RESEARCH PAPER

Effects of flower dimorphism and light environment on arbuscular mycorrhizal colonisation in a cleistogamous herb

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ABSTRACT

Although it is known that floral dimorphism contributes to the maintenance of mixed breeding systems, the consequences of producing progeny of a contrasting genetic background and seeds with differential resource allocation has been practically ignored regarding establishment of belowground organisms–plant interactions. This article evaluates the combined effect of floral dimorphism with cross type and light environment on interactions between *Ruellia nudiflora* and arbuscular mycorrhizal fungi (AMF). *R. nudiflora* produces cleistogamous (CL) flowers that exhibit obligate self-pollination and chasmogamous (CH) flowers with facultative self- (CHs) or cross- (CHc) pollination. We evaluated the establishment of the plant–AMF interaction in progeny derived from each floral type, under two light conditions (shaded *versus* open). We established different scenarios depending on the existence of inbreeding depression (*ID*) and whether the differential resource allocation (*DRA*) to CH and CL flowers affected the *R. nudiflora*–AMF interaction. We predicted that under shaded light conditions there might be an intensification of *ID*, having a negative effect on AMF colonisation. The percentages of hyphae and vesicles in the harvested roots was significantly higher in the shaded plants (F ≥ 4.11, P < 0.05), while progeny of CHc and CHs presented a higher percentage of hyphae and vesicle colonisation compared to CL progeny (F = 15.26, P < 0.01). The results show that DRA to CH flowers and light availability both determines the establishment of *R. nudiflora*–AMF interaction. The results also suggest that even under stressful light conditions, endogamy does not affect this interaction, which may explain the success of *R. nudiflora* as an invasive species.

INTRODUCTION

Since the pioneering work of Charles Darwin, sexual diversity in plants has been one of the subjects most studied by ecologists and evolutionary biologists (Barret 2002). Research into the evolution of sexual diversity in plants has mainly focused on attempting to understand the reasons behind the wide variety of morphological and functional characteristics presented by plants in their flowers (Barret 2002). The answer to this question is based on two closely linked factors: the condition of immobility of plants and avoidance of the negative effects of endogamy (Stebbins 1957; Jain 1976; Charlesworth & Charlesworth 1987). However, although some theoretical models predict that an evolutionary strategy should have one of two relatively stable conditions (*i.e.* predominantly selfing or predominantly crossing species; Lande & Schemske 1985), around 40% of plants with flowers present mixed breeding systems (hereafter MBS; Goodwillie *et al.* 2005) that have the potential to produce progeny with a contrasting genetic 'background' (*i.e.* selfing or crossing progeny).

The genetic consequences of MBS have been widely studied in terms of the effects of inbreeding depression of individual performance (Charlesworth & Charlesworth 1987). However, the consequences of producing selfing or crossing progeny for the establishment of antagonistic or mutualistic interactions have been little explored (*e.g.* Ivey & Carr 2005; Bello-Bedoy &

Núñez-Farfán 2011), particularly in terms of their co-variation with stressful environmental conditions that can intensify inbreeding depression (Armbruster & Reed 2005) and contribute to the generation of plastic responses to heterogeneous environments (Pigliucci 2001).

In species that present MBS it has been demonstrated that endogamous progeny respond differently compared to exogamous progeny in terms of their interaction with aboveground organisms, *e.g.* defence against herbivores and pathogens (Stephenson *et al.* 2004; Kariyat *et al.* 2011) and visits by pollinators (Ivey & Carr 2005). However, in interactions with belowground organisms, practically no evidence exists regarding the consequences of producing seeds with a different genetic background. To our knowledge, only one example exists where it has been proved that progeny derived from cross-pollination presented higher arbuscular mycorrhizal fungi (AMF) colonisation (Collin & Ashman 2010).

