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Effects of nutrient supply and below-ground herbivory by *Diaprepes abbreviatus* L. (Coleoptera: Curculionidae) on citrus growth and mineral content☆

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Abstract

Three-year-old citrus trees were grown in the greenhouse to study the effects of fertilizer concentration and root herbivory on plant growth and mineral concentration. In separate experiments, sour orange (*Citrus aurantium* L.) and Swingle citrumelo (*C. paradisi* Macf. × *Poncirus trifoliate* L.) plants were treated with a complete fertilizer diluted to provide 25, 100, 200, or 400 ppm N and grown for 7 weeks with or without *Diaprepes abbreviatus* L. larvae. Increased fertilizer concentration increased the shoot mass and the shoot:root ratio of both sour orange and Swingle citrumelo. Root herbivory also increased the shoot:root ratio by depressing root growth more than shoot growth. Effects of root herbivory on growth were consistent across the four levels of fertilizer concentration, indicating that tolerance is not a function of nutrient status. For both rootstocks, concentrations of nitrogen in roots and leaves increased with fertilizer concentration, and C:N ratios decreased. In sour orange, root herbivory most strongly affected the concentration of carbon in roots, whereas in Swingle citrumelo, root herbivory most strongly affected leaf nitrogen. In general, herbivory reduced mineral concentrations of roots but the strength, and sometimes the direction, of herbivore effects varied significantly among fertilizer treatments. This research indicates that application of excess, balanced fertilizer is unlikely to offset growth reductions due to root herbivory by *D. abbreviatus*, and suggests that supplementation of specific nutrients may be of value.

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Keywords: Root herbivory; Plant nutrition; Plant–herbivore interactions; C:N ratio

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1. Introduction

Although less studied than folivory, root herbivory significantly affects plants in both natural and managed systems (Brown and Gange, 1990; Blossey and Hunt-Joshi, 2003; Hunter, 2001). In addition to consuming stored photosynthates, root herbivores reduce surface area for water and nutrient uptake and open wounds for pathogen invasion of the host plant (Andersen, 1987; Brown and Gange, 1990; Blossey and Hunt-Joshi, 2003). Such damage by root-feeding herbivores can prompt a variety of responses in individual plants, including changes in physiology (Steinger and Müller-Schärer, 1992; Murray et al., 1996; Urias-Lopez et al., 2000), growth and storage (Karban, 1980; Murray et al., 1996; Morón-Ríos et al., 1997; Dunn and Frommelt, 1998; Nötzold et al., 1998), reproduction (Ganade and Brown, 1997; Maron, 1998, 2001), susceptibility to other insects and pathogens (Masters, 1995; Rogers et al., 1996), and mortality (Strong et al., 1995; Maron, 1998, 2001). The strength of these effects is variable and may depend on biotic and abiotic environmental factors (Dunn and Frommelt, 1998; Gange, 2001) and the temporal pattern and form of herbivory (Andersen, 1987).

Because plant nutrition affects how plants allocate resources to various functions, soil fertility can affect the ability of plants to compensate for herbivory (i.e., affect tolerance; Maschinski and Whitham, 1989; Strauss and Agrawal, 1999). Compared to well-nourished plants, nutrient-stressed plants may exhibit disproportionate reductions in growth due to herbivores (Fay et al., 1996; Houle, 1999). Nutrient deficiency or imbalances may also alter primary and secondary metabolism, and thus foster growth of herbivores (Beanland et al., 2003). In mixture modeling studies that manipulated proportions of minerals available to plants, herbivores performed best on plants grown with proportions of minerals that caused suboptimal plant growth (Busch and Phelan, 1999; Beanland et al., 2003).

In this study we held the proportions of minerals constant and varied the concentration of fertilizer delivered to young citrus to determine how fertilizer concentration and root herbivory affect growth and mineral concentrations of two citrus rootstock varieties. The herbivore, *Diaprepes abbreviatus* L. (*Diaprepes* root weevil), is the most important insect pest of citrus in Florida (Diaprepes Task Force, 1997). Introduced in 1964, *D. abbreviatus* now causes annual losses in Florida estimated at \$ 75 million. These larvae attack roots of more than 40 plant species in 20 families and are considered a major long-term threat for many tropical and sub-tropical crops (Simpson et al., 1996). Larvae feed on bark of thicker roots and snip off thinner, nutrient-gathering roots. This damage reduces root surface area for water and nutrient uptake, induces defense-related proteins (Mayer et al., 1995; Borowicz et al., 2003), and opens wounds that promote invasion by opportunistic root pathogens, especially *Phytophthora* spp. (Rogers et al., 1996; Graham et al., 2003), which magnify the impact of *D. abbreviatus*.

Of the two rootstock varieties used in this study, sour orange (*Citrus aurantium* L.) is relatively susceptible to *D. abbreviatus*, and Swingle citrumelo (*C. paradisi* Macf. × *Poncirus trifoliata* L.) is more resistant (Shapiro and Gottwald, 1995). The results reported here are from a larger study that examined effects of fertilizer concentration on resistance to *D. abbreviatus* larvae (Borowicz et al., 2003). In that study, 3-year-old, well-nourished sour orange trees produced a greater mass of *D. abbreviatus* larvae compared to the most nutrient-stressed plants, and well-nourished sour orange and Swingle citrumelo plants had greater concentrations of total proteins and pathogenesis-related proteins than did severely nutrient-stressed plants. Here, we examine the effects of nutrient supply on growth of the young plants to determine whether or not host plant tolerance to root herbivory is a function of nutrient supply. We also performed mineral assays to determine how nutrient supply and herbivory of nutrient-gathering roots affect the carbon:nitrogen ratio and the balance of other minerals in citrus.

2. Methods

Three-year-old sour orange and Swingle citrumelo plants (approx. 60–100 cm tall) were grown from seed in U.S. Horticultural Research Laboratory greenhouses and were transplanted to 3.75 L pots lined with nylon screen and containing steamed sand. Plants of each rootstock were randomly assigned to fertilizer treatment (4 levels) and to root weevil treatment (0

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