



Modifying orchard planting sites conserves entomopathogenic nematodes, reduces weevil herbivory and increases citrus tree growth, survival and fruit yield

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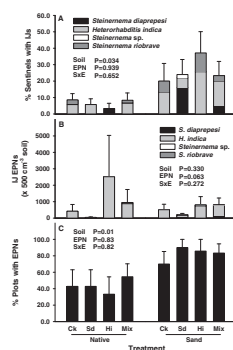
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HIGHLIGHTS

- ▶ Coarse sand in planting holes increased nematode parasitism of root weevils.
- ▶ Coarse sand increased species diversity of entomopathogenic nematodes.
- ▶ Trees grew larger, survived better and produced more fruit in coarse sand.

GRAPHICAL ABSTRACT



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ABSTRACT

In Florida, a root weevil pest of citrus, *Diaprepes abbreviatus*, is more damaging and attains higher population density in some orchards on fine textured, poorly drained “flatwoods” soils than in those on the deep, coarse sandy soils of the central ridge. Previous research revealed that sentinel weevil larvae were killed by indigenous entomopathogenic nematodes (EPNs) at significantly higher rates in an orchard on the central ridge, compared to one in the flatwoods. We hypothesized that filling tree planting holes in a flatwoods orchard with sandy soil from the central ridge would provide a more suitable habitat for EPNs, thereby reducing weevil numbers and root herbivory. Fifty trees were planted in oversized planting holes filled with coarse sand and 50 trees were planted in native soil in a split plot design where whole plots were species of introduced EPNs and split plots were soil type. Each of *Steinernema diaprepesi*, *Steinernema riobrave*, *Heterorhabditis indica*, *Heterorhabditis zealandica*, or no EPNs were introduced into the rhizospheres in 10 plots of each soil type. During four years, EPN numbers in soil samples and the relative abundance of seven species of nematophagous fungi associated with nematodes were measured three times using real-time PCR. The efficacy of EPNs against sentinel weevil larvae was also measured three times by burying caged weevils *in situ*. EPN species richness ($P = 0.001$) and diversity ($P = 0.01$) were always higher in sand than native soil. Soil type had no effect on numbers of EPNs in samples, but EPNs were detected more frequently ($P = 0.01$) in plots of sandy soil than native soil in 2011. Two nematophagous fungi species, *Paecilomyces lilacinus* and *Catenaria* sp. were significantly more abundant in nematode samples from sandy soil on all three sampling dates. Efficacy of EPNs against weevil larvae was greater in sandy soil inoculated with *S. diaprepesi* ($P = 0.03$) in June 2010 and in all treatments in sandy soil in May 2011 ($P = 0.03$). Sixty-eight percent more adult weevils ($P = 0.01$) were trapped emerging from native soil during two years than from sandy soil. By

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May 2011, the cumulative number of weevils emerging from each plot was inversely related ($P = 0.01$) to the numbers of EPNs detected in plots and to EPN efficacy against sentinels. Three trees in sandy soil died as a result of root herbivory compared to 21 trees in native soil. Surviving trees in sandy soil had trunk diameters that were 60% larger ($P = 0.001$) and produced 85% more fruit ($P = 0.001$) than those in native soil. Although it is not possible to characterize all of the mechanisms by which the two soil treatments affected weevils and trees, substitution of sand for native soil was an effective means of conserving EPNs and shows promise as a cultural practice to manage *D. abbreviatus* in flatwoods citrus orchards with a history of weevil damage to trees.

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1. Introduction

The *Diaprepes* root weevil (DRW), *Diaprepes abbreviatus*, is native to the Caribbean Basin and was first detected in Florida in 1964. Not a strong flyer, the weevil nevertheless spread to all major citrus growing areas of the state. Adults feed on expanding leaves and protect the egg mass between two leaves held together by a sticky substance secreted during oviposition. Neonate larvae fall to the soil where they feed on progressively larger roots for several months, depending on soil conditions. Larvae pupate in chambers they create in the soil. Teneral adults emerge from soil throughout the year, but peak emergence occurs during several weeks in spring or early summer, with a secondary peak possible in autumn (Futch et al., 2005). Damage to trees is due to the larval feeding on the root cortex. The older larvae create extensive wounds in the cortex of large structural roots, thereby increasing the infection of roots by the plant pathogenic *Phytophthora* spp. The pest–disease complex quickly debilitates and even kills trees when DRW population densities are high (Graham et al., 2003). At lower densities the damage to roots is cumulative and tree decline is more gradual.

