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SHORT NOTE

Genetic variation in the response of the weed *Ruellia nudiflora* (Acanthaceae) to arbuscular mycorrhizal fungi

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Abstract The main goal of this work was to test for plant genetic variation in the phenotypic plasticity response of the weed *Ruellia nudiflora* to arbuscular mycorrhizal (AM) fungi inoculation. We collected plants in the field, kept them under homogeneous conditions inside a nursery, and then collected seeds from these parent plants to generate five inbred lines (i.e., genetic families). Half of the plants of each inbred line were inoculated with AM fungi while the other half were not (controls); a fully crossed experimental design was then used to test for the effects of treatment (with or without AM fungi inoculation) and inbred line (genetic family). For each plant, we recorded the number of leaves produced and the number of days it survived during a 2-month period. Results showed a strong positive treatment effect (plastic response to AM fungi inoculation) for leaf production and survival. Moreover, in terms of survival, the treatment effect differed between genetic families (significant genetic family by treatment interaction). These findings indicate that the positive effect of AM fungi on plant survival (and potentially also growth) differs across plant genotypes and that such condition may contribute to *R. nudiflora*'s capacity to colonize new environments.

Keywords Genetic variation · Arbuscular mycorrhizae · Phenotypic plasticity · Weed · *Ruellia nudiflora*

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Introduction

Phenotypic plasticity has been defined as the ability for one genotype to express different phenotypes across environments (Alpert and Simms 2002; Lortie and Aarssen 1996) and has been interpreted as an evolutionary response to heterogeneous environmental conditions. Although plant phenotypic plasticity associated to abiotic factors has been extensively studied (see review by Valladares et al. 2007), plant phenotypic plasticity associated to biotic interactions has received less attention. Given that the strength of biotic interactions has shown to vary spatially based on differences in species identity and abundance across sites (Thompson 2005; and see Abdala-Roberts and Marquis 2007), then biotic interactions may represent an understudied source of environmental heterogeneity that acts on plants which may evolve plastic responses to such biotic component (Fordyce 2006 and references therein).

Plant species which are characterized by being successful colonizers under different environmental conditions are proposed to have evolved plastic responses in order to cope with novel and/or varying environmental conditions (Richards et al. 2006). In addition, biotic interactions such as that between plants and arbuscular mycorrhizal (AM) fungi may be of central importance in order for the former to colonize new environments (Callaway et al. 2004; Richardson et al. 2000; but see Reinhart and Callaway 2006; Seifert et al. 2009). Although mycorrhizal interactions have been traditionally considered mutualistic, it is now recognized that they may vary along a symbiotic continuum (i.e., from strong mutualism to antagonism) depending on the environmental conditions (Johnson et al. 1997). In this sense, variation in the sign, intensity, or even occurrence of this interaction suggests that plant responses to AM fungi may be governed by a strong component of

phenotypic plasticity. Importantly, although many studies have shown an impact of AM fungi on plant survival (Pattinson et al. 2004; Ramos-Zapata et al. 2006), growth (Guadarrama et al. 2004; Ramos-Zapata et al. 2009), and reproductive traits (Wolfe et al. 2005) in natural settings, one aspect which has been largely ignored in wild species is the degree of genetic variation in phenotypic plasticity associated to this interaction (Pánková et al. 2008). This condition is especially relevant given that is necessary in order for plasticity to be selected for and evolve (Pigliucci 2001).

Studies on plant phenotypic plasticity, as well as genetic variation in the plasticity response to the interaction with AM fungi, are relevant both from an ecological and an evolutionary standpoint because they may contribute to the understanding of plant colonization ability in novel environments. For instance, it has been shown that AM fungi propagule abundance is lower at disturbed sites (Carrillo-García et al. 1999; McGee et al. 1997), and this condition is expected to limit to some extent the colonization ability of plant species. If different plant genotypes vary in the strength and/or sign of their plasticity response to AM fungi, then this may result in some genotypes better coping with a given set of environmental conditions than others. Thus, not only phenotypic plasticity per se but also genetic variation in such condition within plant populations may increase the availability and diversity of responses and may result in a greater ability to colonize novel sites.

