

Effect of arbuscular mycorrhizal fungi (*Glomus intraradices*) on the oviposition of rice water weevil (*Lissorhoptrus oryzophilus*)

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Abstract Root-feeding insects are important drivers in ecosystems, and links between aboveground oviposition preference and belowground larval performance have been suggested. The root-colonizing arbuscular mycorrhizal fungi (AMF) play a central role in plant nutrition and are known to change host quality for root-feeding insects. However, it is not known if and how AMF affect the aboveground oviposition of insects whose offspring feed on roots. According to the preference–performance hypothesis, insect herbivores oviposit on plants that will maximize offspring performance. In a greenhouse experiment with rice (*Oryza sativa*), we investigated the effects of AMF (*Glomus intraradices*) on aboveground oviposition of rice water weevil (*Lissorhoptrus oryzophilus*), the larvae of which feed belowground on the roots. Oviposition (i.e., the numbers of eggs laid by weevil females in leaf sheaths) was enhanced when the plants were colonized by AMF. However, the leaf area consumed by adult weevils was not affected. Although AMF reduced plant biomass, it increased nitrogen (N) and phosphorus concentrations in leaves and N in roots. The results suggest that rice water weevil females are able to discriminate plants for oviposition depending on their mycorrhizal status. The discrimination is probably related to AMF-mediated changes in plant quality, i.e., the females choose to oviposit more on plants with higher nutrient concentrations to potentially

optimize offspring performance. AMF-mediated change in plant host choice for chewing insect oviposition is a novel aspect of below- and aboveground interactions.

Keywords Arbuscular mycorrhizal fungi (AMF) · Insect root herbivore · Oviposition · Preference–performance hypothesis · Rice · Above- and belowground interactions

Introduction

Ecological linkages between soil organisms and aboveground insect herbivores, mediated by effects on the quality and quantity of the plants as primary resource for both subsystems, are increasingly acknowledged (Bezemer et al. 2003; Soler et al. 2007; Wardle et al. 2004; Wurst and Jones 2003). Recent studies show that the presence and spatial arrangement of soil organisms can affect host plant selection by shoot insect herbivores for feeding and oviposition (Soler et al. 2009, 2010; Wurst and Forstreuter 2010). Among the most important soil microbes are the arbuscular mycorrhizal fungi (AMF), which play a central role in plant mineral nutrition in many ecosystems and can induce physiological changes in their hosts (Rillig 2004). Consequently, AMF can alter plant quality as a host for above- and belowground insect herbivores (Currie et al. 2011; Gange 2001; Wurst et al. 2004). The larval performance of root-feeding insects may be affected by AMF depending on the fungal and insect species (Currie et al. 2011; Gange 2001). One hypothesis that has attempted to link larval performance and female oviposition is the preference–performance hypothesis (PPH), which states that when insect herbivores have offspring with limited capacity to relocate in relation to the host plant, there is a strong selection pressure for the adult to oviposit on plants

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that will maximize offspring performance (Jaenike 1978; Johnson et al. 2006). For phytophagous insects whose life cycles include a larval stage living in the soil, selective oviposition could be a highly beneficial strategy, considering that soil-dwelling larvae may be too small to effectively burrow long distances or too big to passively move between soil pores (Johnson et al. 2006). Therefore, it seems reasonable to question if AMF can alter the oviposition of insects whose offspring feed on the roots.

For insect root herbivores, roots are mostly not accessible to ovipositing females (Städler 2002). In a short review, Johnson et al. (2006) discussed links between insect oviposition aboveground and potential or measured performance of soil-dwelling offspring, pointing to a role of roots or rhizosphere characteristics for shaping oviposition aboveground via plant- and/or soil-mediated semiochemicals. Moreover, insect root herbivores often display highly aggregated spatial distributions in soils (Brown and Gange 1990), and female oviposition behavior has been suggested as one of the main factors driving this aggregation (Brown and Gange 1990). Because AMF populations may also occur aggregated in fields, Gange (2001) suggested that another factor shaping the clustered distribution of root-feeding larvae could be different AMF populations with differential effects on larval survival.

Additionally, from an evolutionary sense, it seems likely that insects with root-feeding larvae have evolved to discriminate between AMF-mediated changes in plants favorable to the performance of their offspring as predicted by the PPH. However, no study, as far as we are aware, has ever tested if AMF can alter the aboveground oviposition of insects whose offspring feed belowground on the roots, which will be the aim of the present study. This is a novel aspect of plant-mediated interactions between belowground soil organisms and aboveground insect herbivores.

