



# A holoparasitic plant severely reduces the vegetative and reproductive performance of its host plant in the Caatinga, a Brazilian seasonally dry forest

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## ABSTRACT

Host-parasite interactions between plants may reduce the vegetative and reproductive performance of the host plant. Although it is well established that parasitic plants may negatively affect the metabolism and the number of vegetative/reproductive structures of their hosts, the effects of this interaction on the reproductive characteristics of the host plant are poorly understood. Here we document the interaction between *Cuscuta partita* (Convolvulaceae) and its main host, *Zornia diphylla* (Fabaceae), in the Caatinga of northeastern Brazil. We measured diverse reproductive/vegetative attributes of *Z. diphylla* in 60 plots randomly distributed in patches that were parasitized and not parasitized by *C. partita*. Both vegetative and reproductive attributes, such as the number of branches, leaves and flowers, and the individual biomass of *Z. diphylla* were significantly reduced by the parasitism. The number of pollen grains and ovules per flower were not affected by the parasitism, but since the parasitism reduced flower production, the total number of pollen and ovules per individual and population may also be reduced. Additionally, pollen viability was significantly reduced in the flowers of parasitized individuals. We conclude that *C. partita* may negatively impact the vegetative and reproductive performance of its main host, *Z. diphylla* in distinct ways in the Caatinga.

**Keywords:** Caatinga, *Cuscuta partita*, floral traits, haustoria, holoparasitic plants, plant-plant interaction, pollen viability, reproductive success, *Zornia diphylla*

Hemi- and holoparasitic plants may significantly impair the metabolism and the development of vegetative and reproductive structures, such as branches, leaves, flowers, seeds and fruits of many host species (e.g. Hibberd *et al.* 1996; Fernandes *et al.* 1998; Puustinen & Salonen 1999; Silva & Rio 1996; Irving & Cameron 2009; Mourão *et al.*

2009; Bahia *et al.* 2015). Additionally, extreme levels of infestation by holoparasitic species may cause host death and changes in plant community composition (e.g. Aukema 2003; Grewell 2008; Graffis & Kneitel 2015; Těšitel *et al.* 2016). In total, holoparasitic plants comprise more than 400 species distributed in 87 genera (Leake 1994; Riches

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& Parker 1995). Currently, *Cuscuta* (Convolvulaceae) is one of the largest genera of holoparasitic plants including 170-200 species (Costea & Stefanović 2010).

Resource acquisition by holoparasitic plants proceeds exclusively via haustoria, which drains water and metabolites from the bundles of the host plant (Pennings & Callaway 2002). In addition to photosynthate reallocation, holoparasitic plants may stimulate the secretion of hormones by the host plant, directly inoculating the host structures with their own hormones or mRNA (Knutson 1979; Ihl *et al.* 1984; Westwood *et al.* 2010). In this sense, holoparasitic plants may negatively impact many metabolic and physiological aspects of their host plants, such as stomata opening, photosynthesis rate, transpiration, hormone secretion or water-use efficiency (Goldstein *et al.* 1989; Fernandes *et al.* 1998; Sala *et al.* 2001; Runyon *et al.* 2008; Prider *et al.* 2009).

Because of the parasitism, host plants may also exhibit reduced individual biomass, which is mainly associated with changes in physiological processes caused by the parasite plant (Irving & Cameron 2009; Westwood *et al.* 2010). Changes in the biomass of parasitized plants are represented by reductions in the number of branches, leaves, flowers and fruits (Gomes & Fernandes 1994; Koskela *et al.* 2002). Additionally, parasitic interactions may negatively affect the root development of host plants (Irving & Cameron 2009). The intensity of damage caused by the parasitic plant to the host species may change depending on the strategies of acquisition of resources by the parasite or on the genetic diversity and origin of the species involved in the parasitic interaction (Koskela *et al.* 2002; Press & Phoenix 2005; Prider *et al.* 2009; Li *et al.* 2012).

