



Astigmatid mite growth and fungi preference (Acari: Acaridida): Comparisons in laboratory experiments

J. Hubert^{a,*}, V. Jarošík^b, J. Mourek^b, A. Kubátová^c, E. Ždárková^a

^aResearch Institute of Crop Production, Drnovská 507, Praha 6, 161 06, Czech Republic

^bDepartment of Zoology, Faculty of Science, Charles University, Viničná 7, Praha 2, 128 44, Czech Republic

^cDepartment of Botany, Faculty of Science, Charles University, Benátská 2, Praha 2, 128 01, Czech Republic

Received 25 July 2003; accepted 12 December 2003

KEYWORDS

Mites;
Feeding;
Preference;
Development;
Microscopic fungi

Summary

The relationship between palatability and suitability of fungi for sustaining mite population growth was tested in the laboratory. The effect of mite fungal preference on spore dispersion was also studied. Eight species of microscopic fungi, *Alternaria alternata*, *Aspergillus niger*, *Aspergillus versicolor*, *Cladosporium cladosporioides*, *Eurotium amstelodami* var. *amstelodami*, *E. amstelodami* var. *montevidensis*, *Mycocladius corymbifer*, and *Penicillium aurantiogriseum* differed in their attractiveness as food and in their suitability to sustain population growth of three astigmatid mites, *Acarus siro*, *Lepidoglyphus destructor* and *Tyrophagus putrescentiae*. The preference for a particular species of fungus and its suitability for sustaining population growth were not correlated. Observed differences among mite species in their population growth were more likely associated with their ability to digest fungi. Fungi were divided into four groups based on their palatability and suitability to sustain population growth: (i) preferred food and suitable for mite growth (e.g. *A. alternata*, *C. cladosporioides*); (ii) preferred, but unsuitable (e.g. *E. amstelodami* var. *amstelodami*); (iii) avoided, but suitable (e.g. *A. versicolor*, *M. corymbifer* and *E. amstelodami* var. *montevidensis*); and (iv) avoided and unsuitable (e.g. *A. niger*). With respect to fungal spore dispersion, mites had the least effect on “avoided and unsuitable” fungal species while preferred fungi were most influenced by mite grazing.

© 2004 Elsevier GmbH. All rights reserved.

*Corresponding author.

E-mail address: hubert@vurv.cz (J. Hubert).

Introduction

Astigmatid mites are common soil dwellers but can also be found in homes and buildings, which they access via rodent and bird nests. Primarily fungivorous (O'Connor, 1979, 1984), astigmatid mites indirectly affect the plant litter decomposition in the soil (Siepel and Maaskamp, 1994) and can also influence storage grain in granaries (Armitage and George, 1986). The fungus–mite interaction can be favourable to the mite, to the fungus, or to both species. A fungus may profit from the selective dispersal of its spores on the body surface or in the digestive tract of a mite (Jacot, 1930; Griffiths et al., 1959; Williams et al., 1998a, b). As migrating mites transport fungal spores to new substrates (e.g. dead leaves), fungi can flourish on these new resources (Hanlon and Anderson, 1979; Hanlon, 1981; Visser et al., 1981). Fungi can also profit from mite-feeding, because moderate grazing induces a fast compensatory growth of the mycelium (Hedlund et al., 1991). This is especially so if the fungus has a patchy distribution (Parkinson et al., 1979; Bengtsson et al., 1993, 1994; Hedlund and Augustsson, 1995). Other fungus–mite interactions include soil fungi, particularly species of *Aspergillus* and *Penicillium*, that develop on fruit and on dead soil animals (Warcup, 1967). There are also fungi that attract soil animals, which lay eggs near their hyphae (Warcup, 1967; Fassatiová and Lýsek, 1982; Nordbing-Hertz, 1988). Subsequently, many of the eggs and developing larvae die, providing a nitrogen source for the fungi (Klironomos and Hart, 2001).

Whether or not a fungus is eaten by a mite is determined by the mycotoxin and secondary metabolite content (Daneshvar and Rodriguez, 1979), the digestive capabilities of the mite (Bowman, 1984; Hubert et al., 2001) and the availability of alternative food (Parkinson et al., 1991a, b). Furthermore, fungi either attract mite grazers by kairomones, or repel them with volatiles (Vanhaelen et al., 1980; Bengtsson et al., 1991; Hartenstein, 1962). As a result, fungi are either palatable or unpalatable as a source of food for mites. In turn, the palatable ones are suitable for mite development, while the unpalatable are not (Sinha and Whitney, 1969; Sinha, 1968; Smrž and Čatská, 1989). Dark pigmented microfungi (*Cladosporium*, *Alternaria* and *Ulocladium*) are considered the most palatable, while fungi of genus *Aspergillus* and *Penicillium* are less palatable fungi. Zygomycetous fungi (*Mucor* and *Mortierella*) and those from the genus *Trichoderma*, *Fusarium* have an intermediate palatability (Maraun et al., 1998, 2003).

The following combinations of fungi preference and suitability for mite growth may exist: (i) preferred and suitable for growth; (ii) preferred, but unsuitable; (iii) avoided, but suitable; and (iv) avoided and unsuitable.

Preferred and palatable fungi are well known (Chen et al., 1995; Sadaka-Laulan et al., 1998) as are avoided and unsuitable ones (Kaneko et al. 1995). Preferred but unsuitable fungi are reported for the mite *Tyrophagus putrescentinae* (see Pankiewicz-Nowicka et al., 1984), some springtails (Klironomos et al., 1992) and sciarid fly larvae (Frouz and Nováková, 2001). In addition, springtails avoid some fungi, which are suitable for their development (Shaw, 1988; Walsh and Bolger, 1990). This confirms the existence of the fourth group of avoided but suitable fungi.