To investigate these interactions, we will focus on the effect of *Glomus intraradices* Schenck & Smith on the oviposition behavior of the rice water weevil, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae). This root-feeding insect is an important biological constraint on rice (*Oryza sativa* L.) yields in the southern USA and has been accidentally introduced into some of the biggest rice-producing regions of Asia and Europe, posing a threat to the global rice production (Hamm et al. 2010; Lupi et al. 2009; Stout et al. 2002; Tindall and Stout 2003). As an adult, the rice water weevil is a foliar herbivore, scraping the epidermis of rice leaves with its mouthparts to produce long narrow slits on leaves called feeding “scars,” which generally do not result in significant losses (Stout et al. 2002). As larva, rice water weevil is a root herbivore, pruning roots severely and reducing plant vigor and grain yields (Stout et al. 2002).

During the early spring, the rice water weevil adults emerge from overwintering sites and migrate to rice fields, where they feed on the leaves of rice plants (Hamm et al. 2010). Rice water weevil, however, is best described as an oligophagous insect, being much restricted to feeding on plants in three families—grasses, sedges. Oviposition does not commence in full until rice fields are flooded (Stout et al. 2002). Being excellent swimmers, the adults are very mobile in the flooded paddies (Hix et al. 2000). The root-feeding larvae, however, can only travel up to 15 cm in the soil (Pathak and Khan 1994), and their feeding is much restricted to roots of the host selected by the ovipositing females. The mating occurs on the shoot, and the females lay eggs within the leaf sheaths at or below the waterline (Stout et al. 2002). In the southern USA where the weevil is indigenous, females are actively ovipositing through most of May, June, and July, and three generations can emerge in 1 year. After hatching, the neonates mine leaf tissue for a short time but eventually move to the roots where they develop through four instars until adulthood (Stout and Riggio 2002).

In many rice production systems, flooding of rice fields few weeks after seeding is a common practice (Hamm et al. 2010), and this initial period under unflooded condition favors the AMF colonization of rice (Dhillion 1992; Secilia and Bagyaraj 1994). Although flooding may reduce the percentage of AMF colonization (e.g., Solaiman and Hirata 1995), several greenhouse and field studies have shown that AMF can affect wetland rice growth and concentrations of nutrients before and after flooding (Dhillion and Ampornpan 1992; Secilia and Bagyaraj 1994; Solaiman and Hirata 1995). Furthermore, *G. intraradices* is known to affect the plant growth, biochemistry, and root architecture of rice (Campos-Soriano et al. 2010; Gutjahr et al. 2009). Using rice as model plant, we tested the hypothesis that rice root colonization by *G. intraradices* affects the aboveground oviposition behavior of rice water weevil females in order to potentially optimize the performance of the root-feeding offspring, according to the PPH.

Materials and methods

Experimental setup

Soil collected from an agricultural site at the campus of Freie Universität Berlin (Germany) was mixed (1:1 v/v) with sand (CEMEX GmbH, Kraatz, Germany) to reduce the nutrient availability and encourage AMF colonization of the roots. To eradicate the indigenous AMF inocula from this soil, the soil/sand substrate was sterilized by autoclaving (20 min at 121°C). Twenty-eight surface-sterilized plastic

containers (150-ml volume) were filled with the sterilized soil/sand substrate, and two treatments were set up, AMF inoculation and non-AMF control. The AMF inoculation consisted of 10 ml of *G. intraradices* inoculum in sand substrate (INOQ GmbH, Germany), with approximately 200 fungal propagules of *G. intraradices*, mixed 4 cm deep into the soil/sand substrate. DNA multiscan[®] showed that no phytopathogens were detected in the inoculum (INOQ GmbH, Germany). Previous studies have shown that an amount of 25 spores of AMF per pot is sufficient to obtain a rice root colonization of 27–43% after 50 days of growth (cited by Dhillion 1992). The non-AMF control consisted of 10 ml of sterile inoculum (autoclaved at 121°C for 20 min), also mixed into the soil/sand substrate, to correct for sand fraction, organic matter, and nutrients of the added AMF inoculum. To create the appropriate microbial control of the AMF inoculation (Koide and Li 1989), a microbial wash was prepared by washing 200 ml of the living *G. intraradices* inoculum in 400 ml of H₂O and filtering the suspension through a 20- μ m sieve. Then, 20 ml of the microbial wash containing a background of non-AMF microbes was added to each non-AMF container. To germinate rice (*O. sativa* ssp. *japonica* “Nipponbare”) seedlings, two surface-sterilized caryopses were sown in each container, and upon germination (4–5 days), the seedlings were thinned to one per container. Each seedling was then grown independently in each container at the greenhouse (16 h light, 22/28°C night/day temperatures) and watered every day. Each treatment (AMF and non-AMF) had 14 replicates.

