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Combined use of zoophytophagous mirids for sustainable biological protection of greenhouse tomato crops

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Abstract

Tuta absoluta and *Bemisia tabaci* are two key worldwide tomato pests. In response to chemical control limits, the use of zoophytophagous mirid predators as biocontrol agents is being increasingly studied and proposed for the management of these pests. However, the use of some mirid species and in particular *Nesidiocoris tenuis*, which naturally occurs in European tomato crops, is controversial due to its ability to inflict significant damage on tomato plants (necrotic rings) in parallel of its high predation capacity. Combining other mirid species such as *Macrolophus pygmaeus* and *Dicyphus errans* with *N. tenuis* could reduce the population growth of *T. absoluta* and of *B. tabaci*, while maintaining *N. tenuis* populations below a critical crop damage threshold. In this study, we tested the effect of combining *N. tenuis* with *M. pygmaeus* (at two densities: 10 and 15 individuals per plant) and with or without *D. errans* (five individuals per plant) on the abundance of all insects (predators and pests) for 8 weeks. We also measured leaf damage by *T. absoluta* and plant and flower damage (necrotic rings, flower abortion rate) by *N. tenuis*. We found that the combined presence of *D. errans*, *M. pygmaeus* and *N. tenuis* rapidly and significantly reduced the densities of *B. tabaci* adults, and *T. absoluta* larvae and damage compared to when *M. pygmaeus* (with both densities) was only present with *N. tenuis*. The presence of *D. errans* was critical to reduce *N. tenuis* population growth and necrotic rings on tomato plants, while higher densities of *M. pygmaeus* density reduced the rate of aborted flowers by *N. tenuis*. The manipulation of *M. pygmaeus* densities added to the presence of *D. errans* could provide a sustainable solution to control multiple pests simultaneously while reducing the damaging phytophagous activity of *N. tenuis* in tomato crops.

Keywords *Bemisia tabaci*, Biocontrol agent, *Dicyphus errans*, *Macrolophus pygmaeus*, *Nesidiocoris tenuis*, *Tuta absoluta*

Introduction

Insects are considered as agricultural pests if crop damage leads to reduced yield and/or quality of the harvested product to an unacceptable level for farmers. Tomato is the most important vegetable crop worldwide, and both greenhouses and open field productions are attacked by many insect pests, among which are the invasive species *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) and *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) (De Barro et al. 2011; Desneux et al. 2011). These two

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species are extremely damaging and attack both greenhouse and open field tomato crops and often cohabit on the same plants (Desneux et al. 2010; Biondi et al. 2018; Ramos et al. 2018; Shen et al. 2021).

The tomato leafminer, *T. absoluta* is now considered as the most devastating pest of tomato in the world (Campos et al. 2017; Mansour et al. 2018; Han et al. 2019; Desneux et al. 2022). Its larvae attack all aerial parts of plant and can cause yield losses up to 100% (Desneux et al. 2010). The whitefly, *B. tabaci* is a very polyphagous and invasive crop pest worldwide which causes significant yield reduction through direct plant feeding but most importantly by vectoring many viral diseases that negatively impact crop yield (De Barro et al. 2011). Methods based on the spraying of synthetic chemical insecticides to control *B. tabaci* and *T. absoluta* have been progressively limited by the rise of population resistances to many molecules (Yao et al. 2017; Biondi et al. 2018; Guedes et al. 2019; Horowitz et al. 2020). In addition, these practices have serious negative impacts on beneficial insect fauna, human health, and the environment (Desneux et al. 2007; Kim et al. 2017; Palma-Onetto et al. 2021; Zafeiraki et al. 2022). Therefore, more sustainable alternative control methods are needed such as the use of natural enemies (Bompard et al. 2013; Campos et al. 2020, Zhang et al. 2022) or botanical insecticides (Ricuperio et al. 2022). One of the most widely investigated options is the use of natural enemies, mainly of which are omnivorous or generalist predators, and can contribute to the simultaneous control of multiple pests.

Several species of mirid predators in the genera *Dicyphus*, *Macrolophus*, and *Nesidiocoris* in particular, are naturally present in tomato crops (Alomar et al. 2002; Ferracini et al. 2019) and their regulation role against pests such as whiteflies, aphids, and lepidopteran eggs and larvae is widely recognized (Calvo et al. 2009; Ingegno et al. 2019; Thomine et al. 2020; Pérez-Hedo et al. 2021a). Their effectiveness can be attributed to their voracious consumption of immature stages (Sylla et al. 2016) and their zoophytophagous feeding behaviour, which allows them to subsist on plants during periods of prey shortage (Thomine et al. 2020; Pérez-Hedo et al. 2021b). *Nesidiocoris tenuis* (Reuter) and *Macrolophus pygmaeus* (Rambur) (Heteroptera: Miridae) are currently mass-produced and commercialized, while European *Dicyphus* species are now also included in biocontrol strategies, mainly through conservation (Castañé et al. 2004; Ingegno et al. 2017). Despite their importance and wide use, the phytophagous feeding mode of these omnivorous predators is a double-edge sword: although it allows the maintenance of populations during periods of prey shortage, they may cause important plant damage, especially at high population densities, which calls for an optimization