Species that present floral dimorphism with the presence of cleistogamous flowers (dimorphic cleistogamy, *sensu* Culley & Klooster 2007) present an ideal opportunity to evaluate the effect of endogamy in below- and aboveground interactions, since these species clearly generate progeny with a contrasting genetic background: seeds derived from obligate self-pollination in cleistogamous flowers (CL) and seeds derived from selfing (CHs) or facultative crossing (CHc) in chasmogamous flowers. Moreover, cleistogamous species constitute a good

model because different floral morphs receive a differential allocation of resources (CL flowers are energetically less costly and produce seeds of lower biomass), which can have consequences for the progeny performance (Clay 1983; Eckstein & Otte 2005; Oakley *et al.* 2007). Together, these characteristics allow evaluation of the combined effect of floral dimorphism and cross type (*i.e.* pollen source) on the performance of the progeny.

In this article, we describe the effects of floral dimorphism and the light environment on interactions between *Ruellia nudiflora* (Acanthaceae) and AMF that affects its growth and survival (Ramos-Zapata *et al.* 2010). *Ruellia nudiflora* is a dimorphic cleistogamous species (Munguía-Rosas *et al.* 2012) with a preference for open sites, and is considered an invasive species in the tropical dry forests of Yucatan state, Mexico (Cervera & Parra-Tabla 2009; Munguía-Rosas *et al.* 2012, 2013a).

We established different scenarios depending on the existence of inbreeding depression (*ID*) and whether the differential resource allocation (*DRA*) to the CH and CL flowers affected the association between *R. nudiflora* and AMF (Table 1), in two different light environments. In conditions of no effect of *ID* and *DRA*, we expected equal colonisation among the progeny (Table 1a). With only *ID*, we expected that the endogamous progeny would present lower AMF colonisation compared to the exogamous progeny (Table 1b), probably due to errors in recognition and signalling between the AMF and plants, or indirectly by affecting the procurement of resources by the plant in order to establish the association (Collin & Ashman 2010). If the *DRA* to CH flowers affects the quality of the host plant, in the absence of *ID* we expected that progeny derived from CH flowers would present higher colonisation (Table 1c), while a combined effect of *ID* and *DRA* would produce higher colonisation in the CHc progeny (Table 1 d). Finally, since *R. nudiflora* is a species that preferentially grows in open spaces, we supposed that low light availability would represent a stressful environment. Under these conditions, there may be an intensification of *ID*, producing a generally negative effect on AMF colonisation (*e.g.* Tester *et al.* 1986), especially in the progeny derive from self-pollination.

In addressing the above, this study advances not only our general understanding of the evolution of the mixed breeding systems and the consequences of floral dimorphism, but also our understanding of the genetic and environmental factors that regulate the association between plants and AMF, a key interaction with strong 'bottom to top' effects at community level (*e.g.* Hodge & Fitter 2010; Venkateshwaran *et al.* 2013).

Table 1. Expected effects in the AMF colonisation of roots of progeny derived from self- and cross-pollination in chasmogamous (CH) and cleistogamous (CL) flowers of *Ruellia nudiflora*: CHc = progeny from cross-pollination; CHs = progeny from self-pollination; CL = progeny from obligate self-pollination.

		inbreeding depression effect	
		no	yes
resource allocation effect	no	(a) CHc = Chs = CL	(b) CHc > CHs = CL
(CH *versus* CL flowers)	yes	(c) CHc = CHs > CL	(d) CHc > CHs > CL

MATERIAL AND METHODS

Study area and species

The study was carried out in two experimental plots that belong to the Universidad Autónoma de Yucatán (20°52'N, 89°36'W, 10 m a.s.l.). The vegetation type is seasonally tropical dry forest dominated by tree species such as *Bursera simaruba* (Burseraceae), *Piscidia piscipula* (Fabaceae) and *Parmentiera millspaughiana* (Bignoniaceae) (Flores & Espejel 1994). The climate is warm sub-humid, with summer rains, mean annual rainfall and temperature are 850 mm and 26.2 °C, respectively (Chico Ponce de León 1999).

