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Collembola and plant pathogenic, antagonistic and arbuscular mycorrhizal fungi: a review

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Abstract

The review focuses on interactions between plant pathogenic, antagonistic, arbuscular mycorrhizal fungi and Collembola to explore the role of these arthropods in the control of plant diseases caused by soil borne fungal pathogens. Approximately forty years ago, the plant pathologist Elroy A. Curl and his co-workers of Auburn University (Alabama, USA) suggested for the first time a role of Collembola in plant disease control. The beneficial effect of springtails for plant health have been confirmed by several subsequent studies with different collembolan and fungal species. Collembola have been found to feed preferably on pathogenic rather than on antagonistic or arbuscular mycorrhizal (AM) fungal propagules, thus springtails can reduce the inoculum of pathogens without counteracting the activity of fungi beneficial for plant growth and health. Fungal characteristics that may affect the grazing activity of Collembola are also examined.

Key words: springtails, soil fungi, plant disease control.

Introduction

Collembola are among the most abundant groups of soil mesofauna; they range in size between 0.2 and 2 mm (Anderson, 1988; Hopkin, 1997). The geographical range of Collembola is enormous, as they live in all climatic environments from the Arctic and Antarctic to tropical areas (Tebbe *et al*., 2006). They feed on different organic materials. The majority of them feed on fungal propagules, and only few species have been considered economic pests for plants under certain environmental conditions (Curl, 1988; Sievers and Hulber, 1990; Bishop *et al*., 2001). The belowground fungal community, in particular that of rhizosphere and rhizoplane, could be subjected to a selective feeding by Collembola, and this could enhance some and limit other fungal species resulting in different effects on plant growth and health.

In this review, results of studies on interactions between Collembola and plant pathogenic, biocontrol and arbuscular mycorrhizal fungi are examined. Fungal features that influence the grazing activity of Collembola are also considered.

Collembola and plant pathogenic fungi

Approximately forty years ago, the plant pathologists Elroy A. Curl and Elizabeth A. Wiggins of the Auburn University (Alabama, USA) observing interactions between some collembolan species and some soil-borne plant pathogenic fungi, postulated for the first time a role for these animals in plant disease control (Curl, 1979; Wiggins and Curl, 1979). These authors suggested that the feeding activity of Collembola on fungal propagules could affect the competitive advantage of a pathogenic fungus at the root surface or in the rhizosphere, and thus influence the disease incidence and severity. They showed that *Proisotoma minuta* (Tullberg) and *Thalassaphorura encarpata* (Denis) (= *Onychiurus encarpatus*), the two prevalent Collembola species in Alabama soils, significantly reduced colony growth of the plant pathogenic fungi *Rhizoctonia solani* Khun, *Fusarium oxysporum* Schlect. f. sp. *vasinfectum* (Atk.) Snyder et Hansen, *Macrophomina phaseolina* (Tassi) Goid., and *Verticillium dahliae* Kleb., separately cultured on agarised medium (Wiggins and Curl, 1979; Curl *et al*., 1985; 1988). These authors also showed that collembolan feeding significantly reduced the germination of *M. phaseolina* and *V. dahliae* microsclerotia, and of *Sclerotium rolfsii* Sacc. macrosclerotia by grazing on germ tubes, whereas the mycelial growth of *S. rolfsii* was only slightly inhibited (Wiggins and Curl, 1979; Curl *et al*., 1985). In subsequent studies carried out under controlled conditions in large glass tubes with field soil, the suppressive effect of Collembola against the *R. solani* disease of cotton seedlings was demonstrated (Lartey *et al*., 1989). More than ten years later, Shiraishi *et al*. (2003) proposed the use of the collembolan *Folsomia hidakana* Uchida et Tamura for the control of the damping-off disease caused by *R. solani* in cabbage and Chinese cabbage in small plots for seedling cultivation. These authors observed that *F. hidakana* specimens actively grazed on *R. solani* hyphae and, after the hyphae were consumed, on sclerotia. They also developed a method for rearing *F. hidakana* to allow the commercial use in preventing disease under greenhouse conditions. Nakamura *et al*. (1992) found that *Sinella curviseta* Brook grazed and reproduced on *F. oxysporum* f. sp. *cucumerinum*. They showed that when *S. curviseta* specimens were added to cucumber seedlings in pots, the potential infection of the pathogen to cause Fusarium wilt disease was suppressed. Lootsma and Scholte (1997) found that *Folsomia fimetaria* L. in combination with the fungivorous nematode *Aphelencus avenae* Bastian, significantly reduced Rhizoctonia stem canker disease on potato plants.