of their use as biocontrol agents. In particular, the intense feeding of *N. tenuis* on tomato plants causes serious plant damage, including necrotic rings, blisters, and flower abscission (Sánchez 2009; Calvo et al. 2009; Pérez-Hedo and Urbaneja 2016; Moerkens et al. 2020). This phytophagous behaviour has significant negative effects on plant growth and productivity (Arnó et al. 2010; Sánchez and Lacasa 2008; Castañé et al. 2011; Chinchilla-Ramírez et al. 2021), which limits its potential to be used as a biocontrol agent (Abraços-Duarte et al. 2021; Ingels et al. 2022). In many European regions, it is considered as a serious tomato pest regardless of the biocontrol services it provides. It pushes growers to repeatedly control their populations with chemical insecticides, which disrupts their biocontrol capacity (Mouratidis et al. 2022). Instead of *N. tenuis*, Integrated pest management (IPM) strategies based on the use of mirid predatory biocontrol agents use *M. pygmaeus*, which has rarely been reported to cause plant damage and is generally considered safe to use (Castañé et al. 2011). However, this species is slow to establish abundant populations on crops (De Backer et al. 2014, Sánchez et al. 2021). In addition, the use of *M. pygmaeus* alone is not always effective in managing *T. absoluta* and *B. tabaci* populations (Calvo et al. 2009; Mollá et al. 2014; Jaworski et al. 2015; Michaelides et al. 2018, Sánchez et al. 2018). Its combination with other biocontrol agents has the potential to improve biocontrol programs (Konan et al. 2021; Yao et al. 2022). Unfortunately, this strategy can be compromised because *M. pygmaeus* population levels tend to decline in favour of *N. tenuis*, which is naturally present and can feed on *M. pygmaeus* nymphs (Moreno-Ripoll et al. 2012; Perdakis et al. 2014; Mouratidis et al. 2022). Intraguild predation (IGP), that is the predation of a natural enemy species upon another one sharing a prey species (Chailleux et al. 2014; Mirande et al. 2015), is frequent among mirid species (Moreno-Ripoll et al. 2012; Perdakis et al. 2014; Abraços-Duarte et al. 2021; Mouratidis et al. 2022). *Dicyphus errans* Fieber (Heteroptera: Miridae) has been studied in the past as potential biocontrol agent but has not been used commercially in augmentative biological control (Madeira et al. 2019; Mouratidis et al. 2022). The high voracity of this predator on different prey combined with low phytophagy could make it an ideal biocontrol agent in commercial greenhouses (Ingegno et al. 2017). In addition, *D. errans* tends to be the higher-order predator in intraguild predation (IGP) interactions with *N. tenuis* (Mouratidis et al. 2022), which could help limit *N. tenuis* population growth and damage. In tomato agroecosystems in Mediterranean regions several species of the genus *Dicyphus*, *Macrolophus* and *Nesidiocoris* co-occur naturally (Ferracini et al. 2019; Mollá et al. 2014; Perdakis et al. 2014). So far, experiments testing the impact

of the combined use of *N. tenuis* and *M. pygmaeus* and/or *D. errans* on the growth of pest populations, *N. tenuis* and their damage to plants have been mainly conducted in the laboratory or in the presence of immobile *Ephestia* eggs (Mollá et al. 2014; Perdakis et al. 2014; Konan et al. 2021; Mouratidis et al. 2022). Therefore, it is necessary to evaluate these interactions at a larger scale including under commercial greenhouse conditions and in the presence of pests.

The present study aims to test the following hypotheses: (i) interactions between predators (*M. pygmaeus*, *D. errans* and *N. tenuis*) increase the biological control of *B. tabaci* and *T. absoluta*, (ii) increasing the density of *M. pygmaeus* helps limit plant damage caused by *N. tenuis* by diverting *N. tenuis* plant feeding towards feeding on *M. pygmaeus* young nymphs in case of prey scarcity, and (iii) the presence of *D. errans* helps maintain *N. tenuis* populations below damaging threshold through intraguild predation. Therefore, we measured the effects of varying the density of *M. pygmaeus* (10 versus 15 individuals released per plant) and of the presence or absence of *D. errans* on the population dynamics and damage on tomato of *T. absoluta*, *B. tabaci* and *N. tenuis*.

Material and methods

Insect rearing

Tuta absoluta and *B. tabaci* colonies were reared in climatic chambers on tomato, *Solanum lycopersicum* L. and tobacco, *Nicotiana tabacum* L. (Solanaceae) plants, respectively. The predators *N. tenuis* and *M. pygmaeus* were supplied by Koppert Biological Systems (France). A colony of *D. errans* was established from individuals collected in Southern France, and identified by Jean-Claude Streito (INRAE Montpellier). The three mirid species were reared on tomato plants in cages (30×30×60 cm) made of insect-proof nylon mesh. They were fed with *E. kuehniella* Zeller (Lepidoptera: Pyralidae) eggs. Eggs of *E. kuehniella* were provided as needed every 2 days. All experiments were performed at the French National Research Institute for Agriculture, Food and Environment (INRAE), Sophia Antipolis (France) under laboratory conditions with 24 ± 1 °C, $65 \pm 5\%$ RH and 16:8 L:D.

Plant growing

Tomato seeds, *S. lycopersicum* L. (cv. Nano) were sown in plastic pots (7.9×7.9×6.5 cm, TEKU, Rixheim, France) in a climate chamber (24 ± 1 °C, $65 \pm 5\%$ RH and 16:8 L:D). Twenty-eight days after sowing, tomato plants with four true leaves were transplanted into plastic pots of 10 cm diameter and 9 cm height before being placed in a greenhouse.

Experimental design

The experiment was established in a glass greenhouse divided into four 40 m² compartments (24 ± 1 °C, $65 \pm 5\%$ RH). We established a full factorial experimental design with two crossed factors. The pests *T. absoluta* and *B. tabaci* and the predator *N. tenuis* were used in all treatments. The first two-level factor varied the density of *M. pygmaeus*, i.e. 10 individuals per plant (Mp10) and 15 individuals per plant (Mp15). The second factor was the presence or absence of *D. errans* (De). Thus, four treatments were tested: Mp10, Mp10De, Mp15 and Mp15De; such labelling is used thereafter to refer to the four treatments. The treatments were replicated four times each, and arranged in a randomized complete block design in the four greenhouse compartments, treated as four blocks. Treatments in each compartment were isolated in tunnels covered with fine mesh netting (height: 2 m, width: 1 m, length: 5 m) to prevent insect transfer (Jaworski et al. 2015). Each tunnel contained two rows of seven tomato plants. To have heterogeneous generations and avoid rapid population decrease, two releases of 30 *B. tabaci* adults per plant were conducted 24 h after tomato plant transplanting and 25 days later. One couple of *T. absoluta* adults per plant (28 individuals per tunnel) and the two densities of *M. pygmaeus* (10 and 15 individuals per plant) were released the same day as the first release of whiteflies. The predators *N. tenuis* and *D. errans* were released 7 days after plants were transplanted, at the following densities: *N. tenuis* and *D. errans* 2 males, 2 females and 1 nymph per plant each; *M. pygmaeus* (Mp10) 4 males, 4 females and 2 nymphs per plant; *M. pygmaeus* (Mp15) 6 males, 6 females and 3 nymphs per plant.