Ruellia nudiflora (Acanthaceae) is a perennial weed that grows preferentially in open and disturbed sites, but can also be found in shaded environments (*e.g.* agricultural fields, disturbed forests, roads); it is considered an invasive species in Yucatan (Cervera & Parra-Tabla 2009; Munguía-Rosas *et al.* 2012, 2013a). *Ruellia nudiflora* exhibits dimorphic cleistogamy (*sensu* Culley & Klooster 2007), characterised by the production of cleistogamous (CL) flowers that are obligate self-pollinated and chasmogamous (CH) self-compatible flowers that are facultative self- or cross-pollinated (Abdala-Roberts *et al.* 2014). The CH flowers present an anthesis of 1 day; the corolla opens early in the morning (*ca.* 07:00 h) and closes around midday. Flowers are pollinated by different species of bees (*e.g. Apis mellifera*, *Trigona fulviventris*), as well as by butterflies (*e.g. Microtia elva*). The fruits of both CH and CL flowers are dry and dehiscent, but those of the CL flowers produce fewer seeds (number of seeds per fruit: CL = 5–7; CH = 10–12; Abdala-Roberts *et al.* 2010) with a significantly lower biomass (mg·seed^{-1}: CL = 2.16 ± 0.05; CH = 2.59 ± 0.05, mean ± SD; Munguía-Rosas *et al.* 2012). Experiments conducted under greenhouse conditions have shown that *R. nudiflora* presents a mutualistic association with AMF, which increases both leaf production and seedling survival, although the effect differs between different plant genotypes (Ramos-Zapata *et al.* 2010).

Experimental design

During March 2011, 20 adult (maternal) *R. nudiflora* plants were extracted from a population located *ca.* 20 km from the experimental site. The selected plants were of similar size and located at least 2 m apart. The plants were immediately transported to a greenhouse at the University of Yucatan, planted in 1.5-l plastic bags with soil taken from the collection site and watered when required. Between the months of April and May, 14 of the plants produced both CL and CH flowers; two hand-pollination treatments were conducted in the latter: cross-pollination (CHc) and self-pollination (CHs). For the CHc treatment, a flower from a different plant was selected as the pollen source, emasculating the anthers in order to avoid self-pollination. In the CHs treatment, pollen from the same plant was used. Hand-pollinations were carried out when the pollen was liberated from the anthers (*ca.* 08:00–09:00 h), ensuring that the stigma was saturated. To avoid pollen contamination in the CHc and CHs treatments, the corollas together with the anthers were removed after each hand-pollination procedure. Each hand-pollinated flower was marked and the fruits produced were collected in individual bags; mature CL fruits were collected and stored under the same conditions as the CH fruits. The CH and CL fruits can easily be distinguished, since

the former are larger and retain the style even when mature (Munguía-Rosas *et al.* 2012).

Due to the fact that not all of the plants produced CH flowers or any fruits, only nine maternal families were obtained under all the treatments: (*i.e.* half-sibs CHc, full-sibs CHs and CL fruits). During July 2011, between ten and 26 seeds from fruits of the three treatments per family were germinated and grown under the same conditions in which the mother plants were maintained. No significant differences in seed germination were observed among treatments (Munguía-Rosas *et al.* 2013a). At the end of September, seedlings with at least one pair of true leaves were transplanted to two experimental plots (6 × 8 m) that were divided in half. In each plot, one of these halves was kept open (*i.e.* open treatment) while the other was shaded with a neutral mesh that reduced the environmental PAR by 50% (*i.e.* the shade treatment). In total, 343 seedlings were planted, some 15–25 cm apart; allocation of the seedlings to the plots and light treatments was systematic in that all the families were represented in both light treatments and in both plots. The order within each plot corresponded to an arbitrary consecutive number allocated to each plant; 163 plants (80 in open and 83 in shade) were planted in the first plot and 180 plants (81 in open and 99 in shade) in the second. In total, 119 CHs, 107 CHc and 117 CL plants were planted, with an average number of seedlings per family of 38 (range 23–52). The plants were watered homogeneously as required throughout the course of the experiment.