Species belonging to Acanthaceae are considered successful colonizers of new environments and in some cases are even catalogued as invasives (Florida Exotic Plant Pest Council 2007; Meyer and Lavergne 2004). In particular, *Ruellia nudiflora* (Engelm. & A. Gray Urb.) has a wide distribution throughout the Gulf of Mexico and is considered a weed (Villaseñor and Espinosa 1998). Although preliminary work has shown that it presents AM fungi colonization in its roots (Ramos-Zapata, unpublished data), the presence of phenotypic plasticity associated to this interaction, as well as genetic variation in such plasticity, has not yet been studied for this species. By inoculating different genotypes of *R. nudiflora* with AM fungi, the present study was aimed at answering the following questions: (a) does AM fungi inoculation have an effect on *R. nudiflora* plant growth and survival? and (b) does this effect vary between *R. nudiflora* inbred lines (i.e., genetic variation in phenotypic plasticity)?

Materials and methods

Study species

R. nudiflora (Acanthaceae) is a perennial herb with wide distribution throughout the state of Yucatan (Flores and Espejel 1994) where it is found mostly at disturbed or managed sites (Villaseñor and Espinosa 1998). It is commonly found in traditional Mayan agricultural systems where it has been very difficult to eradicate (Caamal-Maldonado et al. 2001).

R. nudiflora produces both cleistogamous (CL; closed) flowers which obligately self-pollinate, as well as chasmogamous (CH; open) flowers which are pollinated by several species of bees and butterflies. *R. nudiflora* is completely self-compatible, and CH flowers frequently self-pollinate automatically in the absence of pollinators (Abdala-Roberts et al. 2009). Cleistogamous flowers blossom throughout the year, and it has been hypothesized that CL flower production is favored under heterogeneous environmental conditions (Culley and Klooster 2007). The presence of CL flowers in *R. nudiflora* facilitates the generation of inbred lines (hereafter referred to also as genetic families) because all seeds from a given fruit are full siblings.

Roots of *R. nudiflora* have been shown to present different levels of *Arum*-type AM fungi colonization (sensu Gallaud 1905) based on samples taken from plants of several populations in Yucatan. These observations have indicated the presence of AM fungi species belonging to *Acaulospora* and *Glomus* genus in *R. nudiflora*'s rizosphere (Ramos-Zapata, unpublished data).

Experimental design A fully crossed factorial experiment was conducted which evaluated the effects of (a) AM fungi inoculation (treatment, two levels: AM fungi inoculated or not) and (b) inbred line (genetic family, five levels: families) on leaf production and plant survival. A significant treatment effect would indicate a plastic response of the plant to AM fungi inoculation, a significant genetic family effect would indicate differences in performance between genotypes, and finally, a significant interaction term would indicate differences between plant genotypes in their response to AM fungi inoculation (i.e., genetic variation in the plasticity response; see Pigliucci 2001).

Generation of inbred lines A total of ten adult plants were selected in August 2005 from a *R. nudiflora* population found within the Ecological Preserve of Cuxtal (20°48′ N, 89°42′ W). Plants were randomly selected at this site, taking special care that a minimum distance of 10 m existed between plants and that they were all of approximately the same size (i.e., height, number of leaves). Each plant was unearthed and transplanted to a 1.2-l pot which was filled with of a mix of native unsterilized soil and peat moss (1:1 *v*/*v*). These "parent" plants were then taken to a nursery of the Ecology Department of the Autonomous University of Yucatan, where they were kept under homogeneous conditions in order to minimize maternal effects and maximize the genetic identity within each family (Fornoni

and Núñez-Farfán 2000). Environmental conditions inside the nursery were maintained constant throughout the duration of the experiment: average level of photosynthetic active radiation of 784.78 (±52.1) μ $mol^{-2}s^{-1}$, a 12-h photoperiod, and an average temperature during the day and relative humidity of 30°C (±0.67) and 59% (±2.8), respectively. Plants were watered once a week up to field capacity and were kept inside the nursery for a 6-month period. Finally, each plant's position inside the nursery was rotated weekly.

