Impact of a tarsonemid prey mite and its fungal diet on the reproductive performance of a predatory mite

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Abstract:

Phytoseiid predatory mites are the most important group of biocontrol agents currently implemented in protected cultivations worldwide. The possibility to produce these predators at high densities on factitious prey mites is a crucial factor for their success. Commonly used factitious prey mites comprise mainly species belonging to the cohort of Astigmatina. In the present study, we investigated the potential of tarsonemid prey mites as a food source for the spider mite predator *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae). The oviposition of *N. californicus* on mixed stages of *Tarsonemus fusarii* Cooreman (Acari: Tarsonemidae) was similar to that on its natural prey, the two-spotted spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae). As most tarsonemids are specialized fungus-feeders, we tested the effect of different fungal species on the growth of *T. fusarii*. Subsequently, we analysed the impact on the fungal growing medium on the oviposition of *N. californicus*. The fungal growing medium of *T. fusarii* had a significant effect on the reproductive output of the predatory mite, having a negative effect. When *T. fusarii* was separated from the rearing medium, these detrimental

effects were not observed. The present study shows the potential of using tarsonemid prey mites in the production of predatory mites.

Key words: Tarsonemidae, factitious prey, Phytoseiidae, biological control, mass-rearing

Introduction:

Being one of the largest groups within the Heterostigmata, the family of Tarsonemidae currently consists of 43 genera and over 600 described species (Lofego et al., 2016). Mites from this family have a wide range of feeding behaviours, from true herbivores, algivores, fungivores to egg predators, and they occupy many natural (e.g. plants, soil litter) and human-made habitats (e.g. stored product facilities, plant cultivations) (Lindquist, 1986). Many species live in close association with insects, interacting either directly or indirectly with them. Direct interactions range from commensalism, phoresy to predation. Some species from the genus *Tarsonemus* compete with bark beetle larvae (e.g. *Dendroctonus* sp.) for fungal food, demonstrating indirect associations as well (Lombardero et al., 2003; Scott et al. 2008). For species, such as *Polyphagotarsonemus latus* (Banks), *Phytonemus pallidus* (Banks) and *Steneotarsonemus spinki* Smiley, which are destructive pests of a wide range of agricultural crops, numerous studies have investigated the biology of these species and their control (Easterbrook et al., 2001; Gerson, 1992; Hummel et al., 2009). In contrast, information is scarce on the biology and ecological role of fungivorous species, even though they comprise the majority of the tarsonemids (Lindquist, 1986). Species within the genus of *Daidalotarsonemus* and *Excelsotarsonemus* thrive on algae and fungi growing on the foliage of plants, predominantly in humid areas (Ochoa et al., 1995; Sousa et al., 2018). Fungi are also the primary food source of tarsonemids within the genus *Tarsonemus*. The cosmopolitan species *Tarsonemus fusarii* Cooreman was reported as a

contaminant of fungal laboratory cultures and was shown to feed on a wide range of fungal species (Geeraerts, 1974; Gotz and Reichenberger, 1953). Fungal food preference was tested for *Tarsonemus confusus*, indicating that such preference exists, and specific fungus can alter the mites' functional sex ratio (Belczewski and Harmsen 1997). Together with *Tarsonemus granarius* Lindquist, *T. fusarii* is also found in granaries thriving on a variety of fungi, such as *Chaetomium* and *Aspergillus* (Lindquist, 1972). *Tarsonemus fusarii* is one of the most ecologically widespread species (Kaliszewski & Sell 1990).

Phytoseiid predatory mites are important biocontrol agents used worldwide to control mite and insect pests (McMurtry et al., 2013). The possibility to mass-produce phytoseiids on factitious prey mites has been a major contributor to their successful implementation in biocontrol programs (Calvo et al., 2015; Ramakers and Van Lieburg, 1982). Traditionally, factitious prey mites belong to the cohort of Astigmatina (Zhang, 2003), such as *Carpoglyphus lactis* (L.) (Bolckmans and van Houten, 2006), *Lepidoglyphus destructor* (Schrank) (Castagnoli et al., 2006) and *Suidasia medanensis* (Oudemans) (Midthassel et al., 2013).

Phytoseiids effectively feed on both pest tarsonemids, such as *P. latus* (Duarte et al., 2015), and non-pest tarsonemids, such as *T. fusarii* (Vangansbeke et al., 2018). Here, we assessed the potential of *T. fusarii* to be used as a factitious prey mite in the production of the predatory mite *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae). The latter is typically used as a biological control agent of spider mites (McMurtry et al., 2013; van Lenteren, 2012).

