albidus	*Fusarium avenaceum*	[66]
	Fusarium sporotrichioides	[66]
	Penicillium expansum	[76]
	Botrytis cinerea	[76]
Debaryomyces hansenii	*Botrytis* sp.	[77]
	Penicillium nordicum	[78]
	Mucor circinelloides	[79]
	Aspergillus sp.	[79]
	Fusarium proliferatum	[79]
	Fuasarium subglutinans	[79]
	Penicillium expansum	[80]
	Penicillium verrucosum	[80]
	Penicillium digitatum	[81]
Hanseniaspora uvarum	*Colletotrichum capsici*	[82]
Kloeckera apiculata	*Penicillium italicum*	[58]
Kloeckera apis	*Fusarium guttiforme*	[70]
Lachancea thermotolerans	*Aspergillus carbonarius*	[71]
	Aspergillus parasiticus	[83]
	Penicillium verrucosum	[83]
	Fusarium graminearum	[83]
	Aspergillus flavus	[72]
Metschnikowia andauensis	*Botrytis cinerea*	[84]
	Penicillium expansum	[85]
	Penicillium digitatum	[85]
	Penicillium italicum	[85]

Table 1. *Cont.*

Yeast Species Having Growth Inhibitory Capacity	Inhibited Microorganism	Reference
Metschnikowia pulcherrima	*Penicillium expansum*	[58,63,86]
	Penicilliumroqueforti	[63]
	Aspergillus oryzae	[63]
	Aspergillus parasiticus	[63]
	Aspergillus niger	[87]
	Fusarium sp.	[88]
	Botrytis cinerea	[50,51,58]
Metschnikowia fructicola	*Botrytis cinerea*	*
Pichia guilliermondii	*Fusarium species*	[66]
	Penicillium species	[66,89]
	Alternaria alternata	[90]
Pichia membranifaciens	*Botrytis* sp.	[77,91]
	Penicillium expansum	[92]
	Penicillium italicum	[85]
Pichia kudriavzevii	*Botrytis cinerea*	*
Rhodotorula pinicola	*Fusarium avenaceum*	[66]
Rhodosporidium fluviale	*Botrytis cinerea*	[93]
Saccharomyces cerevisiae	*Penicillium italicum*	[75]
	Fusarium oxysporum	[94]
	Fusarium graminearum	[60]
	Aspergillus flavus	[59]
	Aspergillus parasiticus	[59]
	Penicillium italicum	[75]
	Botrytis cinerea	*
Wickerhamomyces anomalus (Pichia anomala)	*Botrytis cinerea*	* [90]
	Aspergillus flavus	[90]
	Penicilliumroqueforti	[90]
	Aspergillus candidus	[90]
	Penicillium italicum	[90]
	Penicillium expansum	[90]
	Penicillium glabrum	[90]
	Penicillium digitatum	[90]
	Cladosporium cladosporioides	[90]
	Paeciliomyces variotii	[90]
	Monascus ruber	[90]

* result of Enikő Horváth (Figure 1).

In certain cases, the antagonistic effect requires close contact and physical interaction between the yeast and pathogen cells, while in other cases, such contact is not necessary [49,67,74,95,96]. Types of contact depend probably on the mode of the inhibitory mechanism.

Growth Inhibition Happens via Different Mechanisms

Some of these antagonistic yeasts have been widely studied. These studies have revealed that the antagonistic yeasts function via different mechanisms [53,97]. The *Metschnikowia* species are mainly known for their red pigment production, which can cause iron depletion in the environment [50,52,98]. As iron can be a component or a cofactor of several enzymes, a lack of it can inhibit many cellular processes and, thereby, cell multiplication of "adjacent" microbes [99]. The relation between pigment production and antagonistic capacity is supported by the fact that the pigment-less *M. pulcherrima* mutants lacked antifungal activity [50,88]. Further studies have suggested that *Metschnikowia* species were able to produce proteases, cell wall degrading enzymes, or the cells competed for nutrients and space, and all these capacities could also contribute to their antagonistic capacity [50,52,53,55,100].