At the end of the 6-month period, five parent plants were randomly selected and ten mature fruits were collected per plant, all from CL flowers (first generation of self-pollination). Seeds from these fruits were individually germinated in a 1.2-l pot which was filled with a mix of native unsterilized soil and peat moss (1:1 *v*/*v*); experimental conditions were identical for all seeds (e.g., substrate, watering, etc.). All seedlings belonging to the same parent plant were considered a genetic family (families 1 to 5). First-generation seedlings from each of the five parent plants were kept in the nursery for a 5-month period (same conditions as those described for parent plants). Once seedlings had grown and the plants started producing fruits, one individual was randomly selected from each family and its CL fruits were collected. Seeds from these fruits (second generation of self-pollination) were germinated in plastic trays with substrate that was steam-sterilized (see Azcón and Barea 1997). Seedlings obtained from these seeds were used as replicates for each genetic family and were subject to the AM fungi treatment.

AM fungi inoculation Three weeks after the second-generation seedlings had germinated (n=181), they were transplanted to 1.2-l pots which contained steam-sterilized native soil which was then re-inoculated with soil filtrate in order to reestablish the microbial biomass, but excluding AM fungi propagules (Azcón and Barea 1997). AM fungi treatment (M or NM) was applied as following: family 1, n=9 (NM) and 19 (M); family 2, n=18 (NM) and 19 (M); family 3, n=20 (NM) and 20 (M); family 4, n=16 (NM) and 20 (M); and family 5, n=20 (NM) and 20 (M).

Plants subject to the NM treatment were kept in steam-sterilized soil with soil filtrate, whereas M plants were subject to 500 g of AM fungi inoculation. The inoculum was obtained from soil taken at the site where the parent plants were collected; the AM fungi were propagated by means of "trap plants" (sorgum, maize, bean; Feldman and Idczak 1992). Finally, after an 8-month period, propagule density in the inoculum was evaluated following the MPN technique (Porter 1979) which indicated a concentration of >1,000 infective propagules per 100 g (composed mainly of spores of *Acaulospora* and *Glomus* and extraradical hyphae and AM fungi-colonized roots). Arbuscular mycorrhizal fungi percent colonization levels in roots of M and NM plants were estimated by means of a modification of the Trypan blue technique (Phillips and Hayman 1970).

As for parent and first-generation plants, second-generation (treatment) plants were left inside the nursery, under the same conditions throughout the experiment, and their position was randomly rotated every week. For each experimental plant, we recorded weekly both leaf production (number of leaves) and survival (alive or dead) throughout a 2-month period (June 2006 to August 2006) for all experimental plants.

Statistical analyses Kruskal–Wallis test was used to evaluate differences in percent of AM fungi root colonization between families within the M treatment group. The effects of treatment, genetic family, and their interaction on the number of days each plant remained alive and on total number of leaves produced per plant (accumulated value throughout the experiment) were evaluated by means of a mixed model using the GLIMMIX macro in SAS ver. 8e (SAS Institute Inc. 2002, Cary, NC, USA). Both models assumed a Poisson error distribution and log link function, and the model for number of leaves used the number of days each plant remained alive as covariate. These analyses did not consider genetic family 1 because its plants had a very limited leaf production and they died shortly after the experiment had initiated. The use of mixed models allowed us to estimate both fixed (treatment) and random effects (genetic family, treatment×genetic family; Littell et al. 1996). Significant random effects were interpreted as a significant amount of variation among any given set of levels for such factor and not strictly as statistical differences between the levels (the latter interpretation would be for a fixed factor effect; see Herrera 2000). Multiple comparisons between levels for random factors were thus not performed.

Results

Root colonization Roots of M plants were colonized by AM fungi while those of NM plants were not. The average percent of colonization for M plants was 51.97% (±4.47), and there were no significant differences in the percent of AM fungi colonization between genetic families (H=1.37, df=4, P=0.849). Thus, treatment effect differences between genetic families (leaf production and survival) would not be due to variation in AM fungi colonization levels.

Leaf production Significant effects of treatment ($F_{1,\ 151}$= 11.4, P<0.001), genetic family (Z=8.7, P<0.0001), and the covariate ($F_{1,\ 151}$=95.5, P<0.0001) were observed on the total number of leaves produced per plant. Plants that were

subject to AM fungi inoculation (M) produced more than twice the number of leaves compared to NM plants in most genetic families (Fig. 1), and the significant family effect indicated differences in overall performance between genotypes. Finally, although differences in the magnitude of the response between families were observed (Fig. 1), the genetic family×treatment interaction was not significant ($F_{6,\ 151}$=1.3, P=0.24), and all families responded positively to AM inoculation. The lack of a significant interaction term indicated no genetic variation in *R. nudiflora*'s plastic response to the interaction with AM fungi.