For the production of astigmatid prey mites, mixes of bran, wheat germ, and yeast are commonly used food sources (Huang et al., 2013; Ramakers and Van Lieburg, 1982). As mouthparts of Tarsonemidae are stylet-like, adapted for piercing and sucking (Hughes, 1976; Kaliszewski et al., 1995), Nuzacci et al 2002), most species rely on the presence of fungal mycelia to enable food

ingestion. Therefore, we explored two fungi that could be used as a food source for *T. fusarii*. Ideally, such fungal food sources should be 1) of high nutritional value for *T. fusarii*, 2) safe to use for biocontrol companies (absence of toxins) and 3) non-plant pathogenic. Two fungi, which should meet the latter two requirements, are *Aspergillus oryzae* and *Fusarium venenatum*. *A. oryzae* has been used for centuries in fermentation processes of rice and soy products (“koji”) in South-East Asia. It is generally accepted that *A. oryzae*, through years of cultivation, became a domesticated ecotype of *Aspergillus flavus* (Barbesgaard et al., 1992; Machida et al., 2005). During this domestication process, aflatoxins present in *A. flavus* have been eliminated (Domsch et al., 1980). *F. venenatum* is used for the production of mycoprotein for human consumption under the trade name “Quorn” (Wiebe, 2002). The strain A 3/5 (NRRL 26139 = ATCC 20334) used for commercial production does not produce aflatoxins (O’Donnell et al., 1998). Here, we tested the nutritional value of *T. fusarii* for *N. californicus* as compared to its natural prey, the spider mite *Tetranychus urticae*. Secondly, we assessed different food sources for the growth of *T. fusarii*. For this, we compared a standard mix of wheat bran, wheat germ, and yeast with two fungi, *A. oryzae* and *F. venenatum*, grown on bran. Finally, the impact of *A. oryzae* on the reproductive performance of *N. californicus* was investigated.

Material and Methods

Mite colonies

Individuals of *Tarsonemus fusarii* were collected from *Rubus* sp. leaves in Gentbrugge (Belgium) (51.037472, 3.771090) and were maintained on a mixture of bran and wheat germ (50%/50%, w/w) at 22 ± 1 °C, 80 ± 5 % relative humidity and a photoperiod of 16 hours light and 8 hours dark.

Two-spotted spider mites, *T. urticae*, were grown on bean plants in a separate greenhouse department at the greenhouse facilities of Biobest N.V. (Greenlab, Westerlo, Belgium). *Neoseiulus californicus* females used for the experiments were collected from the mass-rearing facilities at Biobest N.V.

Fungal strains

Both *Fusarium venenatum* Nirenberg (ATCC® 20334™) and *Aspergillus oryzae* var. *viridis* Murakami, anamorph (ATCC® 22788™) were grown on petri dishes containing potato dextrose agar (PDA Pronadisa). When the fungi were fully developed, circular pieces were removed from these agar Petri dishes to inoculate a mixture of equal parts of wheat bran and water with 5% (by weight) of potato dextrose broth (PDB Pronadisa). This mixture was incubated for 48 hours at 30°C at 90% R.H. before being offered to the mites. This mixture, as well as the combination of temperature, humidity, and time were previously shown to yield the best results for the mite rearings.

Rearing of *T. fusarii* on bran inoculated with fungus

The mites were reared on each of the two fungal strains that had been grown on the wheat bran + PDB as described previously. The mites were kept at 22 ± 1 °C, 80 ± 5 % relative humidity and a photoperiod of 16 hours light and 8 hours dark.

Experiment 1: *T. fusarii* as a food source for *N. californicus*

In the first experiment, we performed a two-day egg-laying trial of *N. californicus* when provided with either *T. fusarii* or *T. urticae* as a food source. Young gravid female *N.*

californicus were transferred individually from the mass-rearing medium on small PVC arenas (2 x 4 cm). Arenas were placed on wet cotton and the edges of the arena were covered with moist tissue paper to prevent the mites from escaping. Tarsonemid prey mites were offered *ad libitum* by transferring a small spoon of rearing medium (± 0.2 g) onto the PVC arena. For the spider mites, a small piece (1 x 1 cm) of heavily infested leaf was cut from the bean plants and was provided on the arena. Eggs produced by *N. californicus* were removed and counted daily. Per treatment, 12 replicates were set up. As the pre-experimental diet might affect the predator's initial fecundity (Sabelis, 1990), the first day of egg-laying was omitted from the analysis. The average number of eggs produced on the second day were compared using GLM analysis with a Poisson distribution. Contrasts between diets were assessed by stepwise model simplification through aggregation of non-significant factor levels (Crawley, 2013). All statistical analyses were done using the computer software R version 3.6.1 (R Core Team 2014).