Thus there is evidence that four possible combinations of preference and suitability of fungi exist for soil animals. Yet fungi have not been classified as such. In order to provide evidence, using rigorous statistical testing, to support this classification, a laboratory experiment was conducted. Three mite species were used to determine the preference and suitability of fungi: *Acarus siro* L., *Lepidoglyphus destructor* (Schrank) and *Tyrophagus putrescentiae* (Schrank). These mites occur frequently in granaries (Hughes, 1976; Stejskal et al., 2003) and inhabit the same microhabitats as the microfungi upon which they feed (Sinha, 1964; Smrž and Čatská, 1987; Parkinson et al., 1991a, b). In addition, *T. putrescentiae* is a eudominant species in arable soils (Smrž and Jungová, 1989) and is used for studies on the nutritional biology and ecology of mites (Smrž, 2003).

Material and methods

A. siro L., *L. destructor* (Schrank) and *T. putrescentiae* (Schrank) were obtained from a stock culture, reared in the RICP laboratory at $25 \pm 1^\circ\text{C}$ and 85% RH on a standard diet of wheat germ, dried baker's yeast and dried *Daphnia* in a ratio of 2:1:1.

The fungi *Alternaria alternata*, *Aspergillus niger*, *Aspergillus versicolor*, *Cladosporium cladosporioides*, *Eurotium amstelodami* var. *amstelodami*, *E. amstelodami* var. *montevidensis* (anamorpha, synonym *Aspergillus montevidensis*), *Mycocladius corymbifer* and *Penicillium aurantiogriseum* were isolated from poppy seeds infested with mites, which were collected in a granary at Veleliby (Central Bohemia), in April 1999. The fungi were cultured on malt agar at $25 \pm 1^\circ\text{C}$ in the dark.

Fungi preference was tested in a double-choice preference test (Pankiewicz-Nowicka et al., 1984), in which a particular species of fungus and a standard diet (control) were offered simultaneously to each species of mite. Petri dishes (6 cm in diameter) containing a 2 mm thick layer of plaster of Paris mixed with charcoal (ratio 9:1) were used for the tests. Four small plastic discs (0.5 cm in diameter) covered with a 2 mm thick layer of malt agar were placed in the dishes as the patches. Two discs were covered with a standard amount of the fungus, and two with the standard diet of wheat germ, dried yeast and *Daphnia* (0.2 g).

One hundred to 200 mites were placed in each Petri dish. This was replicated six times for each fungus and mite combination. The dishes were incubated in the dark at $25 \pm 1^\circ\text{C}$ and 85% RH. After 6 h the number of mites on the fungus, on the standard diet and the number of trips between discs were counted. Mites on the discs were classified as actively feeding, while those walking between disc as searching for food (Hubert et al., 1999). The proportion of mites on the fungus was used as a measure of preference.

In order to test the suitability of fungi for sustaining mite population growth a vial (volume 250 ml, diameter 25 mm) containing malt agar was inoculated with a given fungus. After a week, when the vial contained abundant fungal growth, 50 mites were added. The vial was covered with mesh, and incubated in the dark at $25 \pm 1^\circ\text{C}$ and 85% RH. There were six replicates of each mite and fungus combination and the number of mites was counted 21 days later.

The data on preference and suitability were analysed by two-way ANOVAs, with mite and fungi species as fixed effect explanatory variables. Differences among particular mite and fungal species were tested by LSD tests (Sokal and Rohlf, 1995). The response variables were (i) preference for fungi, calculated by dividing the number of mites on fungal patches by the total number of mites on fungal plus standard (control) patches, and (ii) suitability of fungi for mite growth, calculated as the natural log of mite numbers after 21 days of growth. The preferences were transformed into logits, $\ln[p/(1-p)]$, where p was the number of mites on the fungal patches expressed as a proportion of the total number on the patches. The errors for preferences were assumed to be binomially distributed and tested by χ^2 approximations (Cox and Snell, 1989). Overdispersion of the binomial errors was treated by Williams' adjustment for unequal binomial denominators (Crawley, 1993, p. 351–353). Logits were weighted by the

total number of mites on both types of patch in order to avoid undue influence of logits that were estimated from replicates based on low mite number. The adequacy of models was checked by plotting standardized residuals against fitted values, and by normal probability plots of the fitted values (Crawley, 1993). Calculations were made using the general linear models in the commercial statistical package GLIM[®] v. 4 (Francis et al., 1994).

The relationships between suitability and preference of the fungi for the mites were analysed using correlation analysis. The first and the second principal axis (e.g. Quinn and Keough, 2002) were calculated for bivariate scattergrams (see Sokal and Rohlf, 1995, p. 586–593) that represented the relationship between suitability and preference for each species. The first principal axis was the major axis of the Model II regression, estimating the line represented by the correlation between the logit weighted preference and the natural log of suitability. The second principal axis was orthogonal with the first, and divided the scattergram for each mite species into quadrants (Fig. 3). The fungal species in the lower left hand quadrants were classified as avoided and unsuitable, those in the upper left hand quadrant avoided and suitable, those in the upper right hand quadrant preferred and suitable, and those in the lower right hand quadrant preferred and unsuitable. To achieve a comparable influence for each mite species, the logit weighted preferences and the natural logs were standardized, to have a mean of zero and variance of one.

Results

Preference

The three mite species reacted differently to the fungi. This was revealed by a highly significant interaction between the proportions of the individual mite species on the individual fungal diets (mite species \times fungal species: $\chi^2 = 34.97$, $df = 14$, $P = 0.001$).