Survival Significant effects of treatment ($F_{1,\ 152}$=19.1, P<0.001), genetic family (Z=8.7, P<0.001), and treatment× genetic family interaction ($F_{6,\ 152}$=2.4, P=0.03) were observed on the number of days plants lived. Plants which were inoculated with AM fungi remained alive significantly longer compared to NM plants. The significant interaction term indicated that the treatment effect varied between genotypes and suggested genetic variation in the plant's response to the interaction with AM fungi. Specifically, families 3 and 4 did not respond to AM inoculation, while families 2 and 5 did show a positive response to AM inoculation (Fig. 2).

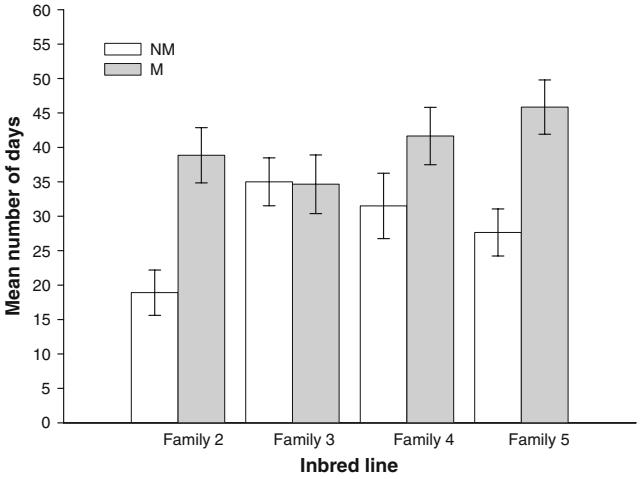

Fig. 2 Number of days that *R. nudiflora* control and AM fungi-inoculated plants remained alive during the experiment. Values given are means±SE. *M* AM fungi-inoculated plants, *NM* noninoculated plants

Discussion

R. nudiflora was benefited from AM fungi inoculation in terms of both leaf production and survival. Moreover, in the case of survival, we found evidence of genetic variation in the response to AM fungi inoculation. These results suggest that the ability for *R. nudiflora* to survive in recently colonized environments may potentially increase when associated to AM fungi and that genetic variation in the response to AM fungi will allow for the selection of genotypes with different degrees of plasticity in their response to this interaction in accordance to the prevailing environmental conditions at each site (e.g., AM fungi abundance, nutrient availability). For example, a recent study by Seifert et al. (2009) reported that *Hypericum perforatum* populations introduced from Europe to North America evolved a reduction in mycorrhizal dependence. Such condition may be taking place at some *R. nudiflora*; however, in other cases, *R. nudiflora* populations may be evolving stronger responses to AM fungi. Which abiotic and biotic conditions favor one scenario or the other remain to be addressed for the study species.

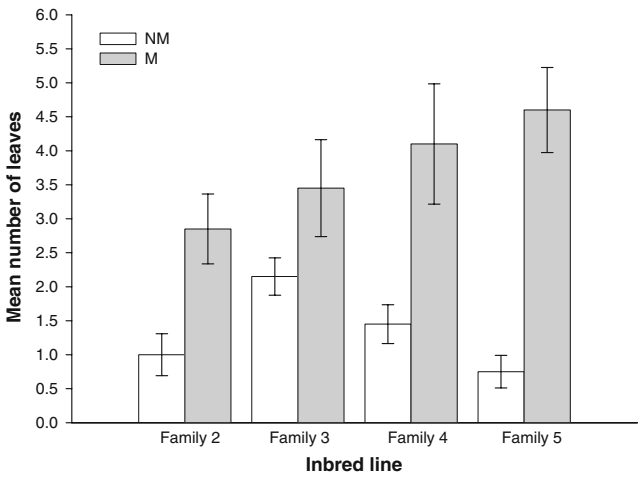

Fig. 1 Number of new leaves produced by *R. nudiflora* control and AM fungi-inoculated plants. Values given are means±SE. *M* AM fungi-inoculated plants, *NM* noninoculated plants