Experiment 2: Growth of *T. fusarii* on different food sources

In this experiment, we compared the population growth of *T. fusarii* when fed on different food sources. These food sources were a bran inoculated with either a yeast (*Saccharomyces cerevisiae*) mix, or with one of the two fungi *A. oryzae* and *F. venenatum*. The food sources were prepared in the same manner as described above and were put in a 30ml insect breeding dish with a ventilated lid. Two thousand *T. fusarii* were added to two grams of each of the food sources and allowed to grow for ten days. At the end of these ten days, the number of mites in each of the food source was estimated by taking a sample (~ 0.100 g) and counting the total number of mobile mites and extrapolating to determine the total amount of mobile mites in each repetition. The average number of mobile *T. fusarii* were compared using GLM analysis with a

normal distribution. Contrasts among treatments were determined with general linear hypothesis testing (function `glht` of the package `lsmeans` in R, Lenth 2016). All statistical analyses were done using the computer software R version 3.6.1 (R Core Team 2014).

Experiment 3: Effect of *T. fusarii* rearing method on the oviposition of *N. californicus*

For this experiment, *T. fusarii* was reared on bran, which was previously inoculated with either *A. oryzae* or *F. venenatum* (see above). *T. fusarii* was grown on the fungal media for more than one month before the start of the experiment. Experimental procedures were similar, as was described for experiment 1. Only now, a small spoon (± 0.2 g) of *T. fusarii* grown on either bran with *A. oryzae* or *F. venenatum* was supplied on the arenas as a food source. Egg-laying of female predators was counted during four consecutive days. For each food source, 12 replicates were used. Again, the first day of oviposition was not used in the analysis. The difference between the food sources was compared using linear mixed-effect models (LME) with diet, time, and their interaction as fixed factors. Individual mite was a random factor. Non-significant interaction and factors were removed until a minimal satisfying model was reached (Crawley, 2013).

Experiment 4: Effect of *T. fusarii* rearing medium on the oviposition of *N. californicus*

Here, we tested whether the *A. oryzae* rearing medium of *T. fusarii* could affect the reproductive performance of *N. californicus*. Therefore, we provided the predatory mite females with *T. fusarii* that were either sieved out from the fungus/bran medium or provided together with the fungus/bran mix. *T. fusarii* were separated from the rearing medium using a 100 μ m sieve. Hence, besides *T. fusarii*, also ample spores and short pieces of mycelia were present in the

sieved out material. The trial set-up and statistical analysis was similar as was described for experiment 2.

Results

Experiment 1: *T. fusarii* as a food source for *N. californicus*

Diet did not affect the oviposition of *N. californicus* (GLM: $\text{Chi}^2=17.939$; $\text{df}= 1, 18$; $p=0.729$), with 1.8 ± 0.3 eggs/female/day and 1.6 ± 0.4 eggs/female per day when offered *T. urticae* and *T. fusarii*, respectively.

Experiment 2: Growth of *T. fusarii* on different food sources

There was a significant effect of the different food sources on the total number of mites (GLM: $F=7.1$; $\text{df}= 2, 16$; $p>0.01$). The number of *T. fusarii* was greater when reared on *A. oryzae* as compared to the other food sources (Figure 1). There were no differences between the total number of mites between the mix with yeast and *F. venenatum* treatments.

Experiment 3: Effect of *T. fusarii* rearing method on the oviposition of *N. californicus*

There was no significant effect of the interaction between time and diet (LME: $\text{Chi}^2=3.394$; $\text{df}= 1$; $p=0.494$) and time (LME: $\text{Chi}^2=1.455$; $\text{df}= 1$; $p=0.483$). Diet had a significant effect on the egg-production of *N. californicus* (Figure 2, LME: $\text{Chi}^2=23.234$; $\text{df}= 1$; $p<0.0001$), with a

twofold increase in oviposition when fed *T. fusarii* that was produced on *F. venenatum* as compared to mites produced on *A. oryzae*.

Experiment 4: Effect of *T. fusarii* rearing medium on the oviposition of *N. californicus*

Time and the interaction between diet and time did not have a significant effect (time= LME: $\chi^2=0.705$; df= 1; $p=0.703$ and diet x time= LME: $\chi^2=0.054$; df= 1; $p=0.973$). Sieving out *T. fusarii* significantly increased the oviposition of *N. californicus* (**Error! Reference source not found.**, LME: $\chi^2=37.069$; df= 1; $p<0.0001$).

Discussion

Augmentative biological control is a key component in integrated pest management, especially in protected cultivation of vegetable and ornamental crops (Naranjo et al., 2015). Phytoseiid predatory mites comprise the most important group of commercially available natural enemies (van Lenteren, 2012). An important factor explaining this success is the possibility to mass-produce these predatory mites at high densities on factitious astigmatid prey (Calvo et al., 2015; Knapp et al., 2018). However, further improvement of the efficiency of mass-production systems remains essential to reliably supply growers with an economic product (Knapp et al., 2018) and to further expand the scope towards open-field applications of biocontrol agents.