Rice water weevil adults were collected from rice fields in Louisiana (USA) in July 2010. The females of this insect are actively ovipositing during this time of the year (Jiang et al. 2008). The weevils were shipped with water and rice leaves in a cold acclimatized package to Berlin (Germany) 3 days prior to use. In order to ensure equal ratios of males and females, weevils were captured *in copula* and placed in small plates prior to infestation. Twenty-eight containers, 14 AMF-inoculated and 14 non-AMF control containers, each with a 14-day-old rice plant, were placed in a plastic basin (75 cm long×45 cm in width×30 cm deep) and distributed in alternate fashion along four rows with approximately 8 cm of distance between plants. The basin was then flooded, submerging the plants with the waterline 5 cm above the shoot basis, and a cage cover (75 cm long×45 cm in width×80 cm in height) screened with a fine nylon mesh was attached on top of the basin. Fourteen mating pairs of weevils were then released into the water surface, and the cage was closed. Weevils were allowed to swim freely between plants, feed, mate, and oviposit for 4 days under constant flooding. The flooding depth and timing as well as the plant density within the arena are consistent with common

agricultural practices (Hamm et al. 2010). Because AMF exhibit small-scale spatial heterogeneities (e.g., Wolfe et al. 2007), the distribution of replicates of both treatments in the choice bioassay mimics this spatial variability.

Harvest and assessments

Weevils were re-collected after 4 days of infestation. Plants were then removed from the flooding and harvested by cutting the shoot at ground level. The roots were carefully washed in water to remove soil and sand particles. The leaf blades were separated, and the leaf sheaths were placed in alcohol (70%) to discolor. To determine the consumed leaf area per plant by feeding of adult weevils, digital images of the leaf blades produced with a scanner (Epson Perfection V700 photo) were analyzed on WinDIAS 3.1 software (Delta-T Devices, UK). To assess the female oviposition behavior, the number of eggs laid per plant was determined with a method adapted from Stout and Riggio (2002). The method consisted in dissecting carefully the discolored leaf sheaths under a stereoscope (Stereomicroscope M165C, Leica) and removing the eggs from the leaf tissue as they were counted. Leaf blades, leaf sheaths, and root were dried in the oven (40°C) for a week and weighed with a precision balance to determine the dry weights. The dried leaf blades and a portion of the dry roots ($n=9$ per treatment) were grounded to fine particles using a ball mill (Retsch MM301), and the concentrations of N and C were determined with a CN Elemental Analyzer (Euro EA, HEKAtech GmbH, Germany) using acetanilide as standard (HEKAtech M.135.17). The P concentration of the ground leaf samples ($n=9$ per treatment) was determined by dry ashing according to Chapman and Pratt (1961) using a spectrophotometer (Blenchmark Plus, Bio-Rad Inc.). To determine the total amount of N, P, and C per plant, the proportion of each nutrient was multiplied by the respective root and shoot dry weights. Percentage of root length colonized by *G. intraradices* was measured after Rillig et al. (1998). Subsamples of the roots of each plant (>20 2-cm-long pieces) were cleared in 10% KOH (water bath, 90°C for 15 min). After decanting the KOH, the subsamples were washed twice with distilled H₂O and acidified in 1% HCl for 15 min. Roots were stained in 0.05% Trypan Blue (water bath, 90°C for 20 min) and then stored in lactoglycerol overnight to remove excess staining. AMF colonization was determined at the microscope (×200 magnification) using the gridline intersection method (McGonigle et al. 1990). Blue-stained hyphae associated with arbuscules or vesicles, with irregular or none cross-wall septation, and branching typically not at a right angle were noted as AMF. Hyphae that did not follow these morphological traits were noted as non-AMF (Rillig et al. 1998).

Statistical analyses

Data were analyzed by analyses of variance (ANOVA) combined with Tukey's Honestly Significant Difference (HSD) test using the R software for statistical computing (R-project.org) with the categorical factor "AMF." Data were tested for normality (Shapiro–Wilk test) and homogeneity of variances (Bartlett's test). When required, data were square root (for count data) or arcsine (for proportion data) transformed to fulfill the ANOVA assumptions.