Once the plants reached reproductive age (*i.e.* production of CH and CL fruits), which occurred in July 2012, the roots of all plants that were still alive were individually harvested per light treatment (open *versus* shade) and per type of flower and cross (CHc, CHs and CL). Harvested roots were washed with tap water and dyed with trypan blue according to Phillips & Hayman (1970), modified by Hernández-Cuevas *et al.* (2008). We subsequently prepared permanent samples with polyvinyl alcohol, lactic acid and glycerine (PVLG) and estimated the percentage of total AMF colonisation by each fungal structure (hyphae and vesicles) in each sample using the intersection method (McGonigle *et al.* 1990). The hyphae are structures that transport nutrients from the soil to the roots and the vesicles constitute organs of storage; both structures therefore reflect colonisation by AMF (Smith & Read 2008). *Ruellia nudiflora* is colonised by unidentified species of the genera *Acaulospora* and *Glomus* (Ramos-Zapata *et al.* 2010). While it is known that different species of fungi can respond differently to environmental conditions (e.g. light *versus* shade), the small distance between plots (3 m) and between the plants themselves, as well as the fact that these plots experienced the same environmental conditions as before the experiment, means that important differences in the fungal community are not expected among treatments. However, future experiments should consider the taxonomic identity of each AMF species since species-specific responses to environmental changes may exist (Smith & Read 2008).

Statistical analysis

The percentages of AMF hyphae and vesicles observed on the roots were analysed with a mixed effects linear model, with the GLM method (Littell *et al.* 1996) in the statistical package SAS version 9.1, using a normal type distribution error and type III

sums of squares (SAS 2002). The GLM method was used because it allows estimation of least expected sum of squares and tests hypotheses concerning the components of variance in the random effects (Littell *et al.* 1996). In this particular case, we were interested in evaluating whether the response varied among the genetic families depending on the light environment and the cross type, given the evidence provided in a previous study that showed genetic variation in the response to AMF (Ramos-Zapata *et al.* 2010). The main factors considered as fixed effects were light treatment, with two levels (open *versus* shaded), the combined effect of the floral dimorphism and cross type (hereafter FDC), with three levels (CHc, CHs and CL), while plot and family (nine families) were considered as random effects. Because all the families were distributed and replicated in the two plots, maternal family was considered a nested effect within each plot. It is important to clarify that two plots were used only in order to have enough space to plant all the seedlings. However, in order to ensure that the availability of ineffective AMF propagules was similar under both light treatments, three compound soil samples were taken from each plot; the most probable number method (Ramos-Zapata *et al.* 2011) showed that there were no differences in the number of ineffective propagules per 50 g of soil (Ramos-Zapata unpublished data). The response variables (*i.e.* percentage of hyphae and vesicles observed) were arcsin transformed in order to comply with the requirement for normality (Zar 1986). On finding significant effects of the main factors, or interaction between the main factors and the family, differences were determined based on pre-planned contrasts (Littell *et al.*1996). In all cases, means (±SE) are presented, calculated from the original percentage colonisation data.

RESULTS

Regardless of treatment, we observed that the percentage of colonisation by hyphae and vesicles in the roots was generally higher under shaded conditions compared to that in open conditions (hyphae: 22.24 ± 1.6 *versus* 18.48 ± 1.9; vesicles: 5.22 ± 0.63 *versus* 3.19 ± 0.55, respectively). For the combined effect of floral dimorphism and cross type (FDC), progeny derived from the CHs treatment had a higher average percentage colonisation by hyphae and vesicles (hyphae: 32.87 ± 2.33; vesicles: 6.9 ± 1.05), followed by the CHc treatment (hyphae: 22.9 ± 1.63; vesicles: 4.61 ± 0.6) and finally the CL treatment, which presented the lowest colonisation (hyphae: 10.92 ± 1.58; vesicles: 1.71 ± 0.32).

The results of the mixed model for the percentage colonisation of roots by AMF hyphae revealed significant effects of light level and FDC, as well as an effect of the interaction between light level effect and FDC (Table 2). The significant effect of the interaction was because plants of the CL treatment presented a significantly higher percentage of hyphae under shaded conditions (Fig. 1). The plants of the treatments CHc and CHs presented the same percentage of hyphal colonisation under both light conditions (Fig. 1).