Many phytoseiids are known to feed, reproduce and control pest tarsonemids, such as the broad mite *P. latus* (Badii and McMurtry, 1984; Duarte et al., 2015; Fan and Petitt, 1994), the cyclamen mite *P. pallidus* (Easterbrook et al., 2001; Tuovinen and Lindqvist, 2010) and *Steneotarsonemus* spp. (Messelink and van Holstein-Saj, 2007; Zhang, 2003). Studies on feeding behaviour of phytoseiids on non-pest tarsonemids, however, are scarce. Only recently,

Neoseiulus barkeri Hughes was reported to feed on *Tarsonemus confusus* Ewing (Li et al., 2018). For *Amblyseius swirskii* Athias-Henriot, feeding on *T. fusarii* resulted in an equally high oviposition rate as compared to feeding on the astigmatid *C. lactis* (Vangansbeke et al., 2018). In this study, also *T. fusarii* proved to be a good food source for the spider mite predator *N. californicus*.

Mites from the genus *Tarsonemus* are considered generalist fungus-feeders (Lindquist, 1986). Some species, such as *Tarsonemus ips* Lindquist and *Tarsonemus krantzi* Smiley & Moser, use their C-tergite ventral flaps to carry fungal spores (Moser, 1985). Other species are associated with feeding on fungal diseases, such as *T. confusus* feeding on *Cladosporium* sp. and *Alternaria* sp. (Belczewski and Harmsen 1997; Van der Walt et al., 2011). Although some instances have been reported where *Tarsonemus* representatives were observed to be associated with plant damage in some ornamental crops, it is believed that this species, and in extension all mites within the genus of *Tarsonemus*, are fungivorous and are never the causal agents of primary plant damage (Zhang, 2003).

Occasionally, *Tarsonemus* species have been reported as pests in mushroom cultivation (*Tarsonemus myceliophagus* (Hussey and Gurney, 1967)) or stored grain facilities (*Tarsonemus granarius* (Lindquist, 1972)).

Here, *A. oryzae* grown on bran was a superior food for *T. fusarii*, with seven-fold larger population numbers as compared to that on a standard astigmatid growing medium consisting of wheat bran, wheat germ and yeast. Although not significantly different, *F. venenatum* also resulted in higher numbers of tarsonemid prey mites. Several factors determine the acceptance

and subsequent performance of a mite feeding on fungus. Besides the ability to digest the ingested fluids (Hubert et al., 2001), the presence of mycotoxins potentially affects the suitability of fungal food source (Parkinson et al., 1991; Rodriguez et al., 1980). As both fungi tested are considered mycotoxin-free, the latter reason seems unlikely. Another explanation for the superiority of *A. oryzae* over *F. venenatum* might be the difference in the production of fungal spores. The *Aspergillus* strain used in our experiments produced an abundance of spores as opposed to the *F. venenatum* fungus, which was not sporulating under the test conditions. The stylet-like mouthparts of *T. fusarii* are equipped with apodemes (being attachment structures for muscles), which are one of the taxonomic determinants for this species. Hence, *T. fusarii* might be adapted to feed on fungal spores as well as fungal mycelium (R. Ochoa, personal communication), which could explain the strong growth response to *A. oryzae*.

While both *A. oryzae* and *F. venenatum* were shown to be suitable food source for growing tarsonemids, other fungi that are preferably mycotoxin-free, could also be considered when producing prostigmatid and astigmatid prey mites used for the production of natural enemies. Several fungal genera, such as *Chaetomium*, *Aspergillus*, *Trichoderma* and *Alternaria* are associated with tarsonemids (Smiley and Moser, 1985; White and Sinha, 1981). Alternatively, other food-safe fungi, like *Rhizopus* sp., *Actinomucor* sp., *Amylomyces* sp., *Mucor* sp., *Monascus* sp., could be tested for their suitability to rear prey mites. However, *Penicillium* sp. was proven to generate detrimental effect onto the development of some *Tarsonemus* species populations (Suski, 1972).