Results

Mycorrhization, plant biomass, and nutrients

At the end of the experiment, after 4 days of flooding, the 18-day-old rice plants inoculated with *G. intraradices* had $4.1\% \pm 1.16$ (mean \pm SE, $n=14$) of the roots colonized by AMF hyphae; additionally, in $0.75\% \pm 0.25$ and $1.35\% \pm 0.53$ of the roots, arbuscules and vesicles, respectively, were noted. No mycorrhization was detected in roots of the non-AMF control plants. In addition, root colonization by non-AMF hyphae was $3.0\% \pm 0.48$ and $2.5\% \pm 0.59$ in the AMF-inoculated and non-AMF control plants, respectively; but these were not significantly different ($F_{(1,26)}=0.56$, $P=0.459$).

The total plant dry weight (dw) of the 18-day-old rice plants was significantly reduced by *G. intraradices*, approximately to half of the non-AMF control plants (Table 1, Fig. 1a). The root to shoot ratio, however, was not affected ($F_{(1,26)}=0.08$, $P=0.769$), i.e., both shoot and root weights were reduced equally. *G. intraradices* significantly reduced the shoot by 46.5% ($F_{(1,26)}=28.50$, $P<0.001$) from 91.9 ± 6.84 to 49.2 ± 4.15 mg dw (mean \pm SE, $n=14$) and the root by 47.4% ($F_{(1,26)}=18.14$, $P<0.001$) from 39.0 ± 3.79 to 20.5 ± 2.15 mg dw (mean \pm SE, $n=14$). However, AMF-inoculated rice plants had a higher nutritional quality. The colonization of rice roots by *G. intraradices* significantly increased the concentrations of N and P and reduced the concentration of C in the leaves of the 18-day-old rice plants (Table 2). The N concentra-

tion in the root was also enhanced by *G. intraradices* colonization, while there was a trend toward an increase in the concentration of C in the root (Table 2). Despite significant reduction of plant dry weight by *G. intraradices*, the content of P in the shoot tended to increase in AMF-inoculated plants, while contents of N and C were significantly reduced (Table 2). The contents of N and C in the root were also significantly reduced by *G. intraradices* (Table 2).

Oviposition and feeding behavior of the rice water weevil

In our experimental setup, rice water weevil females laid a total of 178 eggs and an average of 12.7 eggs per female. The 4 days of bioassay was likely enough for females to visit all plants, since all plants had feeding scars at the end of the experiment, but not enough for females to become limited in available eggs (Jiang et al. 2008). The colonization of rice roots by *G. intraradices* significantly increased the number of laid eggs by females in leaf sheaths per plant, approximately twofold, in comparison to the non-AMF controls (Table 1, Fig. 1b). However, the increased oviposition on AMF-inoculated rice plants was not accompanied by increased leaf consumption. The ANOVA results showed that total consumed leaf area by adult weevils on plants colonized by *G. intraradices* was not significantly different from the non-AMF controls (Table 1, Fig. 1c).

Discussion

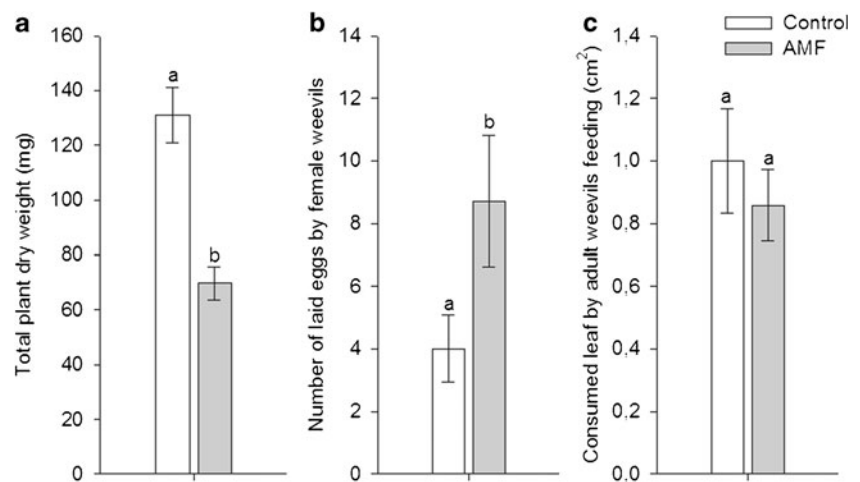
In this experiment, rice water weevil females had a choice between flooded rice plants growing in the presence or absence of *G. intraradices* and laid more eggs on plants colonized by the AM fungus. Although *G. intraradices* reduced the biomass of the 18-day-old rice plants, it increased the concentrations of N and P in the shoot and of N in the roots. These results suggest that rice water weevil females are able to discriminate among plants for oviposition depending on their mycorrhizal status. Extensive choice and no-choice experiments using rice plants in a similar growth stage showed that rice water weevil females prefer to oviposit on bigger plants (M. Stout, unpublished data). These evidences suggest that the ability to discriminate among plants observed in our study is probably related to AMF-mediated changes in plant quality rather than changes in plant quantity, i.e., the females choose to oviposit more on plants with higher concentrations of nutrient to potentially optimize offspring performance (Awmack and Leather 2002).

