European Journal of Plant Pathology **109:** 723–730, 2003.

Post-harvest fungal ecology: Impact of fungal growth and mycotoxin accumulation in stored grain

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Key words: ecology, biotic, abiotic factors, fungal interactions, niche occupation, mycotoxins, insects

Abstract

Grain quality after harvest is influenced by a wide variety of abiotic and biotic factors and has been studied as a stored grain ecosystem. Important factors include grain and contaminant mould respiration, insects and mites, and the key environmental factors of water availability and temperature. Interactions between these factors influence the dominance of fungi, particularly mycotoxigenic species. Studies have shown that growth, mycotoxin production, competitiveness and niche occupation by mycotoxigenic species are influenced by the presence of other contaminant moulds and environmental factors. This has been demonstrated for both *Fusarium culmorum* and deoxynivalenol production, *Aspergillus ochraceus/Penicillium verruscosum* and ochratoxin production and *Fusarium* section Liseola and fumonisin production. Interactions between mycotoxigenic spoilage fungi and insects do occur but have not been studied thoroughly. Some insects disseminate mycotoxigenic species, others are known to use spoilage moulds as a food source, while others avoid certain fungal species. Thus, a more holistic ecological view is needed when considering management approaches to long-term-safe storage of cereal grains after harvest.

Stored grain as an ecosystem

Grain entering store carries a wide range of microorganisms including bacteria, yeasts and filamentous fungi, the population structure being dependent on field climatic conditions and harvesting processes (Magan and Lacey, 1986; Lacey and Magan, 1991). Poor post-harvest management can lead to rapid deterioration in grain quality, severely decreasing germinability and nutritional value of stored grain. Fungal activity can cause undesirable effects in grain including discolouration, contribute to heating and losses in nutritional value, produce off-odours, losses in germination, deterioration in baking and milling quality, and can result in contamination with mycotoxins.

Wallace and Sinha (1981) were the first to consider stored grain as a man-made ecosystem and use multivariate statistics to examine the complex interactions between abiotic and biotic factors to identify key parameters for safe storage. They believed that unless this more holistic and ecological approach was adopted it was not possible to understand the processes occurring and thus improve post-harvest management of stored grain. Factors such as grain type and quality, fungal population and community structure, mycotoxin production and pest infestation were all interlinked (Figure 1). The key environmental factors of temperature, water availability and gas composition influence both the rate of fungal spoilage and the production of mycotoxins.

Generally, provided grain is stored at a moisture content equivalent to $\leq$0.70 water activity (a_w) then no spoilage will occur. However, since grain is often traded on a wet weight basis, inefficient drying systems can lead to fungal activity and concomitant mycotoxin production which renders grain useless for food or feed. During initial storage, fungal inoculum can become redistributed in grain. Mechanical damage is also conducive to entry of spoilage fungi in insufficiently dried grain. It must also be remembered that

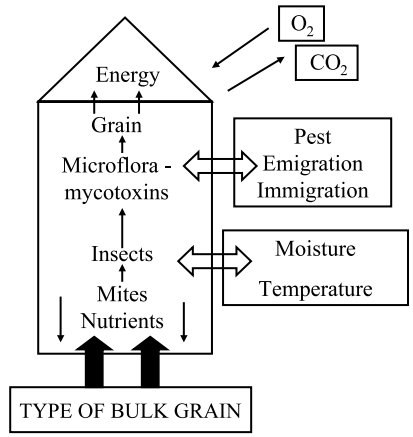

Figure 1. Diagrammatic representation of interactions between biotic and abiotic factors in stored grain ecosystems (adapted from Sinha, 1995).