It is unclear why the oviposition of *N. californicus* decreased in the presence of the *A. oryzae* growing on bran. Some hypotheses explaining this phenomenon are:

- 1) *A. oryzae* growing on bran produces volatiles that negatively impact the predator. When growing on rice, *A. oryzae* has been shown to produce a range of volatile compounds, including aldehydes and ketones. Moreover, production of alcohols and aldehydes increased under more anaerobic conditions (Ito et al., 1990). As *N. californicus* was frequently found hiding inside pieces of bran, oxygen deficiency might have caused a more toxic microenvironment resulting in the observed negative outcome.
- 2) When a fungus such as *A. oryzae* is growing on bran, thereby producing an abundance of spores, prey mites are more difficult to find as compared to sieved our material. Habitat complexity has previously shown to affect both the movement of the predator and their prey capture rate (Lee and Zhang, 2016; Madadi et al., 2007). Hence, when reared on *A. oryzae* on bran, the habitat structure might have impeded *N. californicus* in successfully locating and subduing the tarsonemid prey.
- 3) Fungus growing on the bran substrate might have altered the microclimate, which negatively affects the phytoseiid's performance. Growth of micro-organisms, including fungi, is associated with the production of heat (van Kleeff et al., 1993; Wilson, 1999). As predatory mites are ectothermic organisms with a maximum temperature threshold (Vangansbeke et al., 2015), excessive heat production can result in deleterious effects.

In summary, we demonstrate the potential of using tarsonemid prey mites in the production of the phytoseiid predatory mite *N. californicus*. The impact of the fungal species and its growing media on both the tarsonemid prey mite and *N. californicus* merits further investigation.

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References

- Badii MH, McMurtry JA (1984) Feeding behavior of some phytoseiid predators on the broad mite, *Polyphagotarsonemus latus* (Acari: Phytoseiidae, Tarsonemidae). Entomophaga 29: 49–53. <https://doi.org/10.1007/BF02372208>
- Barbesgaard P, Heldt-Hansen H, Diderichsen B (1992). On the safety of *Aspergillus oryzae*: a review. Appl Microbiol Biotechnol 36:569-572. <https://doi.org/10.1007/BF00183230>
- Belczewski RF, Harmsen R (1997) In vitro feeding preferences of the fungivorous mite *Tarsonemus confusus* Ewing (Tarsonemidae). In: GR Needham, R Mitchell, DJ Horn & WC Welbourn (eds), Acarology IX: Symposia (the proceedings of the Ninth International Conference, Columbus, Ohio, 1994). Ohio Biological Survey, Columbus, Ohio
- Bolckmans K, van Houten Y (2006) Mite composition, use thereof, method for rearing the phytoseiid predatory mite *Amblyseius swirskii*, rearing system for rearing said phytoseiid mite and methods for biological pest control on a crop. World Intellectual Property Organisation, WO 2006/057552.
- Calvo FJ, Knapp M, van Houten YM, Hoogerbrugge H, Belda, JE (2015) *Amblyseius swirskii*: What made this predatory mite such a successful biocontrol agent? Exp Appl Acarol 65 : 419–433. <https://doi.org/10.1007/s10493-014-9873-0>
- Castagnoli M, Nannelli R, Tarchi F, Simoni S (2006) Screening of astigmatid mites for mass-rearing *Neoseiulus californicus* (McGregor) (Acari: Phytoseiidae). Redia 89: 55–58.
- Crawley MJ (2013) The R book, Chichester, West Sussex, UK
- Domsch KH, Gams W, Anderson TH (1980) Compendium of soil fungi. New York, USA
- Duarte MVA, Venzon M, Bittencourt, MC de S, Rodríguez-Cruz FA, Pallini A, Janssen A (2015) Alternative food promotes broad mite control on chilli pepper plants. BioControl 60: 817–825. <https://doi.org/10.1007/s10526-015-9688-x>
- Easterbrook MA, Fitzgerald JD, Solomon MG (2001) Biological control of strawberry tarsonemid mite *Phytonemus pallidus* and two-spotted spider mite *Tetranychus urticae* on strawberry in the UK using species of *Neoseiulus* (*Amblyseius*) (Acari: Phytoseiidae). Exp Appl Acarol 25: 25–36. <https://doi.org/10.1023/A:1010685903130>
- Fan YQ, Pettitt FL (1994) Biological Control of Broad Mite, *Polyphagotarsonemus latus* (Banks), by *Neoseiulus barkeri* Hughes on Pepper. Biol. Control 4 : 390–395. <https://doi.org/10.1006/bcon.1994.1049>