Each species had highly significant specific preferences for individual species of fungi (*A. siro*, $\chi^2 = 59.35$, $df = 7$, $P = 0.001$; *L. destructor*, $\chi^2 = 63.23$, $df = 7$, $P = 0.001$; *T. putrescentiae*, $\chi^2 = 107.0$, $df = 7$, $P = 0.001$). *A. siro* and *T. putrescentiae* selected *C. cladosporioides* and *A. alternata*. Preference of *L. destructor* decreased from *E. amstelodami* var. *montevidense* to *A. niger* (Fig. 1). Within individual species of fungi,

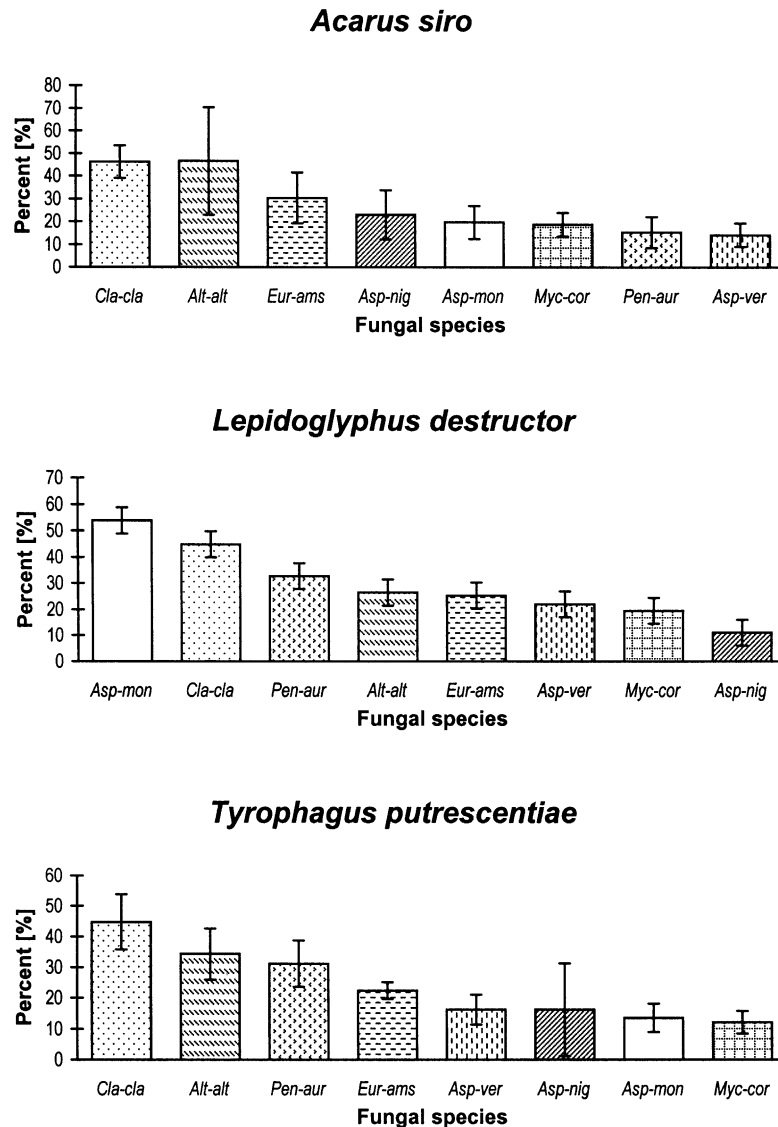


Figure 1. The preference of each mite species for the fungal species. The bars are means and lines are standard deviations. Alt-alt—*A. alternata*, Asp-mon—*E. amstelodami* var. *montevidense*, Asp-ver—*A. versicolor*, Asp-nig—*A. niger*, Cla-cla—*C. cladosporioides*, Eur-ams—*E. amstelodami* var. *amstelodami*, Myc-cor—*M. corymbifer*, Pen-aur—*P. aurantiogriseum*.

T. putrescentiae chose *E. amstelodami* var. *montevidense* significantly less frequently than *A. siro* and *L. destructor*.

Suitability

The three mites reproduced differently on the fungal species (mite species \times fungal species interaction: $F = 20.52$; $df = 16, 151$; $P < 0.001$). For each mite, population growth differed significantly on the individual fungal species (*A. siro*, $F = 20.52$; $df = 16, 151$; $P < 0.001$; *L. destructor*, $F = 64.13$; $df = 8, 45$; $P < 0.001$; *T. putrescentiae*, $F = 42.81$; $df = 8, 45$; $P < 0.001$).

The population of *A. siro* increased significantly faster on *A. versicolor*, *A. alternata*, *M. corymbifer* and *E. amstelodami* var. *montevidense* than on *P. aurantiogriseum*, *C. cladosporioides* and *E. amstelodami* var. *amstelodami*. No growth of *A. siro* was recorded on *A. niger*. The population of *L. destructor* increased significantly faster on *E. amstelodami* var. *amstelodami* than on the other species. No *L. destructor* growth was observed on *E. amstelodami* var. *montevidense*. The population of *T. putrescentiae* grew fastest on *C. cladosporioides* but also increased rapidly on *A. alternata*, *M. corymbifer*, *A. versicolor*, *E. amstelodami* var. *amstelodami* and *E. amstelodami* var. *montevidense*, which differed significantly from the slow