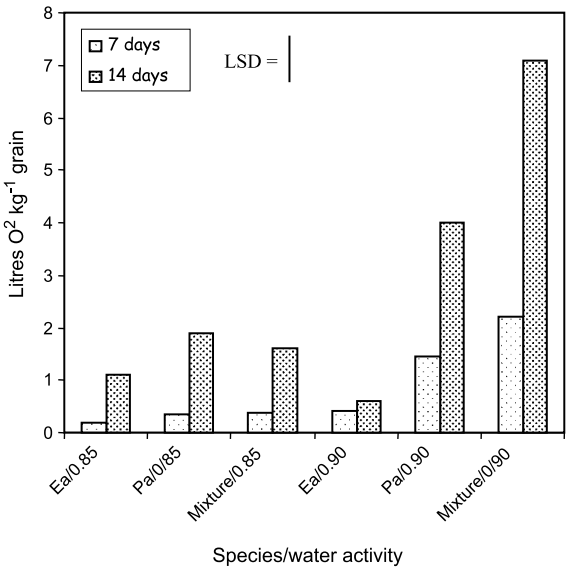

Figure 2. Measurement of the total respiratory activity of *E. amstelodami* (Ea), *P. auratiogriseum* (Pa) or a mixture of the two (mixture) at 0.85 and 0.90 water activity after 7 and 14 days incubation (Magan, unpublished data). Bar indicates least significant difference ($P = 0.05$) between treatments.

stored grain ecosystems offer an excellent but finite nutritional substrate for spoilage fungi.

Ecological considerations of interactions between spoilage fungi post-harvest

Fungi seldom occur on grains in isolation, but usually as a mixed consortium of bacteria, yeasts and filamentous fungi. It is thus inevitable that interspecific and intraspecific interactions will occur depending on the nutritional status of the grain and the prevailing environmental conditions. Indeed, environmental factors may exert a selective pressure influencing community structure and dominance of individual species, especially mycotoxigenic species. Figure 2 shows the effect of a_w on respiration of single spoilage fungi (e.g. *Eurotium amstelodami* and *Penicillium aurantiogriseum*) when grown individually or co-inoculated on wheat grain using an automated electrolytic respirometer system (Willcock and Magan, 2001). Respiration of co-inoculated species was less than additive especially at intermediate a_w conditions after 7 days. After 14 days, patterns changed again when total O_2 utilisation was considered (Hamer and Magan, unpublished data). This is indicative of competition between species. The situation becomes even more complex when a mixture of species colonising cereal substrates is considered.

From an ecophysiological point of view, it has to be remembered that spoilage fungi colonising grain use different primary and secondary strategies to occupy the niche. They may have combative (C-selected), stress (S-selected) or ruderal (R-selected) strategies or merged secondary strategies (C–R, S–R, C–S, C–S–R; Cooke and Whipps, 1993). Primary resource capture of grain is influenced by the germination rate, growth rate, enzyme production and the capacity for sporulation. Subsequent interactions between spoilage fungi result in combat, antagonism and niche overlap which all influence secondary resource capture.

We will consider two approaches which have been used to understand the type of interactions which occur between fungi under different environmental regimes in grain to enable better prediction of not just dominance by key spoilage fungi, but also the potential for production of mycotoxins. Magan and Lacey (1984, 1985) used categories of mutual intermingling (1/1), antagonism (2/2; 3/3) on contact or at a distance respectively, and dominance on contact or at a distance (4/0; 5/0). By giving a higher numerical score to fungi able to dominate *in vitro* rather than antagonism and adding the scores for each species, an Index of Dominance (I_D) was developed to assist with interpreting patterns of colonisation and dominance in grain ecosystems. The I_D was found to significantly change with a_w and temperature, and with grain substrate. Of 15 species, the most competitive species in wheat grain in the United Kingdom were *P. brevicompactum*,

P. hordei, *P. roqueforti*, *Aspergillus fumigatus* and *A. nidulans*. Decreasing the a_w led to conditions increased competitiveness of *P. brevicompactum*. Only *Fusarium culmorum* could compete with storage moulds, at >0.93–0.95 a_w. Interestingly, the rate of growth was not related to dominance. Previously, studies by Ayerst (1969) had suggested that speed of germination and growth were key determinants of colonisation of nutrient-rich matrices, such as grain.

Table 1 shows the effect of interactions between a mycotoxigenic strain of *F. culmorum* and other species in relation to water availability on wheat grain using the I_D scoring system. It is interesting to note that *F. graminearum* is more competitive than *F. culmorum*, regardless of temperature or water availability. *F. culmorum* is, however, dominant against other grain fungi including *Microdochium nivale*. This is indicative of why *F. culmorum* has become such an important pre- and post-harvest pathogen of temperate cereals and also indicates that *F. graminearum* is more competitive when both colonise grain. Thus interactions can change with different abiotic factors and with interacting species. Table 2 gives an example for an ochratoxin (OTA)-producing strain of *A. ochraceus* and other species, both *in vitro* and on maize grain at two different temperatures. *A. ochraceus* is dominant against *A. candidus* and *A. flavus* at 18 °C, but not against the latter at 30 °C *in situ*.