Once parasitic plants have severely reduced host performance, parasitism may lead to changes in competitive interactions between host and non-host plants and impact the community structure, diversity, vegetation cycling and zonation (Pennings & Callaway 2002; Aukema 2003; Grewell 2008; Graffis & Kneitel 2015; Mourão *et al.* 2016). These effects on community structure are often dynamic and may change depending on the performance of the parasite itself or due to environmental conditions (Pennings & Callaway 2002; Press & Phoenix 2005; Grewell 2008; Irving & Cameron 2009; Graffis & Kneitel 2015). An aggressive parasite can drive a preferred host to local extinction, which may, in turn, result in the local extinction of the parasite (e.g. Press & Phoenix 2005; Mourão *et al.* 2009). Additionally, by inducing changes in the physiological processes of host plants, parasitism could influence the occurrence of plant species in particular habitats, depending on local temperature, light intensity and rainfall (Pennings & Callaway 2002; Westwood *et al.* 2010).

The Caatinga is a Brazilian seasonally dry forest characterized by low rainfall that is irregularly distributed throughout the year, with long periods of drought, low levels of air humidity and high temperatures (e.g. Leal *et al.* 2003).

Despite these abiotic restrictions, the Caatinga shows high levels of biodiversity and ecological interactions (*sensu* Leal *et al.* 2003). Many of these interactions related to pollination and seed dispersal have been extensively described for the Caatinga (e.g. Machado *et al.* 1997; Leal *et al.* 2003; 2007; Machado & Lopes 2004 and references therein), while interactions documenting parasitism between plants in this phytogeographical domain are, as far as we know, nonexistent.

Although it is well established that parasitic plants may negatively affect the metabolism, physiology and number of vegetative and reproductive structures of their hosts, the outcomes of this interaction on the host's reproductive process (e.g. number of pollen and ovules and pollen viability) are poorly understood. By using two common herbaceous plant species in the Caatinga, the aim of this study was to understand and quantify the effects of holoparasitism by *Cuscuta partita* Choisy (Convolvulaceae) on the growth and development of the vegetative and reproductive structures of its host *Zornia diphylla* (L.) Pers. (Fabaceae). We hypothesized that the holoparasitic *C. partita* negatively affect the development of the vegetative and reproductive structures of its host plant, *Z. diphylla*.

This study was carried out in a private area named Fazenda Olho d' Água, at Parnamirim, Pernambuco, Brazil (8°5'26"S, 39°34'42"W). The climate in this region is classified as semiarid, with low rainfall, remarkable seasonality and unpredictable precipitation (Nimer 1972). The vegetation in the study site is of the hyperxerophitic type, characterized by the presence of a deciduous forest dominated by shrubs and trees, but with a representative presence of annual herbs in the rainy season mainly in the areas with planosols (CPRM 2005).

*Zornia diphylla* (Fabaceae) is an annual herb largely distributed in South and Central Americas, and in the southern region of North America (Mohlenbrock 1961). It has numerous creeping stems and trifoliate leaves; flowers are yellow and medium-sized (10-20 mm; *sensu* Machado & Lopes 2004) with red macules in the central portion of the flag petal, representing a nectar guide (Fig. 1A) for bees; fruits are legumes with four to six seeds.