Similarly, the mode of inhibition was found to be quite varied in other species [101]. Antagonism of the yeast-like fungus *Aureobasidium pullulans* probably involves competition for nutrients, because the addition of exogenous nutrients reduced its antagonistic activity, while a lower nutrition concentration improved it [49,61,68]. Besides, production of extracellular enzymes, such as β-1,3 glucanase, chitinase, and iron-chalating siderophore, was also detected in this species [49,68,102]. The *Kloeckera apiculata* competes with the phytopathogens for nutrients and vitamins [58], while the *Saccharomyces cerevisiae* is able to produce killer toxin and chitinase [101,103]. Volatiles are also frequently produced materials as inhibitory substrates. *Cyberlindnera jadinii* and *Candida friedrichii* inhibited *Aspergillus flavus* by volatiles [72]. Similarly, *Wickerhamomyces* species inhibited the microbes by the production of volatile compounds; however, these species are also able to produce hydrolytic enzymes (glucanases, chitinases) or killer toxins [65,103–105].

These data demonstrate well that the antagonistic species use various, albeit mostly similar, mechanisms, which separately or together can contribute to the wide spectrum of their inhibitory capacity. Interestingly, the inhibitory effects are related to the living cells, because some studies have shown that the inactivated cells or culture filtrate had no effect on the pathogens [68,106].

As the group of the inhibitable species and details of these inhibitory mechanisms are not fully known, an important task for researchers is to identify those species that can be inhibited by a given yeast and determine the optimal conditions of its antagonism. All these data can help us to set the parameters of a later field or a post-harvest application precisely and can lead to forming new commercially available bio-fungicides, which can expand the range of existing products [53,97].

3. Decrease in Mycotoxin Contamination

The various yeast species can also be very useful in decreasing mycotoxin contaminations. According to research results, numerous yeast species are able to bind the toxins or alter them to become less toxic metabolites.

3.1. Toxin Binding

Several authors have reported that yeasts, like *Saccharomyces cerevisae* or certain *Candida* species, are able to decrease fungal toxins, such as aflatoxins [107], while others, e.g., *Kloeckeraapiculata* or *S. bayanus* cells, could bind OTA [108]. Both intact and heat inactivated *S. cerevisiae* cells have been found to be effective [108–110]. Their toxin adsorption was fast and dependent on cell concentration [109,110]. The positive effect of the living cells also appeared in those experiments where *S. cerevisiae* and *S. pastorianus* strains were able to reduce DON and ZEA levels during wort fermentation [111]. At the end of the fermentation, 11–17% of DON and 31–72% of ZEA were removed by the yeasts [111]. Similarly, selected *Saccharomyces* species and *Schizosaccharomyces pombe* strains successfully removed the fungal toxins from grape juice [110,112]. This is a remarkable result, because the presence of OTA is also rather a difficult problem in wine making. It has been found in various countries both in red and white wine; therefore, the maximum level of OTA has to

be regulated [47,113,114]. However, we have to mention that the degree of OTA binding has been found to be strain-dependent [108,112], thus one of our tasks is to select the most proper yeasts strains.

The results have pointed to the fact that the wall of the yeast cells has an important role in toxin binding, because protoplasts (living cells without cell wall) had lost their adsorption ability [109]. This was confirmed by those data that the yeast-originated cell wall components or their derivatives could also decrease fungal toxin concentration. The cell wall preparations originated from *Saccharomyces cerevisae* or *Candida utilis* bound the ochratoxins (OTs) or deoxynivalenol (DON) [72,115]. Additionally, sulfoethylglucan, a derivative of the cell wall glucan prepared from *S. cerevisiae*, resulted in the reduction in the level of fusaric acid [116], another fungal toxic compound. Binding of these compounds is mostly linked to the high adsorption capacity of the cell wall material [115,117–119]. In order to better understand this binding capacity, the composition of the cell wall isolated from *Saccharomyces cerevisiae* was analysed. Its cell wall contained about 25% dry substances, whose composition was as follows: 40–60% proteins, 25–35% carbohydrates, and a smaller amount of lipids and minerals [115]. As the *Saccharomyces cerevisiae* strains having a higher β-D-glucan content were able to complex larger amounts of ZEA than other strains, it was suggested that the yeast cell wall component β-D-glucan has an especially important role in toxin binding [118]. The results of Jouany et al. showed that there were weak hydrogen and van der Waals bonds in the β-D-glucan-toxin complex [120]. However, protein content, pH, and the size of the cell wall samples and type of the mycotoxins severely affected the binding of the toxins [72,117].