Insect sampling

The population dynamics of each insect species (*N. tenuis*, *M. pygmaeus*, *D. errans*, *B. tabaci*, and *T. absoluta*) were monitored weekly for eight weeks starting one week after predators introduction. Each week, ten plants were selected in each tunnel, excluding the first and last plants of each row to avoid border effects. Adults of *N. tenuis*, *M. pygmaeus* and *D. errans* were observed and counted on the whole plants. Nymphs were not counted, due to the difficulty in identifying them unambiguously at the species level at these stages. Adults of *B. tabaci* were visually observed and counted on both sides of three leaves (1 upper leaf+1 middle leaf+1 lower leaf) randomly selected on each of the ten selected plants, and a mean per leaf was calculated for each replicate. In addition, *T. absoluta* young larvae were counted on the first five apical well-developed leaves, and summed to obtain one number of larvae per five leaves for each replicate.

This choice was made for two reasons: (i) the five apical leaves are considered as females preferential oviposition area, and host the vast majority of young *T. absoluta* larvae, while only older larvae (counted in previous weeks) may be found in older leaves; (ii) while older leaves may be damaged and bear galleries dug by *T. absoluta* larvae, these galleries are most often empty, since such larvae already underwent pupation (Cocco et al. 2015; Konan et al. 2022).

Plant damage

Plant damage due to *T. absoluta* was measured as the proportion of tomato leaves attacked by *T. absoluta* (presence of galleries) in the first five apical leaves inspected for the presence of *T. absoluta*. Plant damage due to the phytophagous activity of *N. tenuis* was measured by counting the number of necrotic rings on stems, young shoots, and petioles, as well as the proportion of aborted flowers (number of flowers which did not form fruits relative to the total number of flowers) from the start of the flowering period.

Statistical analysis

All statistical analyses were performed using R Core Team (2023) version 4.3.0. We analysed the effects of the treatments on insect densities separately over different periods coinciding with the completion of a development cycle at the experimental temperature (24 ± 1 °C; Jaworski et al. 2015; Yao et al. 2022). The development cycles of *N. tenuis*, *T. absoluta* and *B. tabaci* development cycles are 21, 21–22 and 19–20 days, respectively, at 24 °C (Bonato et al. 2007; Sánchez 2009; Desneux et al. 2010), so the corresponding density and damage data were analysed separately on Weeks 1–3, 4–6 and 7–8. The development cycles of *M. pygmaeus* and *D. errans* at 24 °C are 28 and 31 days, respectively (Perdikis and Lykouressis 2002; Ingegno et al. 2017), so the corresponding density data were analysed separately on Weeks 1–4 and 5–8. We performed independent generalized linear mixed models (GLMMs) with a negative binomial error distribution accounting for data overdispersion (function 'glmer.nb', R library 'lme4'; Bates et al. 2105), except for *N. tenuis* density in Weeks 4–6 and 7–8, for which we used a linear mixed model (function 'lmer', R library 'lme4'). The fixed effects were *M. pygmaeus* initial density, the presence/absence of *D. errans*, and their interactions. The random effect was the plant identifier nested in the greenhouse compartment. Similarly, GLMMs were used to analyse the effects of the treatments on the proportion of attacked leaves by *T. absoluta*, the number of necrotic rings and the proportion of aborted flowers due to *N. tenuis* phytophagous activity. The error distributions used were binomial, negative binomial, and

binomial error distributions, respectively, and the fixed and random effects were the same as above. The statistical significance of fixed effects was determined through a stepwise regressive type-II model comparison with an ANOVA and a χ^2 -test. When both factors or the interaction were found to have a significant effect, pairwise mean comparisons between treatments were performed on the best model using the 'emmeans' R function (library 'emmeans'; Lenth 2023). The absence of residual heteroscedasticity and overdispersion was verified in the best model using the functions 'simulateResiduals()' (R library 'DHARMA'; Hartig 2022).

Results

Mirid population densities

The number of *N. tenuis* adults per plant declined from Week 1 to Week 3, then increased up to Weeks 5–6 and finally stabilized or declined again (Fig. 1A). Neither the initially density of *M. pygmaeus* nor the presence of *D. errans* had an effect on *N. tenuis* numbers during the first development cycle (Weeks 1–3; Fig. 1A; Table 1). However, the interaction between *M. pygmaeus* initial densities and the presence of *D. errans* significantly affected the number of *N. tenuis* per plant during the second cycle (Weeks 4–6): both higher initial densities of *M. pygmaeus* and the presence of *D. errans* increased *N. tenuis* densities, but the two effects combined resulted in lower *N. tenuis* densities than in treatments with either effect alone (Mp15 or Mp10De) and than in the control (Mp10) over this period (mean \pm SE of adults per plant: Mp10 5.25 ± 0.21 , Mp10De 5.62 ± 0.21 , Mp15 6.23 ± 0.22 , Mp15De 4.68 ± 0.21 ; Fig. 1A; Table 1). Finally, during the third cycle (Weeks 7–8), both *M. pygmaeus* initial densities and the presence of *D. errans* significantly affected *N. tenuis* densities, but not the interaction term: increasing *M. pygmaeus* initial density increased *N. tenuis* densities, while the presence of *D. errans* had the opposite effect (mean \pm SE of adults per plant: Mp10 5.65 ± 0.21 , Mp10De 3.93 ± 0.20 , Mp15 5.96 ± 0.21 , Mp15De 4.44 ± 0.22 ; Fig. 1A; Table 1).