Studies carried out by Sabatini and Innocenti (2000a;

2000b) indicated that mycelia of *Gaeumannomyces graminis* (Sacc.) Von Arx et Olivier var. *tritici* Walker, *Fusarium culmorum* (Smith et Sacc.) and *Rhizoctonia cerealis* van der Hoeven, the most important responsibles of the foot and root fungal disease complex of winter cereals worldwide, were palatable for Collembola. In multiple-choice experiments, as all these pathogens usually co-exist in the same portion in soil, *F. culmorum* was the most preferred food for *Protaphorura armata* (Tullberg) (= *Onychiurus armatus*), *Kalaphorura tuberculata* (Moniez) (= *Onychiurus tuberculatus*), and *Folsomia candida* Willem (Sabatini and Innocenti, 2000a), whereas *Mesaphorura krausbaueri* Borner did not show any significant preference (Sabatini and Innocenti, 2000b). Furthermore, *G. graminis* var. *tritici*, *R. cerealis* and *F. culmorum* mycelia resulted to be adequate food sources for the reproduction of *F. candida* and *M. krausbaueri*. However, the mycelium of *Bipolaris sorokiniana* (Sacc. in Sorok.) Shoem, another soil fungus responsible of root rot disease of winter cereals, was shown to have lethal/repellent effect on Collembola (Sabatini and Innocenti, 2000a; 2000b). However, long-term experiments demonstrated that conidia of *B. sorokiniana* were palatable and adequate diet for *F. candida* and *M. krausbaueri* reproduction (Sabatini and Innocenti, 2000b). Microcosm studies were subsequently carried out with a tripartite system including wheat plants, *G. graminis* var. *tritici*/*F. culmorum* and *P. armata*, used at a density comparable with that found in the upper 12 cm of Po Valley (Italy) agricultural soils (Sabatini *et al*., 1997). These studies demonstrated that the disease severity was significantly reduced by the collembolan feeding activity (Sabatini and Innocenti, 2001; Sabatini *et al*., 2002). Mesocosm studies confirmed the finding of the previous smaller-scale experiment when soil moisture was optimal for plants, whereas no suppressive effect was shown by Collembola under dry conditions (Innocenti *et al*., 2011). This result confirms the susceptibility of Collembola to soil moisture (Rickerl *et al*., 1989; Frampton *et al*., 2000; Tsiafouli *et al*., 2005). In the study of Larsen *et al.* (2008) *F. culmorum* and *R. solani* confirmed their palatability for *F. candida* and *F. fimetaria*, and both Collembola were able to reproduce on a diet of either fungi.

In a microcosm study carried under laboratory conditions, Wolfarth *et al*. (2013) showed that *F. candida* alone or in combination with the fungivorous nematode *Aphelenchoides saprophilus* Franklin, significantly reduced the biomass content of *F. culmorum*, and the contamination of the mycotoxin deoxynivalenol (DON) in wheat straw. Subsequently, an on-farm experiment confirmed the DON decontamination effect by *F. candida* and *A. saprophilus* (Wolfarth *et al*., 2015). When *F. candida* was used in combination with the detritivorous earthworm *Lumbricus terrestris* L., the reduction of *Fusarium* biomass in wheat straw was mainly due to the degradation ability of *L. terrestris* (Wolfarth *et al*., 2017).

Jørgensen *et al*. (2003) found that *F. fimetaria*, *Isotoma anglicana* (Lubbock), *Parisotoma notabilis* (Schaeffer) (= *Isotoma notabilis*), *Heteromurus nitidus* (Templeton), *P. armata* and *Pseudosinella alba* (Packard) showed differences in feeding preference for some fungi, including *F. culmorum*, grown in soil. These authors concluded that this might in partly explain the coexistence of many species of Collembola in the same soil microhabitats.