- Geeraerts J (1974) Etude de l'attraction exercée par divers champignons sur *Tarsonemus fusarii* Cooreman 1941. Mycoses 17: 27–32. <https://doi.org/10.1111/j.1439-0507.1974.tb04246.x>
- Gerson U (1992) Biology and control of the broad mite, *Polyphagotarsonemus latus* (Banks) (Acari: Tarsonemidae). Exp Appl Acarol 13: 163–178. <https://doi.org/10.1007/BF01194934>
- Gotz H, Reichenberger M (1953) On a mite, ' *Tarsonemus fusarii* Cooreman', destroying fungus cultures. Hautarzt 4: 266–268.
- Huang H, Xu X, Lv J, Li G, Wang E, Gao Y (2013) Impact of proteins and saccharides on mass production of *Tyrophagus putrescentiae* (Acari: Acaridae) and its predator *Neoseiulus barkeri* (Acari: Phytoseiidae). Biocontrol Sci Technol 23: 1231–1244. <https://doi.org/10.1080/09583157.2013.822849>
- 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. [https://doi.org/10.1016/S1164-5563\(01\)01083-4](https://doi.org/10.1016/S1164-5563(01)01083-4)
- Hughes AM (1976) The mites of stored food and houses. H.M.S.O., London.
- Hummel NA, Castro BA, McDonald EM, Pellerano MA, Ochoa R (2009) The panicle rice mite, *Steneotarsonemus spinki* Smiley, a re-discovered pest of rice in the United States. Crop Prot 28: 547–560. <https://doi.org/10.1016/j.cropro.2009.03.011>
- Hussey, N.W., Gurney, B., 1967. Bionomics and control of *Tarsonemus myceliophagus* (Acarina: Tarsonemidae) in mushroom compost. Entomol Exp Appl: 10, 287–294. <https://doi.org/10.1111/j.1570-7458.1967.tb02448.x>
- Ito K, Yoshida K, Ishikawa T, Kobayashi S (1990) Volatile compounds produced by the fungus *Aspergillus oryzae* in rice Koji and their changes during cultivation. J Ferment Bioeng 70: 169–172. [https://doi.org/10.1016/0922-338X\(90\)90178-Y](https://doi.org/10.1016/0922-338X(90)90178-Y)
- Kaliszewski M, Sell D (1990) *Tarsonemus fusarii* Cooreman i *Tarsonemus parafusarii* Kaliszewski (Acari: Tarsonemidae) w Polsce, ze szczególnym uwzględnieniem ekologii [*Tarsonemus fusarii* Cooreman and *Tarsonemus parafusarii* Kaliszewski (Acari: Tarsonemidae) in Poland, with particular regard to their ecology]. Zesz Probl Postepow Nauk Roln 373: 195–216 (in polish with russian and english summaries).
- Kaliszewski M, Athias-Binche F, Lindquist EE (1995) Parasitism and Parasitoidism in Tarsonemina (Acari: Heterostigmata) and Evolutionary Considerations, in: Advances in Parasitology. Elsevier [https://doi.org/10.1016/S0065-308X\(08\)60074-3](https://doi.org/10.1016/S0065-308X(08)60074-3)
- Knapp M, van Houten Y, van Baal E, Groot T (2018) Use of predatory mites in commercial biocontrol: current status and future prospects. Acarologia 58: 7282. <https://doi.org/10.24349/ACAROLOGIA/20184275>
- Lee MH, Zhang Z-Q (2016) Habitat structure and its influence on populations of *Amblydromalus limonicus* (Acari: Phytoseiidae). Syst Appl Acarol 21: 1361–1378. <https://doi.org/10.11158/saa.21.10.7>
- Li L, Jiao R, Yu L, He XZ, He L, Xu C, Zhang L, Liu J (2018) Functional response and prey stage preference of *Neoseiulus barkeri* on *Tarsonemus confusus*. Syst Appl Acarol 23: 2244–2258. <https://doi.org/10.11158/saa.23.11.16>