The number of *M. pygmaeus* individuals per plant declined from Week 1 to Week 3 and stabilized at low densities from Week 3 until the end of the experiment (Fig. 1B). Higher initial densities of *M. pygmaeus* led to higher *M. pygmaeus* densities over both periods tested (Weeks 1–4 and 5–8), but the presence of *D. errans* had no effect (mean \pm SE of adults per plant: Weeks 1–4: Mp10 2.71 ± 0.23 , Mp10De 2.36 ± 0.19 , Mp15 3.71 ± 0.26 , Mp15De 3.38 ± 0.24 ; Weeks 5–8: Mp10 0.29 ± 0.05 , Mp10De 0.46 ± 0.06 , Mp15 1.12 ± 0.10 , Mp15De 1.14 ± 0.10 ; Fig. 1B; Table 1). The number of *D. errans* per plant declined from Week 1 to Week 3, then increased from Week 5 to Week 8 (Fig. 1C).

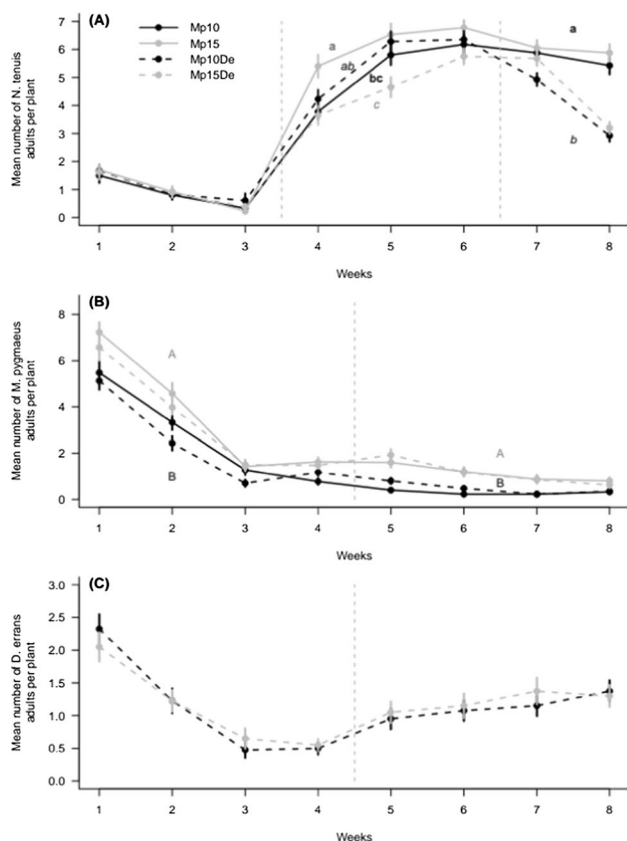


Fig. 1 Mean (\pm SE) number of (A) *N. tenuis*, (B) *M. pygmaeus*, and (C) *D. errans* adults per plant depending on the initial density of *M. pygmaeus* introduced and with or without *D. errans*. 'Mp10' 10 initially introduced *M. pygmaeus*; 'Mp15' 15 initially introduced *M. pygmaeus*; 'De' *D. errans* present. Vertical dashed lines show the time periods used in statistical tests and coinciding with estimated insect generation times. Different letters show significant differences between treatments or groups of treatments within each time period. $N=40$ replicates per treatment and per week (insects counted on 10 plants per tunnel with four tunnels per treatment)

However, the initial densities of *M. pygmaeus* had no effect on *D. errans* densities neither during the first (Weeks 1–4) nor the second cycle (Weeks 5–8; Fig. 1C, Table 1).

Pest densities

The number of *T. absoluta* larvae per five leaves declined through time overall, and it was not affected by the initial density of *M. pygmaeus*, but was affected by the presence of *D. errans* over each of the three periods tested (mean \pm SE of adults per plant: Weeks 1–3: Mp10 2.14 ± 0.21 , Mp10De 1.84 ± 0.19 , Mp15 2.42 ± 0.27 , Mp15De 1.73 ± 0.19 ; Weeks 4–6: Mp10 1.47 ± 0.14 , Mp10De 0.56 ± 0.10 , Mp15 1.11 ± 0.12 ,

Mp15De 0.46 ± 0.08 ; Weeks 7–8: Mp10 0.80 ± 0.12 , Mp10De 0.25 ± 0.07 , Mp15 0.56 ± 0.05 ; Fig. 2A, Table 2).

Similar to *T. absoluta* larvae, the mean number of *B. tabaci* adults per leaf also declined through time overall, and was affected by the presence of *D. errans*, but not the initial densities of *M. pygmaeus* over the three periods tested, except that the interaction term was significantly negative in the first period (mean \pm SE of adults per plant: Weeks 1–3: Mp10 5.29 ± 0.27 , Mp10De 3.98 ± 0.29 , Mp15 3.91 ± 0.27 , Mp15De 3.99 ± 0.27 ; Weeks 4–6: Mp10 2.61 ± 0.16 , Mp10De 1.78 ± 0.16 , Mp15 2.16 ± 0.14 , Mp15De 1.74 ± 0.14 ; Weeks 7–8: Mp10 1.20 ± 0.13 , Mp10De 0.60 ± 0.08 , Mp15 1.12 ± 0.14 , Mp15De 0.50 ± 0.08 ; Fig. 2B, Table 2).

Plant damage

The proportion of leaves attacked by *T. absoluta* per plant was relatively stable through time (Fig. 3A). It was increased in treatments with increased initial densities of *M. pygmaeus* during the first and second *T. absoluta* cycles but not the third, and it was reduced by the presence of *D. errans* during the second cycle only (mean \pm SE percentage of leaves attacked by *T. absoluta* per plant: Weeks 1–3: Mp10 26 ± 2 , Mp10De 20 ± 2 , Mp15 34 ± 3 , Mp15De 27 ± 2 ; Weeks 4–6: Mp10 22 ± 2 , Mp10De 14 ± 2 , Mp15 21 ± 2 , Mp15De 16 ± 2 ; Weeks 7–8, all treatments: 14 ± 1 ; Fig. 3B, Table 3).

