

HOST PREFERENCE AND PHYSIOLOGICAL PERFORMANCE OF THE INVASIVE HEMIPARASITE OF COASTAL COMMUNITIES *CASSYTHA FILIFORMIS* L. (LAURACEAE)

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Abstract

Background: Invasive parasitic species have barely been studied despite their impact on the communities they invade.

Questions: What is the host range used by the invasive parasite *Cassytha filiformis* in the coastal scrubland of northern Yucatan? Does *C. filiformis* show host preference? Does the physiological performance of *C. filiformis* (water deficit and chlorophyll content) vary among hosts on which it establishes and reproduces?

Study species: *Cassytha filiformis*, an invasive hemiparasitic vine of coastal communities.

Study sites and dates: Telchac, Yucatán, México. The study lasted from October 2022 to June 2023.

Methods: The incidence of *C. filiformis* parasitism was recorded. Histological analysis confirmed parasitism, and the water potential and chlorophyll concentration of *C. filiformis* in its main hosts were determined.

Results: *C. filiformis* parasitized 10 species, showing a preference for shrubs. Its main hosts were *Scaevola plumieri*, *Phitecellobium keyense* and *Croton punctatus*. Differences between hosts were observed in water potential variation and total chlorophyll concentration. Differences between stem types (young and mature) in chlorophyll concentration were also observed.

Conclusions: *C. filiformis* prefers shrub species to establish. The physiological performance of *C. filiformis* varied depending on host identity. Differences in chlorophyll concentration between stem types of *C. filiformis* suggest functional physiological differences between them.

Keywords: chlorophyll *a* and *b*, total chlorophyll, water deficit, hemiparasitic plants, host preference, host range.

Resumen

Antecedentes: Las especies parásitas invasoras han sido pobremente estudiadas a pesar del impacto que pueden tener en las comunidades que invaden.

Preguntas: ¿Cuál es el rango de hospederos que utiliza la parásita invasora *Cassytha filiformis*? ¿*C. filiformis* presenta preferencia por hospederos? ¿el desempeño fisiológico (déficit hídrico y contenido de clorofilas) de *C. filiformis* varía entre los hospederos donde se establece y reproduce?

Especie de estudio: *Cassytha filiformis*, liana hemiparásita invasora de comunidades costeras.

Sitio y años de estudio: Telchac, Yucatán México. El estudio abarcó de octubre del 2022 a junio 2023.

Métodos: Se registró la incidencia de parasitismo de *C. filiformis*. Se confirmó el parasitismo mediante análisis histológico y se determinó el potencial hídrico y la concentración de clorofila de *C. filiformis* en sus principales hospederos.

Resultados: *C. filiformis* parasitó 10 especies mostrando preferencia por especies arbustivas. Sus principales hospederos fueron *Scaevola plumieri*, *Phitecellobium keyense* y *Croton punctatus*. Se observaron diferencias entre hospederos en el cambio del potencial hídrico y la concentración total de clorofila. Adicionalmente, se observaron diferencias entre tipos de tallos (jóvenes y maduros) en la concentración de clorofila.

Conclusiones: *C. filiformis* se establece en especies arbustivas. Su desempeño fisiológico varía dependiendo de la identidad del hospedero. Se observaron diferencias en la concentración de clorofila entre tipos de tallo de *C. filiformis* sugiriendo diferencias fisiológicas funcionales entre ellos.

Palabras clave: clorofila *a* y *b*, clorofila total, déficit hídrico, plantas hemiparásitas, preferencia de hospederos, rango de hospederos.

Globally, coastal ecosystems are considered among the most vulnerable due to multiple factors associated with anthropogenic effects that have put the environmental services they provide at risk (Martínez & Psuty 2004, Miller *et al.* 2010, Duarte *et al.* 2013, Mendoza-González *et al.* 2016). Among these factors, urbanization associated with tourist activities is considered one of the most impacted because of the direct effects on the loss or fragmentation of original vegetation (Martínez & Psuty 2004, Grosholz 2002). However, in addition to these effects, the urbanization of coastal ecosystems has numerous indirect effects that increase their fragility. The arrival of invasive species is one of the most important indirect effects since it is one of the main causes of biodiversity loss and ecosystem degradation (Vilà *et al.* 2011, Simberloff *et al.* 2013, van Kleunen *et al.* 2018). It has been suggested that coastal ecosystems around the world are especially susceptible to the invasion of plant species (Castillo & Moreno-Casasola 1996, Grosholz 2002, Del Vecchio *et al.* 2015, Tordoni *et al.* 2021, Martínez *et al.* 2021). For example, in Mexico, it is estimated that nearly 9 % of coastal dune plant species are exotic (*i.e.*, invasive or potentially invasive) (Martínez *et al.* 2021), although locally, this percentage could be higher (*ca.* 30 %; Parra-Tabla *et al.* 2018).