It is known that Collembola may transport mycelial fragments and spores of pathogens on their bodies and/or in their gut (Visser *et al*., 1987; Curl, 1988), thus they can potentially facilitate the colonization of rhizosphere and rhizoplane by pathogens. Nonetheless, studies of Wiggins and Curl (1979), Nakamura *et al*. (1992), and Sabatini and Innocenti (2001) revealed no evidence that the quantity of viable fungal propagules transported by springtails was sufficient to induce disease. Curl *et al*. (1988) observed that the ingested spores of *F. oxysporum* f. sp. *vasinfectum* deposited in fecal pellets retained a low percentage viability, and that larger sclerotia of *S. rolfsii* or microsclerotia of *V. dahliae* and *M. phaseolina* were not ingested. Analysis of gut content of *P. armata* specimens fed with hyphae of *G. graminis* var. *tritici* or hyphae and spores of *F. culmorum*, showed that the majority of these propagules was damaged and lacked cytoplasmic content, therefore no colonies of either pathogens developed from fecal pellets (Sabatini *et al*., 2004). The fate of ingested spores could be related to their shape and size. Spores of *F. culmorum* are multi-celled and have central and dorsal curved surfaces, so their large size and shape could favor the damage during the gut transit. The study of Dromph and Borgen (2001) found that *Onychiurus cebennarius* Gisin, *F. fimetaria*, *P. minuta* and *Orchesella villosa* Geoffroy fed on teliospores of *Tilletia tritici* (Berk.) Wint. Nevertheless, the number of teliospores carried out on the cuticle was low, and transit through the gut almost completely inhibited their germination. In the same study, Dromph and Borgen (2001) also showed that the smaller *Mesaphorura macrochaeta* Rusek did not fed on these spores.

Collembola and biocontrol fungi

Interactions between Collembola and fungi antagonistic to pathogens are important for plant health. Wiggins and Curl (1979) and Curl *et al*. (1985) found that *P. minuta* and *T. encarpata* were repelled by the mycelium of the well known biocontrol fungus *Trichoderma harzianum* Rifai, whereas its spores were ingested and remained viable in fecal pellets. Feeding experiments carried out in Petri dishes subdivided in two sections with an opening that allowed the migration of animals, showed that *T. harzianum* was the least preferred food for *F. candida* or *F. fimetaria* when this fungus was paired with a plant pathogenic fungus (Larsen *et al*., 2008). *Gliocladium virens* Miller, Giddens et Foster and *Laetisaria arvalis* Burds., other biocontrol fungi, were not preferred food sources of *P. minuta* and *T. encarpata* when paired with the pathogen *R. solani* (Lartey *et al*., 1989). Furthermore, *T. harzianum*, *G. virescens* and *L. arvalis* used individually with *P. minuta*, provided a more effective control against *R. solani* disease of cotton seedlings than that obtained with each antagonistic fungus in absence of Collembola (Lartey *et al*., 1991; 1994). Feeding tests where *M. krausbaueri* specimens were added to Petri dishes containing contemporaneously *F. culmorum*, *G. graminis* var. *tritici*, *R. cerealis* and *T. harzianum* colonies, confirmed that springtails were more attracted to pathogenic fungi than to biocontrol fungus (Innocenti *et al*., 1997). The findings of Sabatini *et al*. (2002; 2006) found that spores of *Trichoderma* were eaten by *P. armata*, and that after the transit through the gut, they were able to give colonies of the fungus. The globular shape and the small size of *T. harzianum* spores may reduce the damage during the gut transit. Moreover, in a microcosm experiment where *P. armata* and *T. harzianum* were used together against *G. graminis* var. *tritici* disease of wheat seedlings, it was found that the mode the antagonistic fungus was used, influenced the Collembola control ability (Sabatini *et al*., 2002). Indeed, Collembola showed a suppressive effect only when *T. harzianum* spores were applied to seed, whereas when the spores were mixed in the potting substrate, no biocontrol ability of animals was observed. The authors concluded that the large number of *T. harzianum* propagules, and the fewer pathogen hyphae could have induced springtails to feed on spores of the biocontrol fungus (Sabatini *et al*., 2002). Williams *et al*. (1998) observed that colonies of the mycoparasitic fungus *Coniothyrium minitans* Campbell grew from the majority of fecal pellets of *F. candida* fed on the fungus. These results emphasis the importance of Collembola in the dispersal of biocontrol fungal inoculum.