The number of necrotic rings caused by *N. tenuis* increased rapidly between Weeks 2 and 3, and slowly after that (Fig. 3B). It was lower under higher *M. pygmaeus* initial densities in Weeks 4–6 and 7–8 but not in Weeks 1–3, and it was also reduced by the presence of *D. errans* in Weeks 7–8 only (mean \pm SE number of necrotic rings per plant: Weeks 4–6: Mp10 7.78 ± 0.36 , Mp10De 7.57 ± 0.28 , Mp15 6.78 ± 0.31 , Mp15De 6.49 ± 0.21 ; Weeks 7–8: Mp10 9.63 ± 0.41 , Mp10De 7.50 ± 0.29 , Mp15 8.39 ± 0.33 , Mp15De 6.59 ± 0.28 ; Fig. 3B, Table 3).

Finally, the proportion of aborted flowers, also caused by the phytophagous activity of *N. tenuis*, steadily increased from Week 1 to 4, and stabilised in Weeks 4–5 (Fig. 3C). Similar to the number of necrotic rings, it was reduced under higher initial *M. pygmaeus* densities, but only during the second period (Weeks 4–5), and it was not affected by the presence of *D. errans* (mean \pm SE percentage of aborted flowers per plant, Weeks 4–5: Mp10 27 ± 2 , Mp10De 29 ± 2 , Mp15 23 ± 2 , Mp15De 217 ± 2 ; Fig. 3C, Table 3).

Discussion

In the present study, we evaluated how combining mirid predators can be used to reduce crop damage by *N. tenuis*, a biocontrol agent now considered a serious tomato

Table 1 Response of the number of *N. tenuis*, *M. pygmaeus* and *D. errans* adults per plant to the initial density of *M. pygmaeus* introduced, the presence of *D. errans*, and the second-order interaction. (–) parameters not included in the model

Explanatory variables	d.f	<i>N. tenuis</i>		<i>M. pygmaeus</i>		<i>D. errans</i>	
		χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
1st generation							
<i>M. pygmaeus</i> density * <i>D. errans</i> presence	1	0.283	0.59	0.0907	0.76	–	–
<i>M. pygmaeus</i> density	1	0.006	0.94	18.3	<0.001 *** c	0.0770	0.93
<i>D. errans</i> presence	1	0.438	0.51	2.18	0.14	–	–
2nd generation							
<i>M. pygmaeus</i> density * <i>D. errans</i> presence	1	15.4	<0.001 *** a,e	1.69	0.19	–	–
<i>M. pygmaeus</i> density	1	–	–	37.0	<0.001 *** d	0.0760	0.92
<i>D. errans</i> presence	1	–	–	1.83	0.18	–	–
3rd generation							
<i>M. pygmaeus</i> density * <i>D. errans</i> presence	1	0.235	0.63				
<i>M. pygmaeus</i> density	1	3.97	0.046 * b,e				
<i>D. errans</i> presence	1	56.1	<0.001 *** b,e				

** $P < 0.01$; *** $P < 0.001$; '–' effects not tested

Model coefficients: **a** Intercept 5.25; Mp15 0.983; De 0.367; Mp15De – 1.92. **b** Intercept 5.60; Mp15 0.413; De – 1.63. **c** Intercept 0.930 Mp15 0.336. **d** Intercept – 1.29; Mp15 1.12. 'Mp15' 15 *M. pygmaeus* initially introduced per plant; 'De' *D. errans* present. **e** linear mixed models; the other models used were generalised linear mixed models with a negative binomial error distribution. Generation time: *N. tenuis* 3 weeks (1st generation Weeks 1–3; 2nd generation Weeks 4–6; 3rd generation Weeks 7–8); *M. pygmaeus* and *D. errans* 4 weeks (1st generation Weeks 1–4; 2nd generation Weeks 5–8)

pest in Europe (Moerkens et al. 2020), while increasing biological pest control. We found that increasing *M. pygmaeus* initial density increased the early population growth (second generation) of *N. tenuis*, while the presence of *D. errans* reduced *N. tenuis* population growth durably over a longer time. The presence of *D. errans* also reduced densities of both *T. absoluta* and *B. tabaci*, resulting in reduced leaf damage by *T. absoluta*. Plant damage by *N. tenuis* was also reduced in treatments combining mirid predators.

We expected a faster early population growth of *N. tenuis* when *M. pygmaeus* individuals were released at a higher density. This is because *N. tenuis* can feed on *M. pygmaeus* nymphs (Mouratidis et al. 2022), representing an alternative prey to the primary prey *T. absoluta* and *B. tabaci*. Therefore, increasing the initial density of *M. pygmaeus* would increase the prey resources available to *N. tenuis*, and thereby increase its population growth. We also hypothesized that the higher availability of *M. pygmaeus* nymphs would divert *N. tenuis* from feeding on plant resources, which in turn would decrease plant damage, since low prey densities in crop critically increases the phytophagy of *N. tenuis* (Calvo et al. 2009; Castañé et al. 2011; Yao et al. 2022). Indeed, we found that the number of necrotic rings and the percentage of flower abortion was slightly lower in treatments with higher *M. pygmaeus* initial densities, confirming the results of Yao et al. (2022). Feeding on plants is an essential requirement for *N. tenuis* to optimize the digestion and assimilation of consumed prey (Gillespie and