AMF are known to affect the performance of belowground insect herbivores (Currie et al. 2011; Gange 2001). For instance, root-feeding insect larvae with narrow diet breadth can have higher survival rates when feeding on roots colonized by AMF (Currie et al. 2011). Based on evidences

Table 1 ANOVA results on the effect of *G. intraradices* (AMF) on total plant dry weight, number of laid eggs by female weevils, and consumed leaf area by adult weevils' feeding per plant

	df	Plant weight		Number of eggs		Feeding area	
		F	P	F	P	F	P
AMF	1	26.70	<0.001	5.89	0.022	0.50	0.487
Error	26						

Fig. 1 Total plant dry weight (a), number of laid eggs by female weevils (b), and consumed leaf area by adult weevils' feeding (c) per plant as affected by *G. intraradices* (AMF) compared to the non-mycorrhizal controls (Control). Means \pm SE, $n=14$. For ANOVA results, see Table 1. Bars accompanied by different lower case letters indicate that means differ significantly ($P<0.05$) according to Tukey HSD test



from studies addressing the PPH for insect root herbivores, Johnson et al. (2006) suggested a linkage between below-ground larval performance and aboveground female oviposition preference. In our study, *G. intraradices* enhanced the aboveground oviposition of rice water weevil females, whose larvae are oligophagous root feeders. Documented evidences show that oligophagous insect herbivores generally have a strong relation between female oviposition preference and larval performance (Gripenberg et al. 2010). In our study, the AMF-inoculated rice plants preferred for oviposition had higher concentrations of N and P in shoots and of N in roots than the non-AMF control plants. Positive effects of flooding on oviposition were also associated with increased plant concentrations of N and P in the shoots (Stout et al. 2002). These results suggest that the female oviposition choice of rice water weevil is affected by the nutritional status of the plants. The positive effects of AMF on the survival of root-feeding larvae, recently documented

by Currie et al. (2011), were also associated with an AMF-mediated increase in N concentration of the whole plant. Since we also detected an AMF-mediated increase in the concentration of N in the roots in our study, we suggest that the oviposition preference of rice water weevil females may be related to a potentially better performance of the root-feeding larvae. However, further investigation is required to elucidate the effects of AMF and plant N status on the larval performance of rice water weevil.

The host selection by insect herbivores generally involves plant chemical cues located on the leaf surface or emitted through volatile blends, which encode the host quality (Städler 2002). Several insect species from the family of rice water weevil (Coleoptera: Curculionidae) use induced plant volatiles to locate the host (Ndiege et al. 1996; Perez et al. 1997; Sun et al. 2010; Wakefield et al. 2005; Wang and Kays 2002), and the attractiveness to females and males can vary due to different plant volatiles (Sun et al. 2010). The prior feeding

Table 2 Concentrations (A) and contents (B) of nitrogen (N), phosphorus (P), and carbon (C) in the leaves and N and C in the roots as affected by *G. intraradices* (AMF) compared to the non-AMF controls (Control)

A	Shoot			Root	
	N	C	P	N	C
Concentrations (%)					
Control	5.57 \pm 0.045	41.32 \pm 0.220	0.05 \pm 0.008	1.71 \pm 0.059	27.71 \pm 0.693
AMF	5.95 \pm 0.072	39.15 \pm 0.415	0.12 \pm 0.021	1.99 \pm 0.121	30.61 \pm 1.362
	<i>df</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>
AMF	1	19.47***	21.29***	4.59*	3.56(*)
Error	16				
B					
Contents (μ g)	N	C	P	N	C
Control	4.86 \pm 0.434	35.91 \pm 3.040	0.04 \pm 0.005	0.70 \pm 0.092	11.38 \pm 1.452
AMF	2.82 \pm 0.209	18.56 \pm 1.333	0.06 \pm 0.007	0.41 \pm 0.059	6.41 \pm 0.923
	<i>df</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>
AMF	1	15.10**	25.12***	7.01*	8.36*
Error	16				