- Lindquist EE (1986) The world genera of Tarsonemidae (Acari: Heterostigmata): A morphological, phylogenetic, and systematic revision, with a reclassification of family-group taxa in the Heterostigmata. Mem Entomol Soc Can 118: 1–517. <https://doi.org/10.4039/entm118136fv>
- Lindquist EE (1972) A new species of *Tarsonemus* from stored grain (Acarina: Tarsonemidae). Can Entomol 104: 1699–1708. <https://doi.org/10.4039/Ent1041699-11>
- Lofego AC, Pitton T, Rezende JM (2016) A new genus and new species of Tarsonemidae (Acari: Heterostigmata) from the Brazilian rainforests. Syst Appl Acarol 21: 307–319. <https://doi.org/10.11158/saa.21.3.6>
- Lombardero MJ, Ayres MP, Hofstetter RW, Moser JC, Lepzig KD (2003) Strong indirect interactions of *Tarsonemus* mites (Acarina: Tarsonemidae) and *Dendroctonus frontalis* (Coleoptera: Scolytidae). Oikos 102: 243–252. <https://doi.org/10.1034/j.1600-0706.2003.12599.x>
- Machida M, Asai K, Sano M, Tanaka T, Kumagai T, Terai G, Kusumoto K-I, Arima T, Akita O, Kashiwagi Y, Abe K, Gomi K, Horiuchi H, Kitamoto K, Kobayashi T, Takeuchi M, Denning DW, Galagan JE, Nierman WC, Yu J, Archer DB, Bennett JW, Bhatnagar D, Cleveland TE, Fedorova ND, Gotoh O, Horikawa H, Hosoyama A, Ichinomiya M, Igarashi R, Iwashita K, Juvvadi PR, Kato M, Kato Y, Kin T, Kokubun A, Maeda H, Maeyama N, Maruyama J, Nagasaki H, Nakajima T, Oda K, Okada K, Paulsen I, Sakamoto K, Sawano T, Takahashi M, Takase K, Terabayashi Y, Wortman JR, Yamada O, Yamagata Y, Anazawa H, Hata Y, Koide Y, Komori T, Koyama Y, Minetoki T, Suharnan S, Tanaka A, Isono K, Kuhara S, Ogasawara N, Kikuchi H (2005) Genome sequencing and analysis of *Aspergillus oryzae*. Nature 438: 1157–1161. <https://doi.org/10.1038/nature04300>
- Madadi H, Enkegaard A, Brodsgaard HF, Kharrazi-Pakdel A, Mohaghegh J, Ashouri A (2007) Host plant effects on the functional response of *Neoseiulus cucumeris* to onion thrips larvae. J Appl Entomol 131: 728–733. <https://doi.org/10.1111/j.1439-0418.2007.01206.x>
- McMurtry JA, Moraes GJD, Sourassou NF (2013) Revision of the lifestyles of phytoseiid mites (Acari: Phytoseiidae) and implications for biological control strategies. Syst Appl Acarol 18: 297–320. <https://doi.org/10.11158/saa.18.4.1>
- Messelink GJ, van Holstein-Saj R (2007) Biological control of the bulb scale mite *Steneotarsonemus laticeps* (Acari: Tarsonemidae) with *Neoseiulus barkeri* (Acari: Phytoseiidae) in amaryllis. IOBC/wprs Bull. 30: 81–85.
- Midthassel A, Leather SR, Baxter IH (2013) Life table parameters and capture success ratio studies of *Typhlodromips swirskii* (Acari: Phytoseiidae) to the factitious prey *Suidasia medanensis* (Acari: Suidasidae). Exp Appl Acarol 61: 69–78. <https://doi.org/10.1007/s10493-013-9682-x>
- Moser JC (1985) Use of sporothecae by phoretic *Tarsonemus* mites to transport ascospores of coniferous bluestain fungi. Trans Br Mycol Soc 84: 750–753. [https://doi.org/10.1016/S0007-1536\(85\)80138-8](https://doi.org/10.1016/S0007-1536(85)80138-8)
- Naranjo SE, Ellsworth PC, Frisvold GB (2015) Economic Value of Biological Control in Integrated Pest Management of Managed Plant Systems. Annu Rev Entomol 60: 621–645. <https://doi.org/10.1146/annurev-ento-010814-021005>

- Nuzacci G, Di Palma A, Magowski WL, Aldini P (2002) Mouthparts of *Tarsonemus nodosus* Schaarschmidt, 1959 (Acari: Tarsonemidae): fine structure and functional morphology. In Bernini F, R Nannelli, G Nuzzaci, E de Lillo (eds), *Acarid Phylogeny and Evolution. Adaptations in mites and ticks*, Kluwer Academic Publishers
- Ochoa R, Naskrecki P, Colwell RK (1995) *Excelsotarsonemus kaliszewskii*, a new genus and new species from Costa Rica (Acari: Tarsonemidae). *Int J Acarol* 21: 67–74. <https://doi.org/10.1080/01647959508684045>
- O'Donnell K, Cigelnik E, Casper HH (1998) Molecular Phylogenetic, Morphological, and Mycotoxin Data Support Reidentification of the Quorn Mycoprotein Fungus as *Fusarium venenatum*. *Fungal Genet Biol* 23: 57–67. <https://doi.org/10.1006/fgbi.1997.1018>
- Parkinson CL, Barron CA, Barker SM, Thomas AC, Armitage DM (1991) Longevity and fecundity of *Acarus siro* on four field and eight storage fungi. *Exp Appl Acarol* 11: 1–8. <https://doi.org/10.1007/BF01193724>
- Ramakers PMJ, Van Lieburg MJ (1982) Start of commercial production and introduction of *Amblyseius mckenziei* Sch. & Pr. (Acarina: Phytoseiidae) for the control of *Thrips tabaci* Lind. (Thysanoptera: Thripidae) in glasshouses. *Meded Fac Landbouw Rijksuniv Gent* 47: 541–545.
- Rodriguez JG, Potts MF, Rodriguez LD (1980) Mycotoxin Toxicity to *Tyrophagus putrescentiae*. *J Econ Entomol* 73: 282–284. <https://doi.org/10.1093/jee/73.2.282>
- Sabelis MW (1990) How to analyse prey preference when prey density varies? A new method to discriminate between effects of gut fullness and prey type composition. *Oecologia* 82: 289–298. <https://doi.org/10.1007/BF00317473>
- Scott J J, Oh D-C, Yuceer CM, Klepzig KD, Clardy J, Currie R (2008) Bacterial protection of beetle-fungus mutualism. *Science* 332: 63 <https://doi.org/10.1126/science.1160423>
- Smiley RL, Moser JC (1985) A new species, key to females, and distribution records for *Heterotarsonemus* (Acari: Tarsonemidae). *Int J Acarol* 11: 247–253. <https://doi.org/10.1080/01647958508683425>
- Sousa ASG, Rezende JM, Lofego AC, Ochoa R, Oliveira AR (2018) *Daidalotarsonemus* and *Excelsotarsonemus* species (Acari: Tarsonemidae) found in shaded cacao plantations in Brazil, with a description of a new species. *Int J Acarol* 44: 68–79. <https://doi.org/10.1080/01647954.2018.1471096>
- Suski ZW (1972) Tarsonemid mites on apple trees in Poland X. Laboratory studies on the biology of certain mites species of the family Tarsonemidae (Acarina: Heterostigmata). *Zesz Probl Postepow Nauk Roln* 129: 139–157.
- Tuovinen T, Lindqvist I (2010) Maintenance of predatory phytoseiid mites for preventive control of strawberry tarsonemid mite *Phytonemus pallidus* in strawberry plant propagation. *Biol Control* 54: 119–125. <https://doi.org/10.1016/j.biocontrol.2010.04.006>