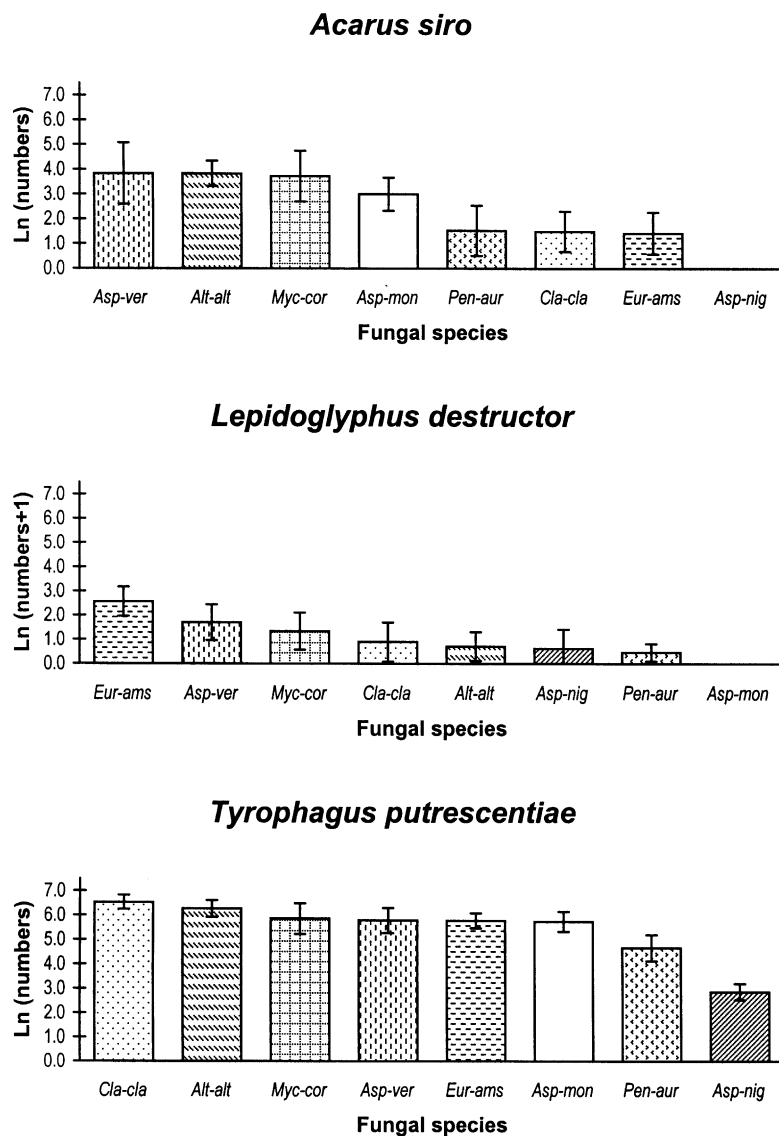


Figure 2. Population growth of each mite species on different species of fungi. The bars are means and lines are standard deviations. Alt-alt—*A. alternata*, Asp-mon—*E. amstelodami* var. *montevidense*, Asp-ver—*A. versicolor*, Asp-nig—*A. niger*, Cla-cla—*C. cladosporioides*, Eur-ams—*E. amstelodami* var. *amstelodami*, Myc-cor—*M. corymbifer*, Pen-aur—*P. aurantiogriseum*.

growth observed on *P. aurantiogriseum* and *A. niger* (Fig. 2). Population growth of *T. putrescentiae* was consistently faster than the other mite species. *A. siro* grew faster than *L. destructor*, except on *A. niger* and *E. amstelodami* var. *amstelodami*.

Relationships between suitability and preference

The feeding preference of the different fungal species and their suitability for mite population growth were not correlated. This was revealed when the standardized logit weighted preferences

and standardized natural logs of suitability for all fungi and mite species were evaluated (Pearson's correlation coefficient $r = -0.17$, $t = -0.81$, $df = 22$, NS; Spearman's rank correlation $\rho = -0.18$, $z = -0.88$, NS; Kendall's rank correlation $\tau = -0.15$, $z = -1.02$, NS) and when the relationship between suitability and preference was assessed separately for each mite species (*A. siro*: $r = -0.11$, $t = -0.27$, $df = 6$, NS; $\rho = -0.43$, $z = -1.16$, NS; $\tau = -0.30$, $z = -1.00$, NS; *L. destructor*: $r = -0.36$, $t = -0.95$, $df = 6$, NS; $\rho = -0.45$, $z = -1.22$, NS; $\tau = -0.29$, $z = -1.00$, NS; *T. putrescentiae*: $r = 0.41$, $t = 1.09$, $df = 6$, NS; $\rho = 0.43$, $z = 1.10$, NS; $\tau = 0.29$, $z = 0.99$, NS).