Collembola and arbuscular mycorrhizal fungi

Collembola coexist in soil with arbuscular mycorrhizal (AM) fungi that are essential for growth and health of plants through their role in transport of water and mineral nutrients, and protection against pathogens (Larsen *et al*., 2008). Multiple-choice feeding experiments where different AM fungi were the only significant variables, showed the preference of *F. candida*, *P. minuta*, and *Protaphorura fimata* (Gisin) (= *Onychiurus fimatus*) for food infected with AM fungi rather than for non-AM infected food. Only one collembolan species, *Xenylla grisea* Axelson, showed the highest feeding activity on non-infected AM material (Thimm and Larink, 1995). In pot tests, hyphae of the AM fungus *Glomus fasciculatus* (Thaxt.) Gerd. et Trappe were observed in *F. candida* gut (Warnock *et al*., 1982). Nevertheless, Collembola seem support the functions of AM fungi (Hishi and Takeda, 2008). A number of laboratory studies have shown that extra-radical mycelia of AM fungi are palatable for springtails, but are not the preferred food, when other nutrient sources such as saprotrophic and pathogenic fungi are available (Klironomos and Kendrick, 1996; Klironomos and Ursic, 1998; Bonkowski *et al*., 2000; Gange, 2000; Gormsen *et al*., 2004; Tiunov and Scheu, 2005; Larsen *et al*., 2008). Larsen and Jakobsen (1996a) examined the interactions between *F. candida* and the external mycelium of the AM fungus *Glomus caledonium* Nicol. et Gerd. in terms of Collembola reproduction, AM-hyphal length and AM-potassium transport. They found that the interactions between Collembola and the AM mycelium were limited under the conditions used, and that the *F. candida* reproduction was unaffected by AM fungus. When the same authors examined the effect of *F. candida* on the symbioses between three AM fungi and *Trifolium subterraneum* L., they confirmed that Collembola grazed on roots and/or hyphae of AM fungi, however they seemed to have little effect on the functioning of AM fungi (Larsen and Jakobsen, 1996b). Ngosong *et al.* (2014) found that the biomass of maize roots inoculated with AM fungi increased in the presence of *P. armata* specimens. These authors found that Collembola did not disrupt plant-mycorrhizal association, nor decreased nutrient transport by AM fungi. AM spores are larger than spores of the majority of fungi, thus they are not usually ingested by Collembola (Gormsen *et al*., 2004). However, spores of the AM fungus *Gigaspora gigantea* (Nicol. et Gerd.) Gerd. et Trappe, were consumed by Collembola. On the contrary, the animals did not ingest the smaller spores of *Glomus deserticola* Trappe, Bloss et Menge (Caravaca and Ruess, 2014).

Mesocosm experiments with wheat plants, AM fungus *Glomus intraradices* Schenk and Smith, *F. culmorum*, and *P. armata*, showed that Collembola did not decrease the root colonization rate by the *G. intraradices* compared to that of mycorrhizal control plants (Innocenti *et al*., 2009). However, the combination of Collembola and AM fungus was not more efficient in reducing the disease severity than animals and AM fungus used separately. Regarding interactions between Collembola and ectomycorrhizal fungi, Hiol Hiol *et al*. (1994) showed that where *P. minuta* was given a choice, *R. solani* was grazed more heavily than the ectomycorrhizal fungi *Laccaria laccata* (Scop.: Fr.) Cooke, *Pisolithus tinctorius* (Pers.) Colker et Couch, *Suillus luteus* (L.) Roussel and *Thelephora terrestris* Pers. ex Fr..

How the preference of Collembola for a fungus occurs?