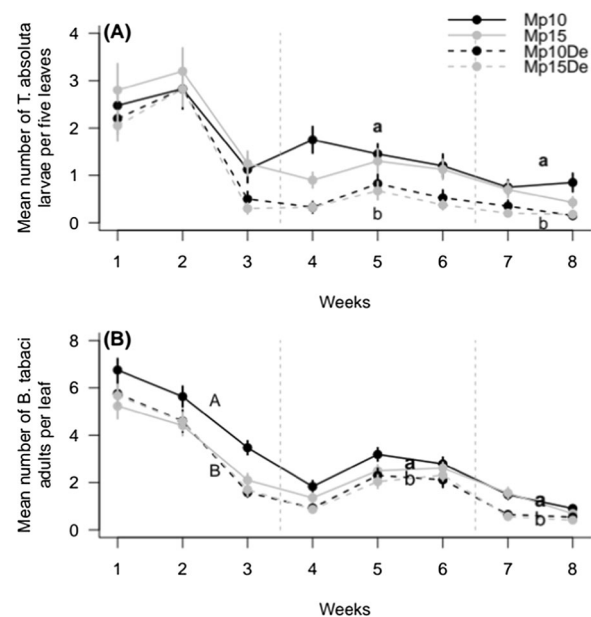


Fig. 2 Mean (\pm SE) number of (A) *T. absoluta* larvae per five leaves, and (B) *B. tabaci* adults per leaf, depending on the initial density of *M. pygmaeus* introduced and with or without *D. errans*. 'Mp10' 10 initially introduced *M. pygmaeus*; 'Mp15' 15 initially introduced *M. pygmaeus*; 'De' *D. errans* present. Vertical dashed lines show the time periods used in statistical tests and coinciding with estimated insect generation times. Different letters show significant differences between groups of treatments within each time period. N = 40 replicates per treatment and per week (insects counted on 10 plants per tunnel with four tunnels per treatment)

Table 2 Response of the number of *T. absoluta* larvae per five leaves and of the mean number of *B. tabaci* adults per leaf to the initial density of *M. pygmaeus* introduced, the presence of *D. errans*, and the second-order interaction. (-) parameters not included in the model

Explanatory variables	d.f	<i>T. absoluta</i> larvae		<i>B. tabaci</i> adults	
		χ^2	<i>P</i>	χ^2	<i>P</i>
1st generation					
<i>M. pygmaeus</i> density * <i>D. errans</i> presence	1	0.577	0.45	4.77	0.029 * d
<i>M. pygmaeus</i> density	1	0.0630	0.80	–	–
<i>D. errans</i> presence	1	4.00	0.046 * a	–	–
2nd generation					
<i>M. pygmaeus</i> density * <i>D. errans</i> presence	1	0.0953	0.76	0.651	0.42
<i>M. pygmaeus</i> density	1	2.77	0.096	1.86	0.17
<i>D. errans</i> presence	1	28.6	<0.001 *** b	14.4	<0.001 *** e
3rd generation					
<i>M. pygmaeus</i> density * <i>D. errans</i> presence	1	0.0637	0.80	0.0188	0.89
<i>M. pygmaeus</i> density	1	1.92	0.17	0.0941	0.76
<i>D. errans</i> presence	1	20.5	<0.001 *** c	28.4	<0.001 *** f

* $P < 0.05$; *** $P < 0.001$; ‘–’ effects not tested

Model coefficients: **a** Intercept 0.823; De – 0.245. **b** Intercept – 0.0566; De – 1.01. **c** Intercept – 0.975 Mp15 0.915. ‘Mp15’ 15 *M. pygmaeus* initially introduced per plant; ‘De’ *D. errans* present. **d** Intercept – 0.834; De – 1.22. **e** Intercept 1.64; Mp15 – 0.307; De – 0.288; Mp15De 0.311. **f** Intercept 0.833; De – 0.310. **f** Intercept 0.0691; De – 0.823. ‘Mp15’ 15 *M. pygmaeus* initially introduced per plant; ‘De’ *D. errans* present. Models used were generalised linear mixed models with a negative binomial error distribution. Generation time: *T. absoluta* and *B. tabaci* ≤ 3 weeks (1st generation Weeks 1–3; 2nd generation Weeks 4–6; 3rd generation Weeks 7–8)

McGregor 2000), and higher availability of *M. pygmaeus* prey likely compensates only partially the need to feed on plants in case of main prey shortage.

We also expected that the presence of *D. errans* would decrease *N. tenuis* population growth through IGP, since *D. errans* preys on *N. tenuis* nymphs (Abraços-Duarte et al. 2021; Mouratidis et al. 2022). The three predator species in the same environment inevitably compete for the shared resource (prey), likely increasing the frequency of encounters with heterospecific individuals, and therefore the likelihood of IGP. A reduction in *N. tenuis* population growth due to IGP by *D. errans* has been previously observed (Mouratidis et al. 2022). Here, the decrease in *N. tenuis* population densities from Week 6 in treatments with *D. errans* could be related to the increase in population densities of *D. errans* from Weeks 3–4 (Fig. 1). This reduction in *N. tenuis* population densities due to *D. errans* predation on *N. tenuis* nymphs also led to reduced necrotic rings by *N. tenuis*, since they have been shown to directly relate to *N. tenuis* density (Sánchez et al. 2009). Reducing densities of *N. tenuis* nymphs is especially important to limit tomato plant damage (Arnó et al. 2010; Calvo et al. 2012). However, the presence of *D. errans* did not influence the proportion of aborted flowers in our experiment, despite a consequently reduced population density of *N. tenuis*. This could be due to the still low *D. errans* densities during the flower sampling period (Weeks 3–6). Madeira et al. (2019) and Mouratidis et al. (2022) reported the necessity

of *D. errans* prior establishment in crops for the efficient control of *N. tenuis* and reduced plant damage.