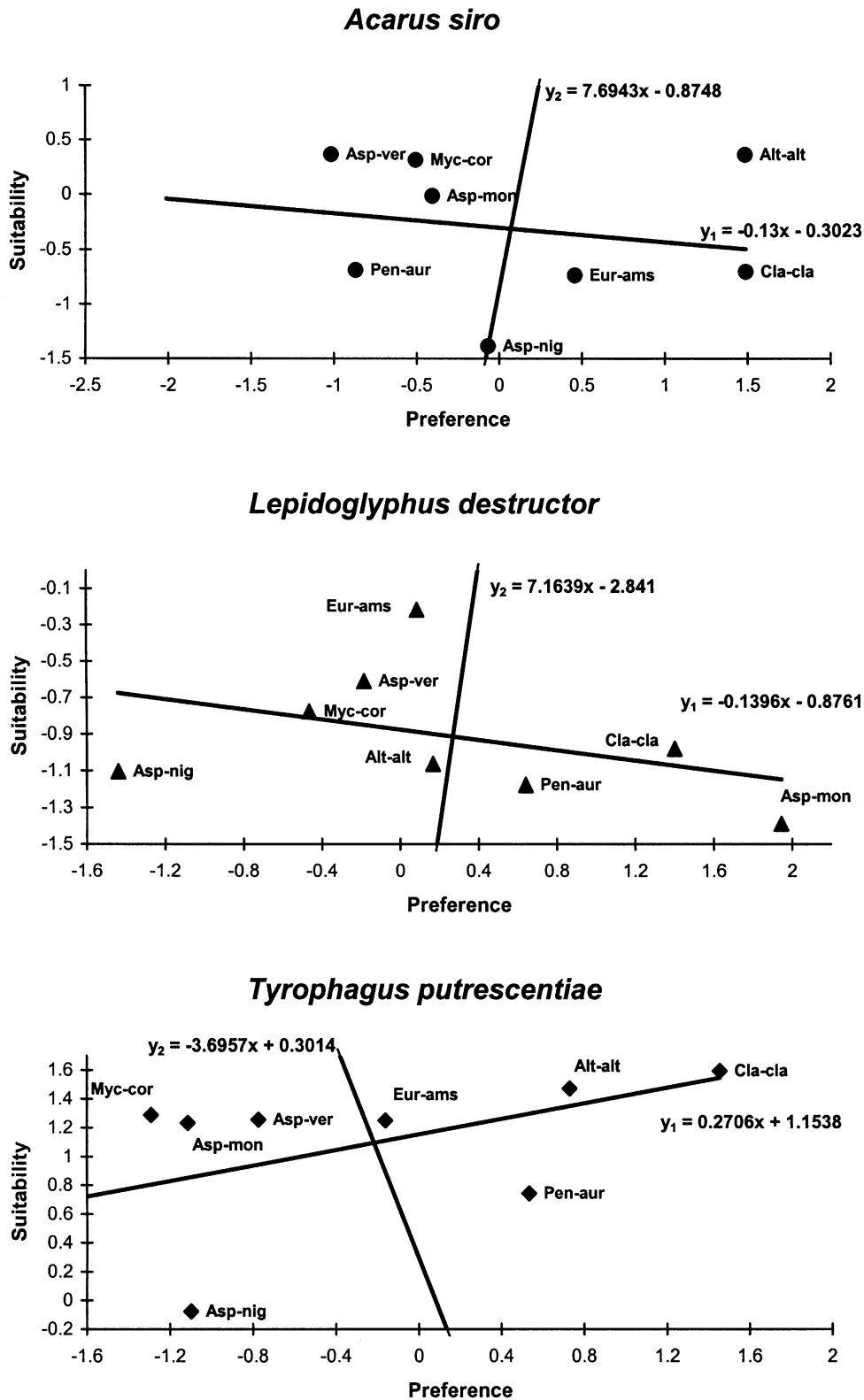


Figure 3. The first (y_1) and the second (y_2) principal axes for the bivariate scattergrams representing the relationships between standardized logit weighted preferences and standardized natural logs of suitability of the fungi for the individual mite species. The fungi in the lower left hand quadrants are avoided and unsuitable, in the upper left hand quadrants avoided and suitable, in the upper right hand quadrants preferred and suitable, and in the lower right hand quadrants preferred and unsuitable. Alt-alt—*A. alternata*, Asp-mon—*E. amstelodami* var. *montevidense*, Asp-ver—*A. versicolor*, Asp-nig—*A. niger*, Cla-cla—*C. cladosporioides*, Eur-ams—*E. amstelodami* var. *amstelodami*, Myc-cor—*M. corymbifer*, Pen-aur—*P. aurantiogriseum*.

Table 1. Separation of the fungi into four groups according to their suitability as food and the preference for them shown by the mites, based on the first and the second principal axes in bivariate scattergrams.

Mite species	Fungal species			
	Suitable + preferred	Unsuitable + preferred	Suitable + avoided	Unsuitable + avoided
<i>Acarus siro</i>	Alt-alt	Eur-ams Cla-cla Asp-nig ^a	Asp-ver Myc-cor Asp-mon	Pen-aur Asp-nig ^a
<i>Lepidoglyphus destructor</i>	Cla-cla	Pen-aur Asp-mon	Eur-ams Asp-ver Myc-cor	Asp-nig Alt-alt
<i>Tyrophagus putrescentiae</i>	Eur-ams Alt-alt Cla-cla	Pen-aur	Myc-cor Asp-mon Asp-ver	

^aUndetermined for preference.

For each mite species, bivariate scattergrams, divided into quadrants by the first and the second principal axes (Fig. 3), separated the fungi into four groups, based on preference as food and suitability for mite growth (Table 1). The fungi *A. versicolor* and *M. corymbifer* were suitable, but were avoided by all mite species. *A. alternata* was classified as a suitable and preferred species for *A. siro* and *T. putrescentiae*, and as unsuitable and avoided by *L. destructor*. *E. amstelodami* var. *montevidense* was unsuitable but preferred by *L. destructor*, and suitable but avoided by *A. siro* and *T. putrescentiae*. *A. niger* was unsuitable for mite growth and its preference as food was undetermined for *A. siro* (Fig. 3), while the same fungus was unsuitable and avoided by *L. destructor* and *T. putrescentiae*. *C. cladosporioides* was suitable and preferred by *L. destructor* and *T. putrescentiae*, and unsuitable but preferred by *A. siro*. Furthermore, *E. amstelodami* var. *amstelodami* was suitable and preferred by *T. putrescentiae*, unsuitable but preferred by *A. siro*, and suitable but avoided by *L. destructor*. Finally, *P. aurantiogriseum* was unsuitable but preferred by *L. destructor* and *T. putrescentiae*, and unsuitable and avoided by *A. siro*.

Discussion

The suitability of a fungus for sustaining mite population growth depends (i) on the mite's ability to utilize the fungus and (ii) on the digestibility of particular fungal species (cf. Maraun et al., 1998, 2003).

In this study, the differences in mite population growth were probably associated with fungal

digestibility. Fungal mycelium is formed of cell walls rich in chitin, and cell contents rich in trehalose (see Luxton, 1972; Siepel and Ruiter-Dijkmann, 1993). The cell walls usually pass through the digestive tracts of mites undigested, while the cell content is digested (Hubert et al., 2001). This indicates that the digestive enzyme trehalase has a key role in fungal digestion (cf. Siepel and Ruiter-Dijkmann, 1993). The trehalase activity is highest in *Tyrophagus*, moderate in *Acarus*, and lowest in *Lepidoglyphus* (Hubert unpublished), which correlates with the population growth of these mites on the fungi—*Tyrophagus* grew fast compared to *Lepidoglyphus*. Based on the presence of the appropriate digestive enzymes, *Tyrophagus* and *Acarus* can digest fungi (Hubert, unpublished). *T. putrescentiae*, which had the highest population growth, preferred more fungal species than *A. siro*, which had an intermediate population growth. The poor ability of *L. destructor* to utilize mycelium accounts for its poor population growth. Sinha (1966, 1968) also recorded a decrease (from *Tyrophagus* and *Acarus* to *Lepidoglyphus*) in the numbers of suitable fungi for mite population growth.