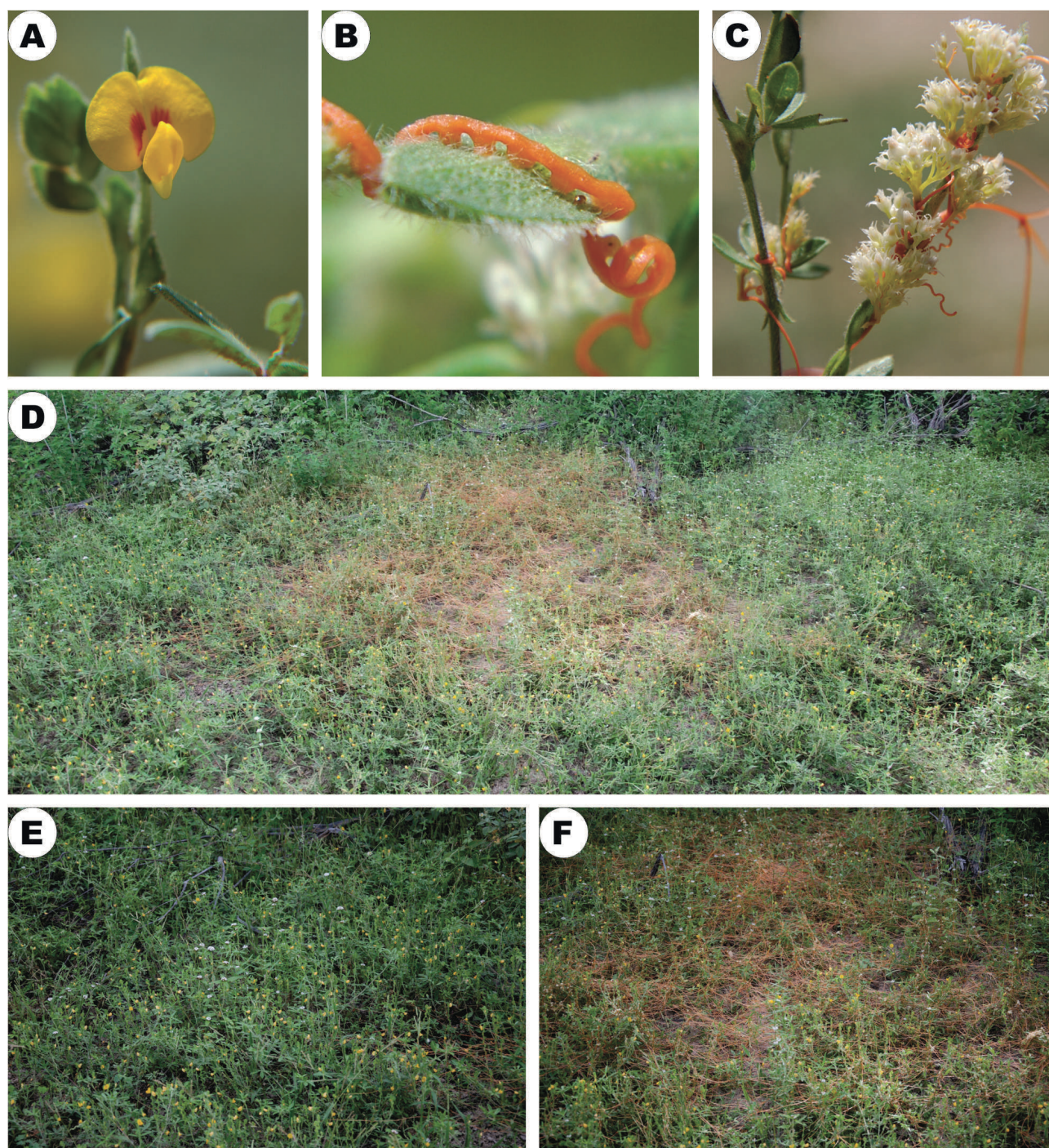
The holoparasitic *C. partita* (Convolvulaceae) lack true roots, leaves and chlorophyll and exhibit numerous haustoria (Prather & Tyrl 1993). It has small white flowers (<10 mm; *sensu* Machado & Lopes 2004) that secrete nectar as a floral reward (Riches & Parker 1995). The species occurs in patches across the study landscape and preferentially parasitizes individuals of *Z. diphylla* in the study site (O Cruz-Neto unpubl. res.) (Fig. 1B-F).

In total, we sampled 40 patches occupied by *C. partita* in the study site. Based on this sampling, we randomly chose 30 patches for our study. Control plots were randomly selected near each selected patch occupied by *C. partita*. In these control plots, individuals of *C. partita* were absent, i.e. not found parasitizing any other plant. We distributed a





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**Figure 1.** (A) Flower of *Zornia diphylla* in the study site, a Caatinga area in northeastern Brazil. (B) Branch of *Cuscuta partita* with many haustoria fixed to a floral bud of *Z. diphylla*. (C) *C. partita* inflorescence. (D) Herbaceous community in the presence of *C. partita*. (E) Non-parasitized patch of herbaceous community in the study site, note the high abundance of *Z. diphylla* (yellow flowers). (F) Patch of *Z. diphylla* parasitized by *C. partita* (Photos: Santos J.C.).

single 0.25 m<sup>2</sup> plot in each parasitized and non-parasitized patch. These two treatments were paired distributed and the distance between plots in a single pair of parasitized and non-parasitized patches ranged from two to six meters. Additionally, the distance between pairs of parasitized and non-parasitized plots ranged from 10 to 15 m. By randomly choosing the patches and the plots, we expected to include

distinct levels of intensity of the parasitic interaction in the study site.