In the percentage colonisation of roots by AMF vesicles, the analysis showed significant effects of light level and FDC, as well as an effect of the interaction family × light level (Table 2). The plants grown under shaded conditions had, on average, a higher percentage colonisation by vesicles compared to those grown in open conditions (5.22 ± 0.63, 3.19 ± 0.55,

Table 2. Percentage colonisation by AMF hyphae and vesicles in roots of *Ruellia nudiflora* of different floral type and crossing treatment (CHc = progeny from cross-pollination; CHs = progeny from self-pollination; CL = progeny from obligate self-pollination) in two conditions of light availability (open *versus* shaded).

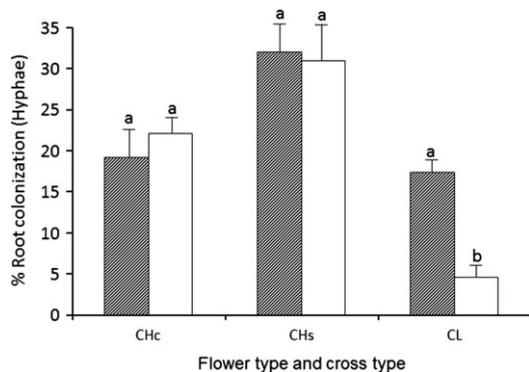| effect	hyphae		vesicles	
	F	P	F	P
type of flower and cross	26.21	**<0.0001**	15.26	**<0.0001**
light	4.11	**0.043**	20.08	**<0.0001**
family (plot)	3.0	0.18	1.42	0.18
type of flower and cross × light	8.79	**0.0002**	0.87	0.41
type of flower and cross × family (plot)	0.71	0.78	0.965	0.49
light × family (plot)	0.20	0.99	2.66	**0.008**

Significant effects are in bold.

Fig. 1. Effect of light environment on the percentage colonisation by hyphae of arbuscular mycorrhizal fungi (mean ± SE) in roots of *Ruellia nudiflora*. Different letters denote significant differences (*P* < 0.05).

Fig. 2. (a) Effect of light environment and (b) type of flower and cross on the percentage colonisation by vesicles of arbuscular mycorrhizal fungi (mean ± SE) in roots of *Ruellia nudiflora*. Different letters denote significant differences (*P* < 0.05).

Fig. 3. Percentage colonisation by vesicles of arbuscular mycorrhizal fungi (mean ± SE) in the roots of nine maternal lines (Families) of *Ruellia nudiflora* grown in shaded (shaded bar) and open (open bar) light conditions. Asterisks (*) denote the families (Fam) in which there are significant differences between the two light treatments (*P* ≤ 0.008 in all cases).

respectively, *P* < 0.0001; Fig. 2a). With respect to FDC, the plants of treatments CHc and CHs presented the same percentage of colonisation by vesicles (CHc= 4.61 ± 0.67 and CHs= 6.92 ± 1.05, respectively; *P* = 0.26). However, the progeny generated from the CH flowers in both cross- (CHc) and self- (CHs) pollination presented a higher colonisation by vesicles with respect to progeny of the CL flowers (1.72 ± 0.32, *P* < 0.0001 in both cases; Fig. 2b).

In general, there was a wide variation in terms of the percentage of colonisation by vesicles between families grown in shaded and open conditions (Fig. 3); while higher colonisation was found under shaded conditions in the majority (7/9) of families (Fig. 3), the significant effect of the interaction between light treatment and family was because colonisation in three of the nine families (Families 1, 4 and 5) was significantly higher in the shade compared to the open treatment (*P* ≤ 0.008 in all cases; Fig. 3).