Interspecific differences in the rate of mite population growth on different fungal diets are commonly reported and are associated with particular feeding adaptations (Sinha and Mills, 1968; Sinha and Whitney, 1969; Pankiewicz-Nowicka et al., 1984; Parkinson et al., 1991a). Mycotoxins or other secondary metabolites possibly account for this variability. For instance, *Tyrophagus* larvae suffered a 13% mortality on diets containing sterigmatocystin produced by *A. versicolor* (Rodríguez et al., 1984). Smrž and Čatská (1987) reported a range (0–10 000 individuals) of population

growths for *Tyrophagus* fed on fungal strains differing in biochemistry. Biochemical differences thus may explain the variability in the population growth of *Tyrophagus* and *Acarus* on *Aspergillus*, *Alternaria* and *Cladosporium* observed in this study. Similar variability has been recorded in other studies (cf. Pankiewicz-Nowicka and Boczek, 1984; Parkinson et al., 1991a, b).

Our results indicate that mite food choice for fungi is not correlated with fungal suitability for development of the compared mite species. Based on this finding we suggest the existence of four fungal groups in terms of mite preferences or fungal attractiveness and fungal suitability for mite development: (i) preferred and suitable for growth; (ii) preferred, but unsuitable; (iii) avoided, but suitable; and (iv) avoided and unsuitable. This grouping, based on species specific relationships between suitability and preference, takes into account the species-specific reactions of the individual mite species to individual fungi, as revealed by the significant mite \times fungus interactions in the analyses of preference and suitability.

The “avoided and unsuitable” fungal species would be the least affected by mite activity. Mite grazing on these species and spore dispersal via mites is minimal. The avoided and unsuitable species, *A. niger*, was rejected both by astigmatid and oribatid mites (Hartenstein, 1962; Sinha, 1966), though, in some case, its spores were found in mite guts (Behan and Hill, 1978; Hubert et al., 2000). These findings could be consistent with the inconclusive preference for fungi by *A. siro* (Figure 3 and Table 1).

The “preferred and suitable”, or “preferred, but unsuitable” fungi attract their micro-arthropod grazers with volatile compounds (Bengtsson et al., 1988, 1991). This behaviour should be adaptive, but it is unknown whether the attractants produced by these fungi enable them to achieve higher metabolic rates and fitness (Bengtsson et al., 1993). In this study, five species of fungi, *A. alternata*, *Cladosporium cladosporioides*, *E. amstelodami* var. *amstelodami*, *E. amstelodami* var. *montevidense* and *P. aurantiogriseum* attracted the mites. Interestingly, the same species attracted both *Acarus* and *Tyrophagus* mites (Table 1). This indicates that the same odour may lure different species of fungivorous mites.

The “preferred and suitable” fungi should profit from the dispersal of their spores in mite faeces, or on the surfaces of mites, to new un-colonized habitats, such as plant litter or uncolonized storage grain in granaries (Sinha, 1979). The preferred and suitable species *A. alternata* and *Cladosporium cladosporioides* occur frequently in plant litter

(Domsch et al., 1993) as well as in granaries (Sinha, 1979), and *Cladosporium* is frequently isolated from oribatid mites (Behan and Hill, 1978). *Penicillium griseofulvum* spores were frequently ingested by *Schelorbates laevigatus* (see Hubert et al., 1999), but gut content analyses of mites indicated that these spores were not digested (Griffiths et al., 1959; Smrř and Čatská, 1987). Consequently, the spore dispersal in mite faeces could be significant, especially if large quantities of spore containing faecal pellets are produced. This mechanism could be more important than dispersal of spores on the body surface of mites. However, in laboratory experiments *T. putrescentiae* consumed a large quantity of fungal mycelium. Thus, high population densities of mites may not be advantageous for fungi since this may result in overgrazing (Bengtsson et al., 1994). The “preferred, but unsuitable” fungi may profit from spore dispersal by mites and, though they are grazed (cf. Hedlund et al., 1991), they are not at risk of overgrazing by mites. That just one fungus was preferred but unsuitable for *T. putrescentiae* can be explained by its ability to digest a wide spectrum of fungi.

Mites have the least effect on “avoided and unsuitable” fungal species, while preferred fungi seem to be the most influenced by mites in terms of mite grazing and dispersion of fungal spores. The extent to which species of mites profit from feeding on various species of fungi depends on the mites’ digestive ability.

Acknowledgements

We are much indebted to Tony Dixon for helpful suggestions and improvement of our English. The authors are also grateful for Mark Maraun’s valuable comments and revision of the manuscript. This work was supported by grants from the Czech Ministry of Agriculture (MZE-000-2700603).

References

- Armitage, D.M., George, C.L., 1986. The effect of three species of mites upon fungal growth on wheat. *Exp. Appl. Acarol.* 2, 111–124.
- Behan, V.M., Hill, S.B., 1978. Feeding habits and spore dispersal oribatid mites in the North American Arctic. *Rev. Écol. Biol. Sol.* 15, 497–516.
- Bengtsson, G., Erlandsson, A., Rundgren, S., 1988. Fungal odour attracts soil Collembola. *Soil Biol. Biochem.* 20, 25–30.