- 491 Van der Walt L, Spotts RA, Ueckermann EA, Smit FJ, Jensen T, McLeod A (2011) The association of
492 *Tarsonemus* mites (Acari: Heterostigmata) with different apple developmental stages and apple core rot
493 diseases. Int J Acarol 37: 71–84. <https://doi.org/10.1080/01647954.2010.539981>
494
495 van Kleeff, BHA, Kuenen JG, Heijnen JJ (1993) Continuous measurement of microbial heat production
496 in laboratory fermentors. Biotechnol Bioeng 41: 541–549. <https://doi.org/10.1002/bit.260410506>
497
498 van Lenteren, J.C., 2012. The state of commercial augmentative biological control: plenty of natural
499 enemies, but a frustrating lack of uptake. BioControl 57, 1–20. [https://doi.org/10.1007/s10526-011-9395-](https://doi.org/10.1007/s10526-011-9395-1)
500 [1](https://doi.org/10.1007/s10526-011-9395-1)
501
502 Vangansbeke D, Audenaert J, Nguyen DT, Verhoeven R, Gobin B, Tirry L De Clercq P (2015) Diurnal
503 Temperature Variations Affect Development of a Herbivorous Arthropod Pest and its Predators. PloS One
504 e0124898. <https://doi.org/10.1371/journal.pone.0124898>
505
506 Vangansbeke D, Duarte MVA, Bolckmans K, Guilbaud MHL, Benavente AM, Pekas, A, Wackers FL
507 (2020) Mite composition and method for growing mites. WO2020070334A1.
508
509 White NDG, Sinha RN (1981) Life history and population dynamics of the mycophagous mite
510 *Tarsonemus granarius* Lindquist (Acarina: Tarsonemidae). Acarologia 22: 353–360.
511
512 Wiebe M (2002) Myco-protein from *Fusarium venenatum*: a well-established product for human
513 consumption. Appl Microbiol Biotechnol 58: 421–427. <https://doi.org/10.1007/s00253-002-0931-x>
514 Wilson MT (1999) A model for predicting mould growth and subsequent heat generation in bulk stored
515 grain. J Stored Prod Res 35: 1–13. [https://doi.org/10.1016/S0022-474X\(98\)00025-3](https://doi.org/10.1016/S0022-474X(98)00025-3)
516
517 Zhang Z-Q (2003) Mites of greenhouses: identification, biology and control. CABI Pub, Wallingford,
518 Oxon, UK
519
520
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Figure captions

Fig1: Mean ($\pm$ standard error) number of mobile *T. fusarii* grown for 10 days on a mix of bran, wheat germ and yeast, or bran, PDB and *F. venenatum*, or *A. oryzae*. Initial population: 2000 mobiles. Bars with different letters differ significantly (contrasts after GLM, $p < 0.05$)

Fig2: Mean ($\pm$ standard error) number of eggs produced by *N. californicus* when fed *T. fusarii* either reared on bran with *A. oryzae* or *F. venenatum* (contrasts after LME, $p < 0.05$)

Fig3: Mean ($\pm$ standard error) number of eggs produced by *N. californicus* when fed *T. fusarii* either provided with the *A. oryzae*/bran medium or sieved out from it (contrasts after LME, $p < 0.05$)