Our results showed a decrease in the three mirid population densities from Weeks 1 to 3 regardless of the treatments applied, due to a slow population establishment after the release. This may be related to increased mortality due to disturbance, and to the lack of prey availability. Indeed, predators were released one week after prey release, and remained at low densities throughout the experiment. The predator population increases from Week 4 coincided with the emergence of new generations. Indeed, between 24 and 25 °C (near experimental temperature 24 ± 1 °C) periods of about 21, 28 and 31 days were required to complete *N. tenuis*, *M. pygmaeus* and *D. errans* developmental cycles, respectively (Perdikis and Lykouressis 2002; Sánchez et al. 2009; Ingegno et al. 2017). The increase in *D. errans* densities from Week 4 onward would therefore coincide with the emergence of a new adult generation (only adult predators were counted), or with the introduction of new prey (second release of *B. tabaci*) 24 days after the first one (i.e. 4 days before the sampling of Week 3). For *Dicyphus* species, prey availability is an important factor for good establishment on crops (Madeira et al. 2019; Abraços-Duarte et al. 2021; Mouratidis et al. 2022) in contrast to *N. tenuis*, which is able to reproduce on plants and grow populations in absence of prey (Arnó et al. 2010; Castañé et al. 2011; Pérez-Hedo and Urbaneja 2016).

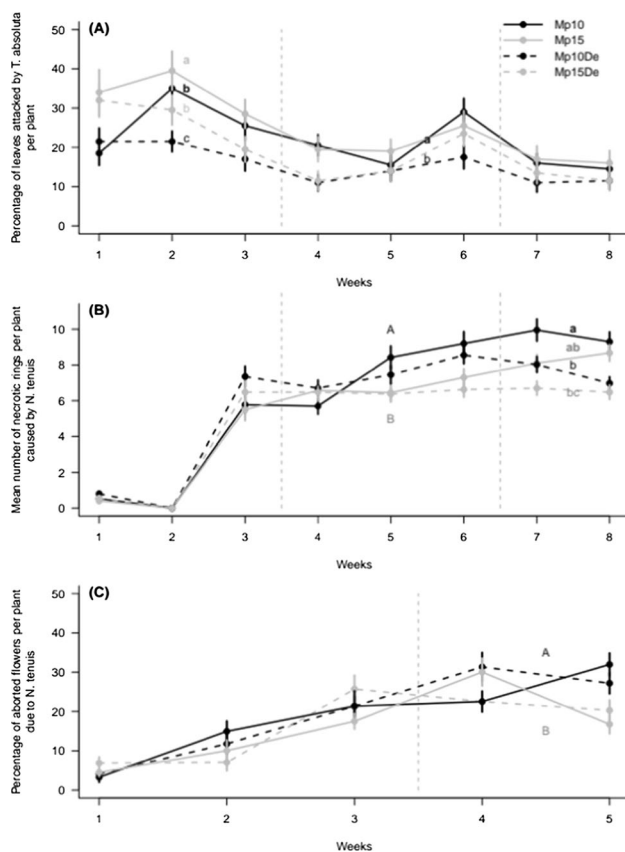


Fig. 3 Damage by *T. absoluta* (A) and by *N. tenuis* (B, C) on tomato plants: **A** percentage of leaves attacked by *T. absoluta* per plant; **B** Number of necrotic rings per plant; **C** Percentage of aborted flowers per plant. 'Mp10' 10 initially introduced *M. pygmaeus*; 'Mp15' 15 initially introduced *M. pygmaeus*; 'De' *D. errans* present. Vertical dashed lines show the time periods used in statistical tests and coinciding with estimated generation times of the insect species causing plant damage. Different letters show significant differences between treatments or groups of treatments within each time period. N=40 replicates per treatment and per week (insects counted on 10 plants per tunnel with four tunnels per treatment)

Unlike *D. errans*, population densities of *M. pygmaeus* declined continuously in our experiment, which is likely mainly due to interactions with its competitors *N. tenuis* and *D. errans*. First, *M. pygmaeus* has been shown to have a low capacity of adaptation and establishment (De Backer et al. 2014; Sánchez et al. 2021). Unlike *N. tenuis*, *M. pygmaeus* reproduction is more difficult under most common temperature regimes in greenhouses tomato crops (Ingegno et al. 2021). Notably, it is identified as the most thermophile species of mirids in the Mediterranean area (Sánchez et al. 2009; Martínez-García et al. 2017). Second, *M. pygmaeus* is less competitive for prey resources: indeed, it is considered less aggressive and preys on *T. absoluta* and *B. tabaci* at a lower rate

compared to other mirid species (Perdikis et al. 2009; Mollá et al. 2014; Sylla et al. 2016; Michaelides et al. 2018). For example, *N. tenuis* is known to occupy the upper plant strata (Perdikis et al. 2014) with a higher prey consumption rate than *M. pygmaeus* (Perdikis et al. 2009; Mollá et al. 2014). This limits the access of *M. pygmaeus* to meristematic plant tissues of higher nutritional quality (Arnó et al. 2010) and to prey such as *T. absoluta* and *B. tabaci*, which prefer the upper strata of tomato plant (Cocco et al. 2015). Montserrat et al. (2004) reported that *M. pygmaeus* was energetically more conservative in foraging than *Dicyphus* predators, leading to a comparably lower encounter and predation rate on whiteflies. Finally, *M. pygmaeus* has a position of IGP prey: predation of *M. pygmaeus* young nymphs by *N. tenuis* females has already been reported (Moreno-Ripoll et al. 2012; Perdikis et al. 2014), and predation by *Dicyphus* predators is also likely (Abraços-Duarte et al. 2021). However, in our experiment we observed that *D. errans* preferred preying on *N. tenuis* rather than *M. pygmaeus* nymphs, which has been demonstrated in other studies (Mouratidis et al. 2022).