DISCUSSION

The results of this study suggest that both differential allocation of resources between the chasmogamous and cleistogamous flowers and differences in the availability of light can determine the colonisation of arbuscular mycorrhizal fungi (AMF) in *R. nudiflora*. Our results also suggest that there is no effect of
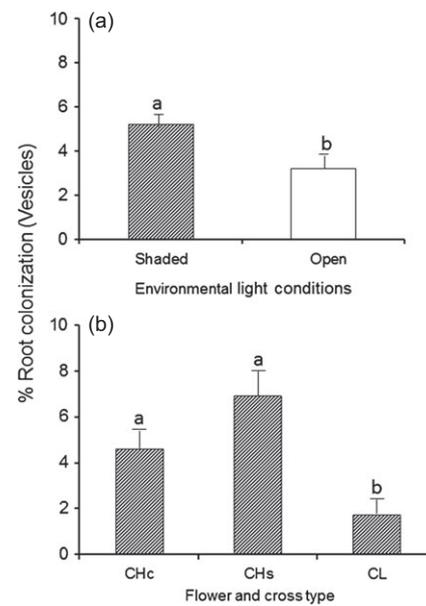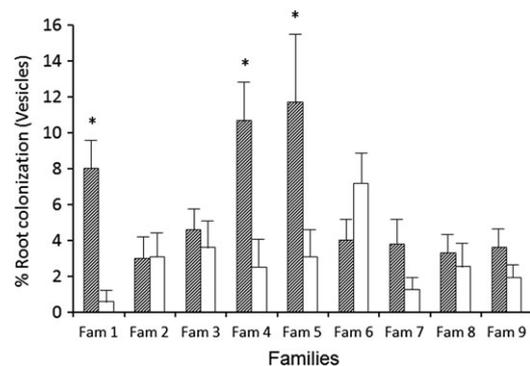
inbreeding depression in the capacity to establish such an interaction, since no differences were observed between progeny derived from cross- (*i.e.* half-sibs CHc) and self- (*i.e.* full-sibs CHs and CL) pollination, even under a stressful light environment. Nevertheless, it is important to recognise that future experiments should consider the taxonomic identity of AMF, since it is known that species-specific responses to different environmental conditions may exist (Smith & Read 2008).

According to our initial predictions regarding the effect of differential resource apportionment to the two floral types (*FDC*) and inbreeding depression (*ID*), our results support scenario (c) described in Table 1. This is because we found that colonisation by hyphae and vesicles was equal in the progeny derived from chasmogamous flowers, regardless of the cross type (*i.e.* self- or cross-pollination), and higher in the progeny

derived from cleistogamous (*i.e.* obligate self-pollinating) flowers. This suggests that differential allocation of resources to the two flower types has consequences for the association established between the progeny of *R. nudiflora* and the AMF. In species with dimorphic cleistogamy, it is known that more resources are allocated to CH compared to CL flowers (Culley & Klooster 2007) and that the progeny derived from CH flowers have higher vegetative and reproductive performance (Clay 1983; Waller 1984; Clay & Antonivics 1985; Eckstein & Otte 2005; but see Culley 2000).

The better performance of the progeny of CH flowers may be related to the generally higher biomass of its seeds than those produced by CL flowers (Culley & Klooster 2007); the relationship between higher seed mass and different adaptive attributes has been widely documented in plants (Fenner & Thompson 2005). In particular, in cleistogamous species it was found that a higher biomass increases germination in CH seeds (Waller 1984; Mitchell-Olds & Waller 1985; Berg & Redbo-Tortensson 1998), and comparisons in different life stages show differences in performance between CH and CL progeny that can be attributed in part to differential resource apportionment (Clay 1983; Clay & Antonivics 1985). In *R. nudiflora*, there are significant differences in the mass of seeds produced by CH and CL flowers, and, while this characteristic does not seem to have an effect on germination (Munguía-Rosas *et al.* 2013a), our results suggest that it has consequences for establishment of the symbiosis with AMF, which in turn has important consequences for the performance of this species (Ramos-Zapata *et al.* 2010). We observed that, regardless of cross type, the progeny of *R. nudiflora* derived from CH flowers, on average, had more than double the percentage colonisation by hyphae and almost five times more colonisation by vesicles on their roots.