Table 1. *F. culmorum* interaction and I_D determined after 30 day incubation at 15 or 25 °C on irradiated wheat grain adjusted to different a_w levels (Hope and Magan, unpublished data)

a_w	Species[a]	Temperature		ID
		15 °C	25 °C	
0.995	F.c : F.g	0[b]/4[c]	0/4	0/8
	F.c : F.p	2/2	1/1	3/3
	F.c : A.t	4/0	4/0	8/0
	F.c : C.h	4/0	4/0	8/0
	F.c : M.n	2/2	4/0	6/2
	F.c : M.m	2/2	4/0	6/2
	F.c : P.v	4/0	2/2	6/2
I_D		16/10	19/7	35/17
0.955	F.c : F.g	0/4	0/4	0/8
	F.c : F.p	0/4	2/2	2/6
	F.c : A.t	4/0	4/0	8/0
	F.c : C.h	4/0	4/0	8/0
	F.c : M.n	4/0	4/0	8/0
	F.c : M.m	0/4	4/0	4/4
	F.c : P.v	2/2	4/0	6/2
I_D		14/14	20/6	34/20

[a]F.c., *Fusarium culmorum*; F.g., *Fusarium graminearum*; F.p., *Fusarium paoe*; A.t., *Alternaria tenuissima*; C.h., *Cladosporium herbarum*; M.n., *Microdochium nivale*; M.m; *M. nivale* var. *majus*; P.v., *Penicillium verrucosum*.

[b]Refers to interaction score for first species only.

[c]Refers to interaction score for second species only.

I_D refers to total addition of scores for an individual species competing with a range of other species based on the interaction scores for each species of 1 : 1 (mutual intermingling), 2 : 2 (mutual antagonism on contact), 3 : 3 (mutual antagonism at a distance), 4 : 0 (first species dominant over the other on contact), 5 : 0 (first species dominant at a distance over the other; from Magan and Lacey, 1984).

More recently, alternative approaches were utilised to understand the relative competitiveness of different species within fungal communities colonising grain. Wilson and Lindow (1994a,b), working with biocontrol systems, suggested that the co-existence of microorganisms particularly on plant surfaces may be mediated by nutritional resource partitioning. Thus *in vitro* carbon utilisation patterns (Niche size) could be used to determine Niche overlap indices (NOI) and thus the level of ecological similarity. Based on the ratio of the number of similar C-sources utilised and those unique to an individual isolate or species, a value between 0 and 1 was obtained. NOI of >0.9 were indicative of co-existence between species in an ecological niche, while scores of <0.9 represented occupation of separate niches. This approach was modified by Marin et al. (1998a) and Lee and Magan (1999) for a multifactorial approach by including water availability and temperature into the system. This demonstrated that based on utilisation of maize C-sources, the NOIs for fumonisin-producing strains of *F. verticillioides* and *F. proliferatum* were >0.90 at >0.96 a_w at 25 and 30 °C, indicative of co-existence with other fungi such as *Penicillium* species, *A. flavus* and *A. ochraceus*. However, for some species, pairing with *F. verticillioides* resulted in NOI values <0.80 indicating occupation of different niches. Figure 3 shows a diagrammatic example of the impact that environmental factors and interaction have on Niche size and NOI for *A. ochraceus* against *Alternaria alternata*. This shows how interactions may change with environment. Table 3 shows results for interactions between an OTA-producing *P. verrucosum* strain and a *Eurotioum* species at 15 and 25 °C. These results suggest that Niche overlap is in a state of flux and significantly influenced by both temperature and water availability. Nutrient status is very important. Lee and Magan (1999) demonstrated that comparison of C-sources in a standard BIOLOG test plate (95 carbon sources) with