3.2. Application of Yeasts as Biotransformation Agents

Numerous studies have investigated biotransformation of fungal toxins. Living cells, from bacteria and yeasts to animal cells, are able to convert toxins into less toxic or non-toxic metabolites through biotransformation [121,122]. The conversions can include different alterations like hydroxylation, oxidation, methylation, demethylation, glycosylation, deamination, and so on [122]. According to previous studies, *Candida*, *Hansenula*, *Pichia*, and *Saccharomyces* genera could alter ZEA to α- or β-zearalenol (stereoisomers) [122,123]. The *Trichosporon mycotoxinivorans* deactivated all OTA in 2.5 h and OTα (hydrolysis product of OTA) appeared at the end of the experiment [124]. Further studies, which investigated the fate of patuline (PAT), reported that *S. cerevisiae* or *Sporobolomyces* sp., as well as *Rhodosporidium paludigenum* or *Rhodotorula mucilaginosa*, could metabolise this toxin [125–128]. Alteration of PAT was an inducible mechanism, which depended on oxygen supply, temperature, and cell density of the yeasts [125,127,128]. A transcriptional analysis revealed that complex mechanisms were activated in *Sporobolomyces* cells in the presence of patulin, and genes of, e.g., oxidation-reduction processes, glutathione, and thioredoxin systems were up-regulated [129]. Moreover, the *Rhodosporidium* cells transformed patulin and they probably produced desoxypatulinic acid as a degradation product, which was not toxic to *Escherichia coli* and *Arabidopsis thaliana*, in contrast to patulin [127].

McCormick and co-workers studied the yeasts of *Trichomonascus* clade and their biotransformation capacity. They found that these yeasts have different target sites on T2 toxin, thus different detoxification mechanisms are responsible for protection against this toxin. These include 3-OH conjugations: 3-acetylation and 3-glucosylation [130]. In another study, the main enzymatic detoxification mechanism of the trichothecenes was acetylation caused by *S. pastorianus* cells [131].

Although these alterations can result in lower toxicity, we cannot rule out that the masked forms of toxins may be transformed to their original forms by the intestinal microbioms after eating [132], thus the best approach can be inhibition of the fungal cell division, both on the surface of crops and in agricultural products.

4. Problems Related to Silage

Toxin contamination of food, especially of milk and dairy products, is a serious problem and can occur in various countries. The toxin level of milk can strongly depend on seasons and feed [133,134]. As silage is a significant part of feed used for cows, its quality is very important. The plant materials are not steril, thus silage can contain various microorganisms from bacteria to toxin producing fungi [135,136]. Generally, these microbes have an important role, because the fermentation and, thereby, characteristics of silage depend on them. When, for example, the fermentation process in the silo does not progress properly, the occurrence of the pathogenic fungi and level of mycotoxins can be high [48,137]. If toxins are present in the silage, they can cause reduced feed intake or milk production and contaminated milk [48,133,134].

To decrease the toxin concentration of silage, inhibition of toxin producing fungi could be achieved by inoculation of the antagonistic yeasts. However, it is difficult to find the optimal strain because there are special conditions in the silo. In addition, several "in-house" yeast species can survive in the silo and they often start to grow when the silage is exposed to air, for example, after silo opening. When these yeast species are lactate-assimilating species, their growth can result in degradation of lactic acid produced by bacteria, leading to an increase in pH. These changes allow further undesirable bacteria and molds to grow. This means that, when we want to use antagonistic yeast in the silo, we have to choose them very carefully. Only those antagonistic yeast strains that are incapable of assimilating lactate and can tolerate a lower pH can be suitable. A previous study demonstrated that *Penicillium roqueforti* was inhibited in the silo by yeasts [56], while another one proved that *Saccharomyces* and *Pichia* species were able to reduce the growth of *Aspergillus flavus* in the mini-silo [106]. This experiment also proved that mixed yeast inoculums can function as a useful strategy to decrease the number of undesirable fungi [106]. When we can find the proper yeast species, it or they can also improve the vitamin and protein level of the silage [138].

5. Conclusions

Although mechanisms involved in yeast antagonism against toxin-producing fungi and bio-detoxification of agricultural products are not entirely clear and require further investigations, yeasts can be attractive alternative solutions in detoxification.

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