- Bengtsson, G., Hedlund, K., Rundgren, S., 1991. Selective odor perception in the soil Collembola *Onychiurus armatus*. *J Chem Ecol* 17, 2113–2125.
- Bengtsson, G., Hedlund, K., Rundgren, S., 1993. Patchiness and compensatory growth in a fungus-Collembola system. *Oecologia* 93, 296–302.
- Bengtsson, G., Hedlund, K., Rundgren, S., 1994. Food and density-dependent dispersal: evidence for a soil collembolan. *J Anim Ecol* 63, 513–520.
- Bowman, C.E., 1984. Comparative enzymology of economically important astigmatid mites. In: Griffiths, D.A., Bowman, C.E. (Eds.), *Acarology* 6, Vol. 2. Ellis Horwood, Chichester, pp. 993–1001.
- Chen, B., Snider, R.J., Snider, R.M., 1995. Food preferences and effects of food type on history of some soil Collembola. *Pedobiologia* 39, 496–505.
- Cox, D.R., Snell, E.J., 1989. *Analysis of Binary Data*. Chapman & Hall, London.
- Crawley, M.J., 1993. *GLIM for ecologists*. Blackwell Scientific Publications, Oxford.
- Daneshvar, H., Rodriguez, J.G., 1979. Fungi dietary of *Caloglyphus berlessei* Mich. (Acarina: Acaridae). *Proceedings of the Fourth International Congress Acarology, Akadémiai Kiadó, Budapest*, pp. 593–598.
- Domsch, K.H., Gams, W., Anderson, T.H., 1993. *Compendium of soil fungi*. Vol. 1. IHW-Verlag, Eching.
- Fassatiová, O., Lýsek, H., 1982. Ovicidal fungi in soil ecological system. *Acta Univ. Carol. Biol.* 9, 297–334.
- Francis, B., Green, M., Payne, C., (Eds.) 1994. *The GLIM System. Release 4 Manual*. Clarendon Press, Oxford.
- Frouz, J., Nováková, A., 2001. A new method for rearing the sciaroid fly, *Lycoriella ingénue* (Diptera: Sciaridae), in the laboratory: possible implications for the study of fly–fungal interactions. *Pedobiologia* 45, 329–340.
- Griffiths, D.A., Hodson, A.C., Christensen, C.M., 1959. Grain storage fungi associated with mites. *J. Econ. Entomol.* 52, 514–518.
- Hanlon, R.D.G., 1981. Influence of grazing by Collembola on the activity of senescent fungal colonies grown on media of different nutrient concentration. *Oikos* 36, 362–367.
- Hanlon, R.D.G., Anderson, J.M., 1979. The effects of Collembola grazing on microbial activity in decomposing leaf litter. *Oecologia (Berlin)* 38, 93–99.
- Hartenstein, R., 1962. Soil Oribatei. I. Feeding specificity among forest soil Oribatei (Acarina). *Ann. Entomol. Soc. Am.* 55, 202–206.
- Hedlund, K., Boddy, L., Preston, C.M., 1991. Mycelial responses of the soil fungus, *Mortierella isabellina*, to grazing by *Onychiurus armatus* (Collembola). *Soil Biol. Biochem.* 23, 361–366.
- Hedlund, K., Augustsson, A., 1995. Effects of enchytraeid grazing on fungal growth and respiration. *Soil Biol. Biochem.* 27, 905–909.
- Hubert, J., Šustr, V., Smrž, J., 1999. Feeding of the oribatid mite *Scheloribates laevigatus* (Acari: Oribatida) in laboratory experiments. *Pedobiologia* 43, 328–339.
- Hubert, J., Kubátová, J., Šárová, J., 2000. Feeding of *Scheloribates laevigatus* (Acari: Oribatida) on different stadia of decomposing grass litter (*Holcus lanatus*). *Pedobiologia* 44, 627–639.
- Hubert, J., Žilová, M., Pekár, S., 2001. Feeding preferences and gut contents of three panphytophagous oribatid mites (Acari: Oribatida). *Eur. J. Soil Biol.* 37, 197–208.
- Hughes, A.M., 1976. *The mites of stored food and houses*. Technical Bulletin 9, Ministry of Agriculture, Fisheries and Food, London.
- Jacot, A.P., 1930. Moss mites as spore-bearers. *Mycologia* 22, 94–95.
- Kaneko, N., Mclean, M.A., Parkinson, D., 1995. Grazing preference of *Onychiurus subtenuis* (Collembola) and *Opiella nova* (Oribatei) for fungal species inoculated on pine needles. *Pedobiologia* 39, 538–546.
- Klironomos, J.N., Widden, P., Deslandes, I., 1992. Feeding preferences of the collembolan *Folsomia candida* in relation to microfungus successions on decaying litter. *Soil Biol. Biochem.* 24, 685–692.
- Klironomos, J.N., Hart, M.M., 2001. Animal nitrogen swap for plant carbon. *Nature* 410, 651–652.
- Luxton, M., 1972. Studies on the oribatid mites of a Danish beech wood soil—I.; Nutritional biology. *Pedobiologia* 12, 434–463.
- Maraun, M., Migge, S., Schaefer, M., Scheu, S., 1998. Selection of microfungus food by six oribatid mite species (Oribatida, Acari) from different beech forests. *Pedobiologia* 42, 232–240.
- Maraun, M., Martens, H., Migge, S., Theenhaus, S., Scheu, S., 2003. Adding to “the enigma of soil animal diversity”: fungal feeders and saprophagous soil invertebrates prefer similar food substrates. *Eur. J. Soil Biol.* 39, 85–95.
- Nordbing-Hertz, B., 1988. Nematophagous fungi: strategies for nematode exploitation and for survival. *Microbial Sci.* 5, 108–116.
- O’Conor, B.M., 1979. Evolutionary origins of astigmatid mites inhabiting stored products. In: Rodriguez, J.G. (Ed.), *Recent Advances in Acarology*, Vol. I. Academic Press, NY, pp. 273–278.
- O’Conor, B.M., 1984. Acarine–fungal relationships: the evolution of symbiotic associations. In: Wheeler, Q., Blackwell, M. (Eds.), *Fungus–insect relationships: Perspectives in ecology and evolution*. Columbia University Press, NY, pp. 354–381.
- Quinn, G.P., Keough, M.J., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- Pankiewicz-Nowicka, D., Boczek, J., 1984. A comparison of food preference of some acarid mites (Acari: acaroidae). In: Griffiths, D.A., Bowman, C.E. (Eds.), *Acarology* 6., Vol. 2. Ellis Horwood, Chichester, pp. 987–993.
- Pankiewicz-Nowicka, D., Boczek, J., Davis, R., 1984. Food selection in *Tyrophagus putrescentiae* (Schränk) (Acaria: Acarididae). *J. Georg. Entomol. Soc.* 19, 317–321.
- Parkinson, D., Visser, S., Whittaker, J.B., 1979. Effects of collembolan grazing on fungal colonization of leaf litter. *Soil Biol. Biochem.* 11, 529–535.