Table 2. *In vitro* and *in situ* interaction scores and I_D between *A. ochraceus* and other species in relation to environmental factors (adapted from Lee and Magan, 2000a,b)

a_w	Species[a]	*In vitro*		*In situ*	
		18 °C	30 °C	18 °C	30 °C
0.95	*A. ochraceus* : *A. candidus*	4[b]/0[c]	5/0	4/0	4/0
	A. ochraceus : *A. flavus*	4/0	4/0	4/0	0/4
	A. ochraceus : *A. niger*	4/0	0/4	0/4	0/4
	A. ochraceus : *E. amstelodami*	2/2	2/2	0/4	0/4
Index of Dominance[d]		14/2	11/6	8/8	4/12

[a]Interacting fungal species.
[b]Refers to interaction score for *A. ochraceus* only.
[c]Refers to interaction score for interacting species only.
[d]Refers to total addition of scores for an individual species competing with a range of other species based on the interaction scores for each species of 1 : 1 (mutual intermingling), 2 : 2 (mutual antagonism on contact), 3 : 3 (mutual antagonism at a distance), 4 : 0 (first species dominant over the other on contact), 5 : 0 (first species dominant at a distance over the other; from Magan and Lacey, 1984).

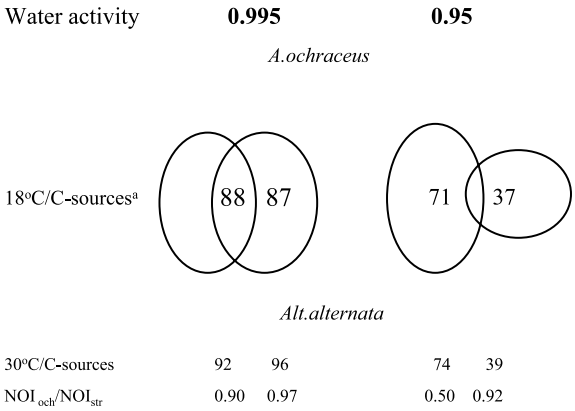

Figure 3. Diagrammatic representation of the Niche size and NOI for *A. ochraceus* when interacting with *A. alternata* at different temperatures and water activity levels (adapted from Lee and Magan, 1999). [a]Number of C-sources utilised out of 95; NOI_{och}, number of C-sources in common divided by total number utilised by *A. ochraceus*; NOI_{str}, number of C-sources utilised in common divided by the number utilised by *A. alternata*.

those only relevant to maize grain (18 carbon sources) gave very different results in terms of Niche size and NOI under different environmental conditions. This approach confirms that interactions and dominance are dynamic, not static, and emphasises the importance of taking account of such fluxes in any integrated approach to understanding and controlling the activity of mycotoxigenic spoilage moulds in the stored grain ecosystem.

Table 3. Example of impact of environmental factors on Niche size and NOI between *P. verrucosum* and other spoilage fungi (Cairns and Magan, unpublished data)

Water activity	0.995		0.93	
	Niche size[a]	NOI_{Pv}/ NOI_{Sp}	Niche size	NOI_{Pv}/ NOI_{Sp}
15 °C				
P. verrucosum	92		74	
A. ochraceus	71	0.71/0.92	52	0.50/0.74
F. culmorum	90	0.88/0.92	63	0.58/0.74
P. aurantiogriseum	90	0.78/0.92	75	0.69/0.74
25 °C				
P. verrucosum	85		69	
A. ochraceus	88	0.84/0.85	63	0.55/0.69
F. culmorum	89	0.82/0.85	51	0.45/0.69
P. aurantiogriseum	74	0.84/0.85	64	0.59/0.60

[a]Niche size, the total number of carbon sources utilised by a species based on Biolog GN plate of 95 Carbon sources.
NOI_{pv}, total number of carbon sources utilised in common divided by the total number utilised by *P. verrucosum* only, under each set of conditions.
NOI_{sp}, total number of carbon sources utilised in common, divided by the total utilised by the competitor, under each set of conditions.