In each plot, we counted the number of flowers of *Z. diphylla*. We sampled only individuals that were totally included, or with at least 90 % of their branches, in the limits of each plot. The number of leaves, branches and flowers was counted for each individual of *Z. diphylla*. Additionally,





the length of the branches (cm) and the size of the flag petal (mm) from different flowers (N= 120) were measured in the field. The size of the flag petal was represented by its width, which together with floral symmetry, has a direct influence on attractiveness to floral visitors (e.g. Hileman 2014; Potts 2016). All the sampled plants of *Z. diphylla* were collected, dried at 56-60°C for 36-48 hours and finally weighed to obtain their individual biomass (g).

We also randomly collected one pre-anthesis floral bud of *Z. diphylla* per plot in order to check the number of ovules per ovary, number of pollen grains per flower and pollen viability. Based on the 30 collected flower buds per treatment, we randomly choose 20 for the measurements and counting. All buds were fixed in 70 % alcohol. A Neubauer chamber was used to estimate the total number of pollen grains per flower (Maêda 1985). Pollen viability was inferred by the presence of cytoplasmatic content in each grain using a staining technique with 1.2 % acetic-carmin solution (Radford *et al.* 1974), where stained grains are considered viable and non-stained, i.e. without cytoplasmatic content, are inviable. Because the absence of cytoplasmatic content in a pollen grain is impeditive for its germination, a significantly higher number of grains without such content may predict lower pollen viability. To obtain the number of ovules per bud/flower, we longitudinally sectioned the ovaries to access and count the ovules.

We used the Kolmogorov-Smirnov test to check the normality of the data. The data were log transformed except for the number of ovules per ovary and number of flowers per plot and per individual. To investigate the changes of vegetative and reproductive attributes of *Z. diphylla* between parasitized and non-parasitized plots, we used a paired T test or Wilcoxon signed-rank test, depending on the normality of the data. The statistical significance was assessed by the one tailed p-value ( $P < 0.05$ ). All the tests were performed using the software Infostat/F v.2013 (Rienzo *et al.* 2013).

All of the analyzed vegetative attributes of *Z. diphylla* were negatively impacted by interaction with *C. partita* (Tab. 1). The individual biomass of *Z. diphylla* was significantly reduced by 33.1 % by the parasitism. In this case, individuals of *Z. diphylla* exhibited an average biomass of 12.7 g in non-parasitized patches and 8.5 g in parasitized ones. These changes in biomass were represented by significant reductions of 53.9 % in the number of leaves, 29.8 % in the production of branches and 18.7 % in the length of branches in parasitized individuals of *Z. diphylla*.

Regarding reproductive traits, the average number of *Z. diphylla* flowers per plot was significantly reduced by 77.3 % in plots with the presence of the parasite (Tab. 1). The non-parasitized plants had an average of 20.2 flowers/day per individual during the field observations, while parasitized plants exhibited an average of 5.6 flowers/day, indicating a significant reduction of 72.1 % in flower production per individual.

In the case of the flower morphology, the average size of the flag petal, the number of ovules per ovary and the

number of pollen grains per flower were not significantly affected by the parasitism of *C. partita* (Tab. 1). However, when we consider that the parasitism reduced the number of flowers per individual, it consequently reduced these traits per individual/population. Additionally, pollen viability was significantly reduced on average from 94.4 % in non-parasitized plants to 59.3 % in parasitized plants of *Z. diphylla*.

The deleterious effects of the parasite on the vegetative and reproductive performance of *Z. diphylla* may be caused by the establishment of haustoria on many of the host plant's structures. Haustoria may act as drains that redirect photosynthates into the parasite and thus change the physiological patterns of its host (Ihl *et al.* 1984; Bock & Fer 1992; Parker & Riches 1993). Specifically, parasitic interactions associated with the establishment of haustoria may lead to changes in the photosynthetic parameters of host species, such as the average of CO<sub>2</sub> partial intracellular pressure and photosynthetic electron transport rates (e.g. Gomes & Fernandes 1994; Fernandes *et al.* 1998; Runyon *et al.* 2008; Prider *et al.* 2009; Li *et al.* 2012). Because of these changes, parasitized plants may exhibit a reduced number of leaves, branches, flowers and individual biomass, relative to non-parasitized plants, as may be the case for *Z. diphylla* in the Caatinga.