- Parkinson, D., Barron, C.A., Barker, S.M., Thomas, A.C., Armitage, D.M., 1991a. Longevity and fecundity of *Acarus siro* on four field and eight storage fungi. *Exp. Appl. Acarol.* 11, 1–8.
- Parkinson, D., Jamieson, N., Eborall, J., Armitage, D.M., 1991b. Comparison of the fecundity of three species of grain store mites on fungal diets. *Exp. Appl. Acarol.* 12, 297–302.
- Rodriguez, J.G., Potts, M.F., Patterson, C.G., 1984. Mycotoxin-producing fungi: effects on stored product mites. In: Griffiths, D.A., Bowman, C.E. (Eds.), *Acarology* 6, Vol. 2. Ellis Horwood, Chichester, pp. 343–350.
- Sadaka-Laulan, N., Ponge, J.F., Roquebert, M.F., Burry, E., Boumezzough, A., 1998. Feeding preferences of the collembolan *Onychiurus sinsensis* for fungi colonizing holm oak litter (*Quercus rotundifolia* Lam). *Eur. J. Soil Biol.* 34, 179–188.
- Shaw, P.J.A., 1988. A consistent hierarchy in the fungal feeding preferences of the collembola *Onychiurus armatus*. *Pedobiologia* 31, 179–187.
- Siepel, H., Rüter-Dijkman, E.M., 1993. Feeding guilds of oribatid mites based on their carbohydrase activities. *Soil Biol. Biochem.* 26, 1491–1497.
- Siepel, H., Maaskamp, F., 1994. Mites of different feeding guilds affect decomposition of organic mater. *Soil Biol. Biochem.* 26, 1389–1394.
- Sinha, R.N., 1964. Ecological relationship of store-products mites and seed-borne fungi. *Proceedings of the First International Congress of Acarology. Acarologia* 6, 372–389.
- Sinha, R.N., 1966. Feeding and reproduction of some stored-product mites on seed-borne fungi. *J. Econom. Entomol.* 59, 1227–1232.
- Sinha, R.N., 1968. Adaptive significance of mycophagy in stored-product Arthropoda. *Evolution* 22, 785–798.
- Sinha, R.N., 1979. Ecology of microflora in stored grain. *Ann. Technol. Agric.* 28, 191–209.
- Sinha, R.N., Mills, J.T., 1968. Feeding and reproduction of the grain mite and the mushroom mite on some species of *Penicillium*. *J. Econom. Entomol.* 61, 1548–1552.
- Sinha, R.N., Whitney, R.D., 1969. Feeding and reproduction of the grain and the mushroom mite on wood-inhabiting Hymenomycetes. *J. Econom. Entomol.* 62, 837–840.
- Smrž, J., 2003. Microanatomical and biological aspects of bacterial associations in *Tyrophagus putrescentiae* (Acari: Acaridida). *Exp. Appl. Acarol.* 31, 105–113.
- Smrž, J., Čatská, V., 1987. Food selection of the field population of *Tyrophagus putrescentiae* (Schrank) (Acari: Acaridida). *J. Appl. Entomol.* 104, 329–335.
- Smrž, J., Čatská, V., 1989. The effect of the consumption of some soil fungi on the internal microanatomy of the mite *Tyrophagus putrescentiae* (Schrank) (Acari: Acaridida). *Acta Univ. Carol.-Biol.* 33, 81–93.
- Smrž, J., Jungová, E., 1989. The ecology of a field population of *Tyrophagus putrescentiae* (Acari: Acaridida). *Pedobiologia* 33, 183–192.
- Sokal, R., Rohlf, F.J., 1995. *Biometry* 3rd Edition. Freeman, San Francisco.
- Stejskal, V., Hubert, J., Kučerová, Z., Munzbergová, Z., Lukáš, J., Ždárková, E., 2003. The influence of the type of storage on pest infestation of stored grain in the Czech Republic. *Plant Soil Environ.* 49, 52–62.
- Vanhaelen, M., Vanhaelen-Fastré, R., Geeraerts, J., 1980. Occurrence in mushrooms (Homobasidiomycetes) of cis and trans-octa-1,5-dien-3-ol, attractants to the cheese mite *Tyrophagus putrescentiae* (Schrank) (Acarina, Acarididae). *Experientia* 36, 406.
- Visser, S., Whittaker, J.B., Parkinson, D., 1981. Effects of collembolan grazing on nutrient release and respiration of a leaf litter inhabiting fungus. *Soil Biol. Biochem.* 13, 215–218.
- Walsh, M.I., Bolger, T., 1990. Effects of diet on the growth and reproduction of some Collembola in laboratory cultures. *Pedobiologia* 34, 161–171.
- Warcup, J.H., 1967. Fungi in soil. In: Burges, A., Raw, F. (Eds.), *Soil Biology*. Academic Press, London, UK, pp. 51–110.
- Williams, R.H., Whipps, J.M., Cooke, R.C., 1998a. Role of soil mesofauna in dispersal of *Coniothyrium minitans*: Transmission to sclerotia of *Sclerotinia sclerotiorum*. *Soil Biol. Biochem.* 30, 1929–1935.
- Williams, R.H., Whipps, J.M., Cooke, R.C., 1998b. Role of soil mesofauna in dispersal of *Coniothyrium minitans*: Mechanisms of transmission. *Soil Biol. Biochem.* 30, 1937–1945.