Effect of interactions on growth and mycotoxin production

Figure 4 shows effects of fungal interactions and a_w on growth of *F. culmorum* on layers of irradiated wheat grain at two different a_w levels. The results show that when interacting with some species, e.g. *M. nivale* or

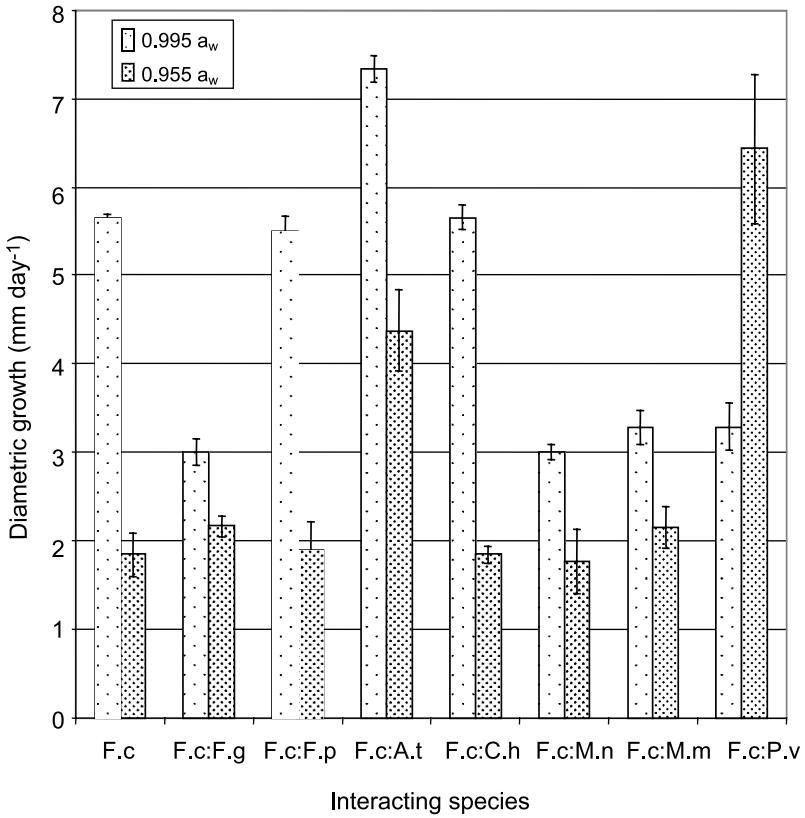

Figure 4. Effect of environmental factors on relative growth (diametric extension ± SE) of *F. culmorum* when paired with other interacting fungi on wheat grain at 0.995 and 0.955 water activities and 25 °C. Growth rates are means of five replicates per treatment. Key to fungi: F.c., *Fusarium culmorum*; F.g., *Fusarium graminearum*; F.p., *Fusarium paoe*; A.t., *Alternaria tenuissima*; C.h., *Cladosporium herbarum*; M.n., *Microdochium nivale*; M.m.; *M. nivale* var. *majus*; P.v., *Penicillium verrucosum* (Hope and Magan, unpublished data).

P. verrucosum, growth of *F. culmorum* is significantly faster than when growing alone on grain. Similar effects on growth and on OTA production were observed for *A. ochraceus* on maize grain (Lee and Magan, 2000b).

The question arises whether such effects on growth also influence mycotoxin production in poorly stored grain. *In vitro* and *in situ* studies have previously suggested that interaction between some species can result in a significant accumulation of mycotoxins, while in other cases an inhibition of mycotoxin production is observed. For example, interactions between section Liseola *Fusarium* species with *A. niger* resulted in a tenfold increase in fumonisin production especially at 0.98 a_w, although under drier conditions no increase in fumonsin occurred on maize grain (Marin et al., 1998b). Also in maize, *A. flavus*, *A. niger* and *E. amsteladami* all significantly inhibited OTA production by *A. ochraceus* (Figure 5; Lee and Magan, 2000b).

Recent studies with *F. culmorum* show that interaction with *M. nivale* stimulated DON production on wheat grain with freely available water (= 0.995 a_w), while under drier conditions (0.955 a_w) interaction with *A. tenuissima*, *Cladosporium herbarum* and *P. verrucosum* reduced DON production (Table 4, Hope and Magan, unpublished data). OTA production by *P. verrucosum* was also influenced by competition with other spoilage fungi on wheat grain (Table 5).