R. nudiflora is typically found in recently disturbed open sites and in agricultural areas of southeast Mexico (Caamal-Maldonado et al. 2001; Villaseñor and Espinosa 1998). We observed that *R. nudiflora* plants subject to AM fungi inoculation showed *Arum*-type colonization which is common for weeds that grow at disturbed sites (Yamato 2004) and is characterized by presenting high rates of expansion (Smith and Read 2008), while providing the host with a continuous flow of nutrients (Dickson 2004). Results from this study suggest that, regardless of conditions present at a given site, this mutualism has increased *R. nudiflora*'s capacity to colonize new environments and thus expand its distribution range throughout the Yucatan Peninsula, across heterogeneous plant communities (Flores and Espejel 1994) and soil conditions (Bautista et al. 2005).

In addition to finding that inoculated plants produced significantly more leaves and lived longer, the treatment effect on survival varied across families. Such genetic variation in *R. nudiflora*'s survival response to AM fungi

may be partly due to a potentially high level of environmental uncertainty regarding the occurrence, establishment, and/or degree of benefit obtained by the plant from this interaction, depending on site-specific conditions. Such scenario will potentially favor the maintenance of high levels of plant genetic variation in phenotypic plasticity associated to this mutualism, at least for the studied *R. nudiflora* population. This condition may be relevant at disturbed sites where the abundance of AM fungi propagules is lower or unpredictable (Carrillo-García et al. 1999; McGee et al. 1997) because the availability of *R. nudiflora* genotypes in a population which respond differentially to the association with AM fungi in terms of survival will assure that at least some individuals will be able to survive independently of AM fungi availability.

Plants are able to modulate the strength of the interactions they establish with AM fungi based on the degree of dependence they have on the latter and/or due to prevailing environmental conditions (Graham et al. 1997); some species have shown not to respond to AM fungi inoculation (e.g., Gao et al. 2007; Richter and Stutz 2002; Schroeder and Janos 2004) while for others, this response has been shown to vary between plant genotypes (e.g., Bago et al. 2006; Grandcourt et al. 2004; Pánková et al. 2008). The effect of genotype on the plant's response to the interaction with AM fungi has been mostly evaluated for cultivated species such as maize inbred lines (Kaeppler et al. 2000), *Citrus* cultivars (Menge et al. 1978), and wheat varieties (Al-Karaki and Al-Raddad 1997). Such studies have commonly found significant variation between genotypes in the response to AM fungi inoculation (e.g., Bryla and Koide 1998; Khaosaad et al. 2006; Zhu et al. 2003). However, this test has rarely been conducted for wild species, with only a few exceptions including this study. For instance, Sylvia et al. (2003) showed that aerial biomass production in *Uniola paniculada* (pioneer species in coastal dunes) increased as a result of its interaction with AM fungi and that this response varied between plant genotypes, a result which agrees with survival results for *R. nudiflora* in this study. In contrast, Fumanal et al. (2006) reported an increase in leaf production, height, and total dry weight for the invasive annual *Ambrosia artemisiifolia* as a result of its interaction with AM fungi; nonetheless, this response did not vary between plant genotypes. Results from this latter study agree with those found here for leaf production in *R. nudiflora*.

A final observation worth mentioning is that, within the mycorrhizal treatment, all inbred lines converged to similar average survival values, while in the absence of the mycorrhizal association (NM treatment), the data suggest differences in survival between genotypes (Fig. 2). This finding suggests that at sites with high densities of AM fungi propagules, plant genotypes will not only have a greater chance of surviving, but that survival will be more similar for all genotypes. In other words, mycorrhizal interactions may have the potential to homogenize survival probabilities between plant genotypes.

We conclude that AM fungi have a positive effect on *R. nudiflora* survival and growth, which in this study was given by a plastic response to fungi inoculation. Nonetheless, the strength of the response to this interaction (in terms of survival) can vary between plant genotypes. Based on these findings, we suggest that *R. nudiflora*'s potential to colonize new sites may be at least partly due to the benefit it obtains from its association with AM fungi, as well as due to the presence of genetic variation in the response to this interaction which will guarantee the availability of genotypes within a population which respond adequately according to site-specific conditions.

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