Regarding reproductive structures, parasitic interactions often affect the reproductive performance of the host by reducing the production of flowers and fruits and the seed quality (e.g. Silva & Rio 1996; Puustinen & Salonen 1999; Mourão *et al.* 2009). Indeed, in the case of parasitism in *Z. diphylla*, we documented a reduction of 72 % in flower production. Despite the fact that parasitism reduced the production of flowers of *Z. diphylla*, changes in petal dimensions between parasitized and non-parasitized plants were not significant. We emphasize that floral traits such as dimensions of petals are mostly related to genetic and natural selection factors in many plant species (*sensu* Weiss *et al.* 2005; Krizek & Anderson 2013), as may be the case for *Z. diphylla*.

Floral dimensions such as the symmetry of floral parts, scent and color and size of petals may exert a strong influence on pollinator attraction and thus on the fruit and seed set of many plant species (e.g., Giurfa *et al.* 1996; Galen 1999; Karron & Mitchell 2012; Hileman 2014; Potts 2016). Because the size and symmetry of the flag petals of *Z. diphylla* were not affected by interaction with *C. partita*, it is possible that this parasitic interaction does not affect the individual attractiveness of the host plant flowers. On the other hand, *C. partita* may possibly impact the nectar secretion and anthesis of *Z. diphylla*, since the parasite plant may drain water and essential metabolites and promote changes in the flower physiology of the host species.

Surprisingly, although the numbers of ovules and pollen grains per flower were similar in parasitized and nonparasitized individuals of *Z. diphylla* (these numbers



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**Table 1.** Reduction of vegetative and reproductive attributes (mean  $\pm$  S.D) of *Zornia diphylla* (L.) Pers. (Fabaceae) by the holoparasite *Cuscuta partita* Choisy (Convolvulaceae) in a Caatinga area in northeastern Brazil.

Attributes of host plant	N	Holoparasitism		Intensity of reduction (%)	Statistical tests	d.f.	P
		Absent	Presence				
<b>Vegetative attributes</b>							
Leaves/individual	30	181.1 ± 112.2	83.4 ± 43.5	54	T = -4.53	29	< 0.001
Branches/individual	30	8.4 ± 4.1	5.9 ± 2.5	29.8	T = -3.07	29	0.002
Branches length (cm)	30	62.1 ± 23.4	50.5 ± 13.4	18.7	T = -2.3	29	0.01
Individual biomass (g)	30	12.7 ± 7.1	8.5 ± 4.3	33.1	T = -2.74	29	0.005
<b>Reproductive attributes</b>							
Flowers/patch	30	61.1 ± 24.4	13.9 ± 11.9	77.3	Z = -4.8	-	<0.001
Flowers/individual	30	20.2 ± 25.8	5.63 ± 4.3	72.1	Z = -3.8	-	<0.001
Flower size (mm)	30	10.6 ± 0.7	10.5 ± 1.1	-	T = -0.26	29	0.4
Pollen grains/flower	20	5,480 ± 544.1	5,333.5 ± 444.8	-	T = -1.14	19	0.1
Pollen viability (%)	20	94.4 ± 3.1	59.3 ± 10.7	37.2	T = -13.79	19	<0.001
Ovules/Ovary	20	5.1 ± 0.8	4.6 ± 0.8	-	Z = -2.4	-	0.08

were clearly reduced when considering the reduction caused by parasites to the number of flowers per individual), pollen viability was significantly reduced by the parasitism. We emphasize that the parasitism of *C. partita* on *Z. diphylla* may act beyond the redirection of resources and the hormonal control of the host plant, as has been described for many interactions involving other species of parasitic plants (e.g., Knutson 1979; Puustinen & Salonen 1999; Pennings & Callaway 2002; Runyon *et al.* 2008). In this sense, cell division processes during the development of vegetative and generative cells of pollen grains of *Z. diphylla* may also be affected by parasites.

In conclusion, parasitism by *C. partita* is severely impairing the development of the vegetative and reproductive structures of *Z. diphylla* in the Caatinga. The direct effect of parasitism by *C. partita* on the reproductive success of *Z. diphylla* is related mainly to the reduction of the number of flowers and, consequently, of the fruit and seed sets of the host plant. The indirect effect is associated with the reduction in the number of pollen grains and in the quality of the pollen released by the flowers of *Z. diphylla* in parasitized patches, which would result in even more reduced fruit and seed sets. Future studies aiming to investigate the reproductive success of host and parasitic plants in different generations should be useful to identify the relative roles of the direct and indirect effects of parasitism in herbaceous communities in the Caatinga.

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