Mean \pm SE, $n=9$. Significant or almost significant *F* values are italicized or followed by an asterisk between brackets, respectively [0.05<(*) P <0.10, * P <0.05, ** P <0.01, *** P <0.001]

by armyworm (*Spodoptera frugiperda* J.E. Smith) on rice has been reported to reduce rice water weevil oviposition (Hamm et al. 2010) and to induce the emission of plant volatiles (Yuan et al. 2008), whereas AMF can change plant volatile patterns induced by armyworm herbivory (Leitner et al. 2010). As observed in our experiment, adult weevils feed on rice leaves throughout the ovipositional period, which likely induces the emission of chemical volatile cues and in turn could inform females on the AMF-mediated changes in plant quality. However, considering that weevils crawl up and down along the shoot during mating, the chemical characteristics of leaf surfaces, via the surface waxes, the trichomes or the boundary layer, could also play a role in discrimination by the females (Städler 2002).

The aboveground feeding of rice water weevil adults, measured as consumed leaf area per plant, was not affected by *G. intraradices*. Gange (2001) reported negative effects of different magnitude of *Glomus mosseae* and *Glomus fasciculatum* on the leaf area consumed by black vine weevil adults on strawberry plants. The inconsistency between our neutral result and previous reports of negative effects on consumed leaf area by adult feeding might be due to the host plant–AMF species specificity (Dhillion 1992; Klironomos 2003), which may determine AMF effects on plant growth and quality and shape the leaf consumption by chewing insects. Furthermore, the adult of rice water weevil might be more tolerant to changes in plant quality for feeding than for oviposition. This has been observed in previous studies (Stout and Riggio 2002; Stout et al. 2002; Tindall and Stout 2003), where the discrimination between different host species, rice lines, or watering regimes were less evident for adult feeding than for female oviposition.

The 18-day-old rice plants inoculated with *G. intraradices* had a percentage of root colonization of 4.1%. *G. intraradices* is an extensive root colonizer, producing only limited hyphal biomass in soil (Hart and Reader 2002). Although the root colonization of 4.1% was low, this is not surprising given the short period of plant growth. In addition, species specificity between AMF and rice cultivars can influence both AMF colonization and its effect on plant growth (Dhillion 1992). However, the percentage of AMF root colonization has frequently been observed not to correlate with the benefits to the host plant (e.g., Klironomos 2000). In our study, the low AMF root colonization was associated with increased concentration of N and P. *G. intraradices* may have contributed directly to the nutrient uptake (Smith and Read 2008), but because this fungus can also induce a more profusely branched root system in rice (Gutjahr et al. 2009), the nutrient uptake via the root itself could have been enhanced in the AMF-inoculated plants. On the other hand, *G. intraradices* may activate the basal defense mechanisms in rice, which are common to pathogen infection, without affecting its symbiotic performance (Campos-Soriano et al.

2010). In their study, the plant height was apparently reduced on mycorrhizal plants until the 28th day of growth, compared with the non-AMF plants, while *G. intraradices* had positive effects on plant biomass only after 42 days post inoculation (Campos-Soriano et al. 2010). Thus, it is possible that the negative effects of *G. intraradices* on the 18-day-old rice plants observed in our study might be restricted to the early stage of vegetative growth and resulted from a tradeoff between growth and defense (Herms and Mattson 1992) as a response to *G. intraradices* activation of basal defense mechanisms (Campos-Soriano et al. 2010).

In our study, the flooding of the experimental containers was only applied at the end of the experiment to simulate the conditions during the initial oviposition attack of rice water weevil in the field. Because of the short period of the flooding, the low AMF colonization observed in our experiment was likely due to other reasons than flooding. Despite the low root colonization, *G. intraradices* changed the biomass and nutrient levels of the plant, and had a significant effect on the oviposition of rice water weevil females. This suggests that even low levels of AMF in the roots which occur under flooded conditions in the field may play a role in shaping rice water weevil attack.

In summary, our study showed that rice water weevil females were able to distinguish between rice plants growing in the presence and absence of AMF and most likely adjust oviposition behavior to optimize their offspring performance, which is a novel aspect of below- and aboveground ecological interactions. This discrimination may be related to AMF-mediated changes in plant quality, possibly detected through alteration of chemical plant cues attractive to females. However, further investigation is needed to elucidate the role of AMF on the PPH of insect herbivores and to clarify precisely the mechanisms involved.

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