Relationship between insects and mycotoxin producing fungi in stored grain

It is important to remember that insect pests are a common problem in stored grain ecosystems. They grow and multiply at water availabilities much drier than those allowing fungal growth. Insects can produce

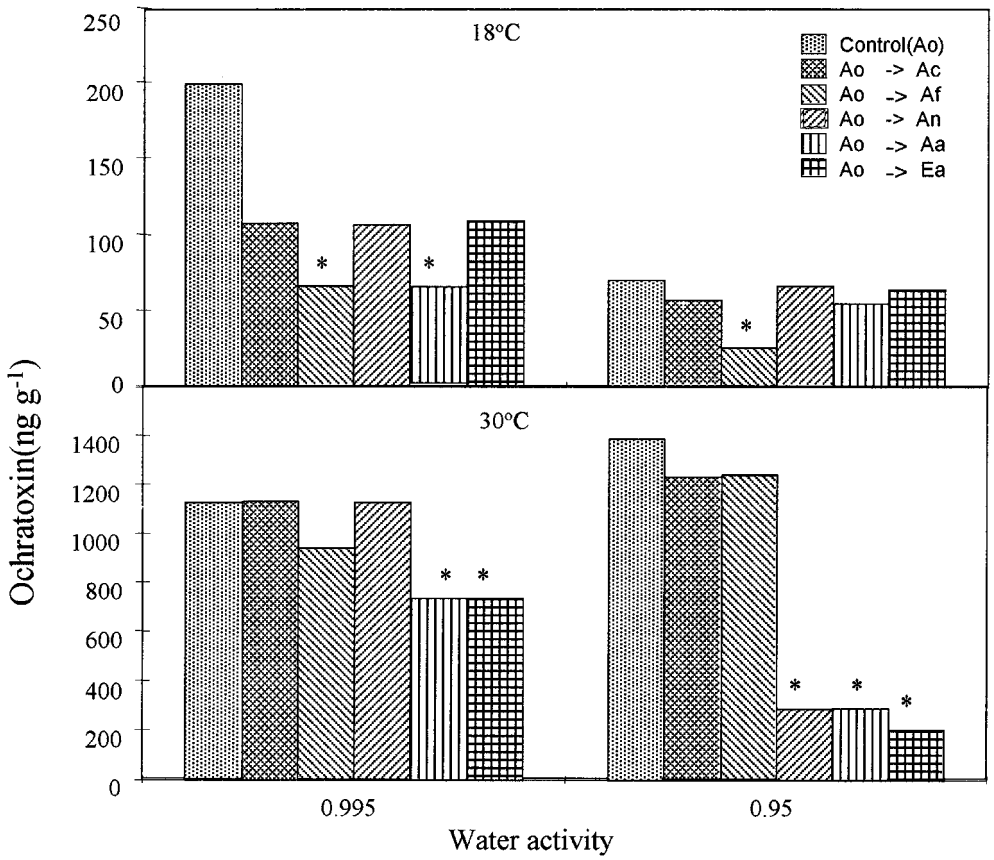

Figure 5. Effect of temperature and water activity on relative ochratoxin production by *A. ochraceus* when interacting with other fungi on maize grain at 18 and 30 °C when compared to *A. ochraceus* colonisation alone. Key to fungi: Ao, *Aspergillus ochraceus*; Ac, *Aspergillus candidus*; An, *Aspergillus niger*; Aa, *Alternaria alternata*; Ea, *Eurotium amstelodami* (adapted from Lee and Magan, 2000b). *Indicates significant differences from the control ($P = 0.05$).

Table 4. Effect of interactions between *F. culmorum* and other species on deoxynivalenol and nivalenol (ng g^{-1} grain) production on irradiated wheat grain at two water activity levels at 25 °C (Hope and Magan, unpublished data)

	Mycotoxin			
	Deoxynivalenol		Nivalenol	
Water activity	0.995	0.955	0.995	0.955
F. culmorum	7669	447	289	298
F. culmorum + *C. herbarum*	634	0	316	412
F. culmorum + *A. tenuissima*	459	444	0	288
F. culmorum + *M. nivale*	451	600	868	0
F. culmorum + *M. majus*	0	440	292	0
F. culmorum + *P. verrucosum*	3264	450	0	0

LSD ($P = 0.05$): DON = 180.5: NIV = 123.2.
Key to fungi: F, *Fusarium;* A, *Alternaria*; M, *Microdochium; M. majus*, *M. nivale* var. *majus*; P, *Penicillium verrucosum*.

metabolic heat which generates water via condensation on surfaces due to temperature differentials and develop classic hot spots which can quickly result in heating and complete spoilage. Pre-harvest insect infection can lead to increased post-harvest production of aflatoxin in maize (Sauer et al., 1984).

