

Beneficial worm allies warn plants of parasite attack belowground and reduce aboveground herbivore preference and performance

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Abstract

We investigated responses of tomato to two functional guilds of nematodes - plant parasite (*Meloidogyne javanica*) and entomopathogens (*Heterorhabditis bacteriophora*, *Steinernema feltiae* belowground, and *S. carpocapsae*) - as well as a leaf mining insect (*Tuta absoluta*) aboveground. Our results indicate that entomopathogenic nematodes (EPNs): 1) induced plant defense responses, 2) reduced root knot nematode (RKN) infestation belowground and 3) reduced herbivore (*T. absoluta*) host preference and performance aboveground. Concurrently, we investigated the plant signaling mechanisms underlying these interactions using biochemical and transcriptome analyses. We found that both entomopathogen and parasite triggered immune responses in plant roots with shared gene expression. Tomato plants responded similarly to presence of RKN or EPN in the root zone, by rapidly activating polyphenol oxidase (PPO) and guaiacol peroxidase (GP) activity in roots, but simultaneously suppressed this activity in aboveground tissues. We quantified changes in gene expression in tomato that may play essential roles in defense response to RKN, which were also coincidentally triggered by EPN. Overall, EPN inoculation directly mediated enhanced plant defense and reduced subsequent RKN infection. Likewise, we show that EPNs modulate plant defense against RKN invasion. Inoculation of tomato roots with EPNs belowground reduced both host preference and performance of the aboveground herbivore, *T. absoluta*. Inoculations of roots with EPN also triggered an immune response in tomato which could explain an observed decrease in egg laying and developmental performance exhibited by herbivores on EPN-inoculated plants. Our results support the hypothesis that subterranean EPNs activate a battery of plant defenses associated with systemic acquired resistance (SAR) and/or induced systemic resistance (ISR) with antagonistic effects on temporally co-occurring subterranean plant pathogenic nematodes a

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