Study of progeny of contrasting genetic background in cleistogamous species is complicated by the fact that it is not possible to clearly separate the effects of endogamy from the differential allocation of resources to the different floral types (Culley & Klooster 2007). However, by controlling the pollen source in the CH flowers in our study, we ensured that any differences in AMF colonisation between progeny derived from CHs and CL would probably be due to differential resource allocation, since both progeny types have the same genetic background (*i.e.* full-sibs). We therefore suggest that, in contrast to results of studies evaluating inbreeding depression on establishment of the association between plants and AMF (Botham *et al.* 2009; Collin & Ashman 2010), this effect does not appear to inhibit this interaction in *R. nudiflora*.

Overall, our results agree with previous findings showing that inbreeding depression is infrequent in cleistogamous species due to the continual selfing to which they are exposed, a process that results in a continuous purging of deleterious alleles (Jain 1976; Oakley *et al.* 2007). However, in contrast to our initial predictions, which were based on evidence that the effect of inbreeding depression is intensified in stressful environments (Armbruster & Reed 2005), we did not observe an effect on the symbiosis between *R. nudiflora* and AMF in the shaded environment. Our results therefore indicate that endogamy does not affect this symbiosis; however, this does not mean that it is not expressed in other growth or reproductive characteristics, as observed in other cleistogamous species (*e.g.* Clay 1983; Clay & Antonivics 1985). Indeed, in *R. nudiflora* in shaded conditions, the progeny of cross-pollination derived

from CH flowers had higher biomass and heavier fruits compared to the endogamous progeny of self-pollinated CH flowers and of CL flowers (Munguía-Rosas *et al.* 2013b).

Our results also show that shaded conditions favour AMF colonisation in *R. nudiflora* roots, in contrast with results of other studies that report higher colonisation with a higher availability of light (*e.g.* Bethlenfalvay & Pacovsky 1983; Tester *et al.* 1986), since the cost of maintaining AMF increases under shaded conditions. However, while it is known that the cost of transferring carbon to the fungi is higher in shaded conditions, it has also been observed that the result of the symbiotic association responds to complex interactions between the light conditions and the availability of phosphorus in the soil (Facelli *et al.* 1999; Olsson *et al.* 2010). For example, it has been suggested that in conditions of low *P* availability, it may be beneficial for the host plant to maintain the symbiosis even in shaded conditions (Facelli *et al.* 1999). This could be the case with *R. nudiflora*, since in the sites where this species is found in Yucatan there is a strong soil phosphorus limitation that affects the establishment, growth and survival of several plant species (Ceccon *et al.* 2004; Salinas-Peba *et al.* 2014). This evidence, together with the fact that *R. nudiflora* presents increased growth and survival when associated with AMF (Ramos-Zapata *et al.* 2010), could explain why in shaded conditions the percentage of both hyphae and vesicles was significantly higher than found in the open treatment.

Olsson *et al.* (2010) recently observed in *Trifolium subterraneum* that the increased cost of carbon for the host plant under shaded conditions does not reduce the flow of carbon to the fungi, and proposed that allocation of carbon to the extraradical mycelium in shaded plants could be a strategy that has evolved to find new hosts when the capacity for carbon allocation is reduced in the original host. This hypothesis could be applied to invasive species and weeds that maintain interactions with AMF, since they are faced with highly variable environments in which the most advantageous strategy could be to maintain plastic responses to the environmental heterogeneity (Pigliucci 2001). Plastic responses have been observed in *R. nudiflora* in terms of phenological characteristics under different light conditions, *e.g.* in duration of flowering and changes in the production of different flower types (Munguía-Rosas *et al.* 2012, 2013a), as well as variable responses to different soil types and even in the interaction of this species with different types of herbivore (Ortegón-Campos *et al.* 2012).

These plastic responses in *R. nudiflora*, together with genetic variation in response to the association with the AMF and an apparent capacity to 'modulate' the intensity of interaction with the AMF under different light conditions, are characteristics that may contribute to the high capacity for dispersal that has led to this species being considered invasive in Yucatan.

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