Some storage insects are disseminators of storage fungi, while others are exterminators (Sinha, 1971). Some storage fungi attract insects as food sources and promote population increases. Some fungi produce metabolites which repel insects. Indeed, loss in calorific value is due to the combined effects of spoilage fungi and insects. These interactions have often been neglected, although they are important. Physiological and biochemical similarities between fungi and early developmental stages of insects mean that potential exists for combined insecticidal/fungicidal control.

Table 5. Effect of interactions between *P. verrucosum* and two other mycotoxigenic *Fusarium* species (*F. culmorum*, *F. poae*) on ochratoxin production (ng $g^{-1} \pm$SE) on wheat-based medium under different water activity and temperature conditions after 56 days incubation

Water activity	Temperature (°C)			
	15		25	
	0.99	0.95	0.99	0.95
P. verrucosum alone	3000 ± 327	1800 ± 645	150 ± 36	3600 ± 409
P. verrucosum + *F. culmorum*	0	10 ± 7	0	0
P. verrucosum + *F. poae*	60	200 ± 18	0	0

There are no recent studies of interactions between insects and mycotoxigenic fungi. Dix (1984) found that *Penicillium* spp. and *A. flavus* were associated with *Sitophilus zeamais*. As adults they carried a high density of spores without succumbing to aflatoxicoses. Earlier Eugenio et al. (1970) showed that the lesser mealworm and the confused flour beetle retained zearelenone (ZEA) through metamorphoses from larvae to adult. Wright (1973) found that neither ZEA or T-2 toxin produced by *F. graminearum* and *F. tricinctum*, respectively, caused any mortality in the life-cycle of *Tribolium confusum*. Since this insect also feeds on these fungi, it may be a non-propagative vector or disperser of these fungal metabolites.

Dunkel (1988) carried out elegant studies to examine the efficacy of different concentrations of OTA, citrinin, rubratoxin B and patulin on larval weights and development time of three different insect species at between 0 and 1000 ppm concentrations. Larval weight of *T. confusum* was only significantly affected by citrinin, rubratoxin B and patulin at 1000 ppm concentration, with little effect on adult emergence. Of the three insect pests examined, only *Attagenus megatoma* was significantly affected at 100–1000 ppm of the mycotoxins. Surprisingly, no studies have been conducted with regard to fumonsins, DON or nivalenol. Such studies are necessary to evaluate the interactions which might occur between insect pests and spoilage moulds in stored grain ecosystems.

Conclusions

The activity of mycotoxigenic fungi in stored grain must be examined in the context of the ecosystem as a whole in order to understand the dominance of certain species under certain environmental conditions. Interactions between these fungi and other contaminants are complex and are significantly affected by the prevailing and changing environmental factors. Niche overlap and dominance of mycotoxigenic species have been shown to fluctuate with environmental factors. Studies *in vitro* and *in situ* suggest that interactions between toxigenic species and other spoilage fungi markedly influence mycotoxin production, with some species stimulating and others inhibiting production. The role of insect pests should not be neglected as they may be integrally involved in the dominance of mycotoxigenic species by helping in dispersal and acting as vectors and carriers of the toxin through grain. Overall, conditions in stored grain are not in a steady state and thus the dynamics of the system will vary over time. This needs to be taken into account in determining safe storage times for cereals without risks of spoilage and mycotoxin contamination. Any decision support system must take all these factors into account for the effective development of good management systems post-harvest.

Acknowledgements

Parts of this research were funded by the European Commission, Quality of Life and Management of Living Resources Programme (QOL), Key Action 1 on Food, Nutrition and Health, Contract Nos. QLK1-CT-1999-00433 and QLK1-CT-1999-00996.

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