The epidemiology and economic importance of DRW in Florida citriculture varies in different parts of the state. Flatwoods regions in Florida are characterized by shallow soils of variable texture with high water tables that require soils to be bedded to allow adequate citrus rooting volume. Soils on the central ridge are very deep with textures generally comprised of >95% uncoated sand particles. *Diaprepes* damage to trees tends to be greatest in orchards on poorly drained, fine textured soils (McCoy, 1999; El-Borai et al., 2012). Such soil conditions may predispose trees to greater damage in response to herbivory (El-Borai et al., 2012) as well as favor infection by *Phytophthora*. However, soil conditions also affect the population density of DRW which is a major cause of variation in damage by the weevil. The average number of adult DRW trapped during three years in three flatwoods citrus groves was approximately an order of magnitude greater than that from three groves on the central ridge (Futch et al., 2005).

The reasons that weevil abundance differs in different regions are unknown. In greenhouse studies, fewer weevil larvae were recovered after 6 and 9 months from pots containing citrus seedlings in coarse ridge sand than from pots with flatwoods soils (fine sand or sandy loam); however, it was not determined whether the differences reflected different survival or different rates of development and emigration (El-Borai et al., 2012). Duncan et al. (2003a) reported a higher average rate of DRW parasitism by native entomopathogenic nematodes (EPNs) during two years in a central ridge orchard (39% per week) compared to that in a flatwoods orchard on sandy loam soil (12% per week). Such differences in rates of biological control suggest the possibility that soils affect DRW spatial patterns in Florida indirectly by influencing the activities of the weevil's natural enemies (Duncan et al., 2007; Stuart et al., 2008). A recent geospatial survey of citrus orchards to quantify 7 EPN species reported from various Florida habitats detected greater species richness and diversity on the central ridge than in

the flatwoods, but did not find regional differences in the overall abundance of EPNs (Campos-Herrera et al., 2010, 2012). Therefore, if EPNs play a role in affecting DRW spatial patterns across the peninsula, it is likely to be mediated by how soils and/or EPN community structure affect rates at which EPNs prey on weevil larvae.

Entomopathogenic nematodes are a major class of natural enemy of soilborne insects. They inhabit nearly all habitats, having been reported from every continent except Antarctica (Griffin et al., 1990). The predominant EPN genera, *Steinernema* and *Heterorhabditis*, function in obligate symbioses with species of entomopathogenic bacteria in the genera *Xenorhabdus* and *Photorhabdus*, respectively. The third stage infective juvenile (IJ) migrates through soil and penetrates insects via body openings or occasionally by penetrating the cuticle. In the insect haemocoel, the nematode expels the bacteria from its intestine. The bacteria then reproduce, producing metabolites that kill the insect host and prevent invasion by secondary organisms (Griffin et al., 2005). The nematode completes several generations within the insect cadaver until nutrients are exhausted, at which time development arrests at the infective stage. Tens or hundreds of thousands of infective juveniles can be produced from a single insect.

A great deal of research has focused on methods to use EPNs for insect pest management. Invasive mole crickets in Florida are managed with the orthopteran-specific EPN species *Steinernema scapterisci* imported from Uruguay, the mole cricket center of origin, but this is the only reported success using EPNs for classical biological control (Adjei et al., 2006; Nguyen and Smart, 1991). The possibility of managing soils to achieve conservation biological control of insects by EPNs has been considered, but not tested (Lewis et al., 1998; Barbercheck and Hoy, 2005; Stuart et al., 2008). Rather, commercially grown and formulated EPNs are most often used to augment native populations of EPNs in soil. Augmentation of EPNs can provide effective suppression of soil-borne insects and sometimes even those in cryptic aboveground habitats (Shapiro-Ilan et al., 2005). However, introducing large numbers of nematodes to soil initiates strong responses by populations of nematophagous mites, fungi and other organisms that help to quickly reestablish a given habitat's equilibrium density for EPNs, thus requiring periodic treatment to maintain effectiveness (Duncan et al., 1996, 2003a, 2007; El-Borai et al., 2007; McCoy et al., 2000; Ekmen et al., 2010; Greenwood et al., 2011).

Here we describe an experiment that tests a conservation biological control strategy for DRW by EPNs. Essentially, we modified the soil texture in a flatwoods citrus orchard by filling planting holes with coarse sand from the central ridge and adding EPN species that are common on the central ridge or applied regularly to control weevils. We hypothesized (1) that the native soil would not support an EPN community as rich or diverse as would sand and (2) that parasitism of *D. abbreviatus* by all EPN species would be less in the finer textured native soil than in the coarse sand. If correct, we expected over time to find greater EPN species diversity, fewer DRW and better growth rates and survival of trees in sand than in native soil.

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