The ability of a fungus to attract/repel Collembola could be related to many morphological and physiological characteristics such as hyphal architecture and pigmentation, aerial, appressed or submerged mycelium on the growth medium, presence of crystals or other deposits at the hyphal surface, nutritional value, flavour, odour, toxic or repellent secondary metabolite content, growth medium composition (Scheu and Simmerling, 2004; Larsen *et al*., 2008; Staaden *et al*., 2011). Generally, food preference seems match fitness parameters such as animal growth and reproduction (Sabatini and Innocenti, 2000b; Hedenec *et al*., 2013). However, Larsen *et al*. (2008) examining the relationship between collembolan reproduction and soil fungi from different ecological niches, found that the fungi with the highest reproductive value were often not the most preferred food. Collembola seem able to differentiate fungi of different palatability and toxicity by their odour (Staaden *et al*., 2011). It is also well known that the substrate on which fungi are cultured, strongly influences their attractiveness (Bengtsson *et al.*, 1988; Jørgensen *et al.*, 2003). In an olfactometer experiment, volatile metabolites released from the mycelium of *Verticillium bulbillosum* Gams et Malla cultured in agar, attracted specimens of *P. armata* more than those produced by other fungi in the same conditions; however, the preference of *P. armata* switched to the other species when the same fungi were grown in soil (Bengtsson *et al.*, 1988). Studies with *F. candida* and four saprotrophic fungi grown on different substrates found that the substrate influenced the grazing preference of animals more than fungal species, and that the most preferred fungus did not support the highest reproduction (Hedenec *et al.*, 2013). Scheu and Simmerling (2004) and Bollman *et al.* (2010) pointed out the role of melanin in the feeding preference. These authors observed that dark pigmented fungal propagules were most attractive for Collembola than not melanized ones. Similarly, Sabatini and Innocenti (2000a) found that melanized conidia of *B. sorokiniana* were fed by *F. candida* and *P. armata*, and were adequate for reproduction, whereas young hyaline hyphae of the same fungus were repellent/lethal. Similar behavior has been shown for other soil animal taxa such as mites. This preference seems not due to the melanin itself, because the melanin is hard to digest for animals (Schneider *et al.*, 2004).

Concluding remarks

Forty years after Curl and Wiggins postulated a role of Collembola in the control of plant diseases caused by soil borne fungi, the potential beneficial effect of springtails for plant health has been confirmed by several subsequent studies with different collembolan and fungal species. It has been found that Collembola feed preferably on pathogenic rather than on antagonistic or AM fungal propagules, thus springtails may reduce the inoculum of pathogens without counteracting the activity of beneficial fungi. However, most of the research has been carried out on laboratory media, or in soil under controlled conditions, whereas to date there is no clear evidence for collembolan feeding preferences in agricultural soils under field conditions. Analyses of the gut content of field-collected Collembola seem to indicate that these animals are less selective than suggested by results obtained in laboratory assays (Tebbe *et al.*, 2006). Furthermore, the impact of Collembola on pathogenic, antagonistic or MA fungi clearly appears to be density dependent. The number of Collembola used in the experiments was not always comparable with that found in the agricultural soil. Rickerl *et al.* (1989) studying the effect of different soil tillage techniques and crop rotations on Collembola and *R. solani* populations, showed that the animal density was too low under all tested conditions for any biocontrol effect against the pathogen.

In conclusion, we believe that the cycle of plant diseases caused by soil borne fungi could not be fully understood without considering the role of Collembola on survival, germination, and dispersal of pathogen propagules. According to what has been reported so far, it would be important to improve the knowledge on effect of crop management practices on Collembola communities. Coulibaly *et al.* (2017) studying the Collembola in function of crop rotation (annual vs perennial), rate of nitrogen fertilization (low vs high), tillage intensity (deep vs reduced), and crop residues management (restitution vs removal) under field conditions over four years, demonstrated that shifting from conventional to conservative cropping system had a strong positive effects upon density and species richness of springtails. However, Sabatini *et al.* (1997) in a study carried out after 15 years of three continuous tillage techniques (minimum tillage, ploughing to 25 or 50 cm) and extended over a four-year period, showed large variations in Collembola abundance in the various years, and found few significant tillage effects on overall abundance and species richness of Collembola; however some species were significantly more abundant under minimum tillage and others under ploughing.

The impact of pesticides on Collembola is another very important aspect to consider. Since 2016, for plant protection products additional testing of effects on soil arthropods and in particular on *F. candida* and on the mite *Hyposaspis aculeifer* (Canestrini), is required if the product is applied directly on or into the soil, in accordance with the EU regulation No 284/2013 setting out the data requirements for plant protection products regulation No 1107/2009, concerning their placing on the market. All these arguments are worth of a further paper.

In our opinion, the combination of Collembola with other biocontrol agents could be a correct strategy for the future mainly for greenhouse crops. Thus multidisciplinary long-term researches involving zoologists, agronomists and plant pathologists are recommended.

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