We found that an increased total predator pressure—either through high *M. pygmaeus* densities or through the presence *D. errans* along with *N. tenuis* populations—was necessary to improve the control of *B. tabaci* and *T. absoluta* populations, leading to lower leaf damage by *T. absoluta*. The combination of predators can have a complementary or additive effect in controlling pest populations. In fact, Yao et al. (2022), under the same experimental conditions showed a beneficial effect of the joint use of *N. tenuis* and *M. pygmaeus* on *B. tabaci* whitefly and *T. absoluta* population densities reduction. This may be due to complementary ecological niches of coexisting predators and / or avoidance of IGP (Perdikis et al. 2014; Aparicio et al. 2020; Konan et al. 2021; Chen et al. 2022; Cruz-Miralles et al. 2022). According to Lucas and Alomar (2002), the level of *B. tabaci* predation was higher in the lower part of the plant when *Dicyphus tamaninii* (Hemiptera: Miridae) and *M. pygmaeus* coexisted than when each predator species was alone. Similarly, a high predation of *T. absoluta* eggs was observed by Konan et al. (2021) when *N. tenuis* and *M. pygmaeus* were combined. The rapid reduction in *B. tabaci* adult and *T. absoluta* larval populations when *D. errans* was present could result from the effectiveness of the *D. errans*—*N. tenuis* combination in controlling these pests (Calvo et al. 2012; Ingegno et al. 2019; Mollá et al. 2014; Madeira et al. 2019). This could explain why pest density decreased when *D. errans* density increased. In the absence of *D. errans*, the number of *T. absoluta* larvae still declined, although more slowly and progressively.

Table 3 Response of the proportions of attacked leaves by *T. absoluta*, and of the number of necrotic rings and the proportion of aborted flowers due to *N. tenuis* to the initial density of *M. pygmaeus* introduced, the time (date of the sampling), the presence of *D. errans* as well as all the pairwise interaction (GLMM following a negative binomial distribution). (-) parameters not included in the model

Explanatory variables	d.f	Proportion of leaves attacked by <i>T. absoluta</i>		Number of necrotic rings caused by <i>N. tenuis</i>		Proportion of aborted flowers due to <i>N. tenuis</i>	
		χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
1st generation							
<i>M. pygmaeus</i> density * <i>D. errans</i> presence	1	0.00450	0.95	0.0547	0.82	0.767	0.38
<i>M. pygmaeus</i> density	1	9.60	0.0020 ** a	0.368	0.54	0.249	0.87
<i>D. errans</i> presence	1	8.11	0.0044 ** a	1.51	0.22	1.12	0.29
2nd generation							
<i>M. pygmaeus</i> density * <i>D. errans</i> presence	1	0.522	0.47	0.00072	0.99	0.825	0.36
<i>M. pygmaeus</i> density	1	0.196	0.66	5.83	0.016 * c	6.70	0.00907** e
<i>D. errans</i> presence	1	6.87	0.0086** b	0.0946	0.76	0.0101	0.92
3rd generation							
<i>M. pygmaeus</i> density * <i>D. errans</i> presence	1	0.00630	0.97	0.00120	0.97		
<i>M. pygmaeus</i> density	1	0.0935	0.76	6.12	0.013 * d		
<i>D. errans</i> presence	1	3.19	0.074	19.7	<0.001 *** d		

** $P < 0.01$; *** $P < 0.001$; '-' effects not tested

Model coefficients: **a** Intercept – 1.11; Mp15 0.388; De – 0.355. **b** Intercept – 1.62; De – 0.341. **c** Intercept – 0.975 Mp15 0.915. 'Mp15' 15 *M. pygmaeus* initially introduced per plant; 'De' *D. errans* present. **c** Intercept 1.99; Mp15 – 0.149. **e** Intercept – 0.976; Mp15 – 0.332. 'Mp15' 15 *M. pygmaeus* initially introduced per plant; 'De' *D. errans* present. Models used were generalised linear mixed models with a binomial error distribution for proportion of attacked leaves and proportion of aborted flower, and with a negative binomial error distribution for number of necrotic rings. Generation time of pests causing damage: *T. absoluta* and *N. tenuis* 3 weeks (1st generation Weeks 1–3; 2nd generation Weeks 4–6; 3rd generation Weeks 7–8). Flowers were only counted in Weeks 1 to 5

The controversial status of *N. tenuis* – both a predator and a pest causing extensive damage on tomato – questions its use as biocontrol agent. This calls for new solutions for the integrated management of *N. tenuis* and other tomato pests. Our study demonstrated that combinations of biocontrol agents offers interesting avenues by manipulating interactions between predators (competition for food, complementarity, IGP, etc.). The combined use of *M. pygmaeus* and *D. errans* where *N. tenuis* is naturally present provides an efficient control of *B. tabaci* and *T. absoluta* populations, while limiting tomato plant damage by *N. tenuis*. Future studies should focus on investigating the optimal densities and release times of predators in these multiple biocontrol agent approaches. Such approaches could also be integrated with the use of service plants or alternative host plants to reduce *N. tenuis* phytophagy and damage on crop plants (Biondi et al. 2016, Konan et al. 2021; Chailieux et al. 2022; Castillo et al. 2022). Since top-down effects of predators on pest populations can be strongly modulated by bottom-up effects such as the manipulation of inputs to crop plants, it would be interesting to investigate how bottom-up effects affect intraguild interactions and the pest control efficacy of predator combinations (Becker et al. 2021; Han et al. 2022). The optimization of these new IPM tools should provide more sustainable perspectives in the management of

zoophytophagous mirids and other pests in vegetable agrosystems.

Author contributions

Conceptualisation KAJK, BG, CCJ, ND; Data collection KAJK, MZ, RB; Biological material provision: BG, RS; Data analysis KAJK, LSM, CCJ; Funding acquisition ND, TM, BG; Writing first draft KAJK, LSM, CCJ, MFNK; writing review and editing KAJK, CCJ, AVL, ND.

Funding

This study was supported by AMRUGE/C2D 2 granted by AFD and IRD to KAJK, the project ACOR (Casdar) to ND, and the ADOPT-IPM project funded by the European Union programme Horizon Europe (grant Number 101060430) to ND.

Availability of data and materials

Data are available upon request to authors.

Declarations

Competing of interests

All the authors declare that they have no competing interests.

Received: 23 May 2023 Accepted: 7 August 2023

Published online: 28 August 2023

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