However, despite the growing evidence that shows the harmful effects of invasive species in coastal ecosystems (*e.g.*, Hertling & Lubke 2000, Gallego-Fernández *et al.* 2019, Cai *et al.* 2020) and the increasing presence of these species, particularly in Mexican coasts, few studies focus on understanding the mechanisms that determine the invasion success (Ramírez-Albores *et al.* 2019, Martínez *et al.* 2021, but see Parra-Tabla *et al.* 2021). Coastal communities of the north of the Yucatan peninsula, characterized by their high species richness, phylogenetic diversity, and endemisms (Espejel 1987, Durán *et al.* 2007, Torres *et al.* 2010, Angulo *et al.* 2018), have been subjected during the last three decades to a severe deterioration that has promoted the arrival of an important number of exotic species (Parra-Tabla *et al.* 2018). Among these, the hemiparasite *Cassytha filiformis* L. (Lauraceae) stands out for colonizing a large part of the northern coast of the Peninsula and for attacking shrubs that are considered keystone species in Mexican coastal dunes, as well as in other coastal regions of the world (Nelson 2008, Ovando-Hidalgo *et al.* 2020, Cai *et al.* 2020, Hernández-Mendoza *et al.* 2023, Parra-Tabla *et al.* 2024).

In contrast with competitive interactions for resources that are established between native and invasive plants (Theoharides & Dukes 2007, Golivets & Wallin 2018, Traveset & Richardson 2020, Ni *et al.* 2021), invasive-native plants' parasitic interactions have been rarely studied (*e.g.*, Cai *et al.* 2020). This kind of interaction is particular since the first barrier that an invasive parasitic species confronts when arriving in a new ecosystem is finding suitable hosts in which they can grow and reproduce. Although parasitic plants are typically considered generalist (Kelly *et al.* 1988, Press 1998, Callaway & Pennings 1998, Pennings & Callaway 2002), it has been reported that numerous parasitic plants show a certain level of specialization, or they switch during their life cycle to specialized use of host plants (Musselman & Press 1995, Kokubugata & Yokota 2012, Zhang *et al.* 2022). For example, parasitic species of the genus *Cassytha* (Lauraceae) occupy different hosts during their growth that only serve as a "bridge" until they find definitive hosts in which they sexually reproduce, thus ensuring the establishment and dispersion of their populations (Zhang *et al.* 2022).

Different characteristics such as the life form, the host plant architecture, and the parasite-host compatibility are determinants in the process of selection of an adequate host (*e.g.*, Press & Phoenix 2005, Kaiser *et al.* 2015, Li *et al.* 2015, Lara *et al.* 2021). Once parasitic plants are established, their hosts are expected to provide the parasites with the necessary resources to grow and reproduce. If this is the case, this selection should be reflected in the physiological performance of the parasitic plant. For example, an adequate host would be one that could offer sufficient resources such as water, and photosynthates (Kelly *et al.* 1988, Pennings & Callaway 1996, Koch *et al.* 2004, Lara *et al.* 2021). Thus, it could be predicted that a parasitic plant would prefer hosts that minimize water deficit and, in turn, can reduce its photosynthetic activity. Therefore, the success of an invasive parasitic plant will depend not only on host plant availability but also on the extent to which the hosts provide the necessary resources to establish long-term viable populations (Pennings & Callaway 1996, Press & Phoenix 2005).

On the other hand, the importance of the identity of the native host plant selected by the invasive parasites relies on the fact that it might be a crucial factor that determines the impact on the invaded ecosystem (Gibson & Watkinson

1989, Callaway & Pennings 1998, Cai *et al.* 2020. In this sense, if the invasive parasites attack hosts that play a key role in the community structure, their effect would be more critical than if they parasitize species that are not dominant or have a limited role in the community (Caviers 2021, Parra-Tabla *et al.* 2024). For example, some species are key in coastal communities as soil nutrient enrichers, nurse plants, or erosion controllers (Espejel 1987, Acosta *et al.* 2009, Hernández-Mendoza *et al.* 2023). In these ecosystems, it has been found that when invasive parasites attack these plants, their functionality is severely affected (Nelson 2008, Cai *et al.* 2020).

Although the pattern of spatial distribution of the invasive hemiparasitic species *C. filiformis* and its effects on some of the parasitized species are known on the northern coast of the Yucatan Peninsula (Parra-Tabla *et al.* 2024), the total range of hosts used by this species is unknown, as well as whether it shows any preference for the life form or species. It is also unclear whether there are differences in “host quality” regarding the physiological performance of *C. filiformis* when establishing and reproducing sexually. Filling these information gaps will help us to understand the mechanisms that allow invasive parasitic species to invade fragile ecosystems such as coastal communities.

In this work, we aim to answer the following questions: What is the host range used by the invasive parasite *Cassytha filiformis* in the coastal scrubland of northern Yucatan? Does *C. filiformis* show host preference? Does the physiological performance of *C. filiformis* (using water deficit and chlorophyll content as proxies) vary among hosts on which it establishes and reproduces?

Materials and methods

Study site and species. The study was carried out in an area of coastal scrubland located in Telchac Puerto, Yucatan, Mexico (21° 20' 11.7" N, 89° 20' 12.5" W; with an altitude from 0 to 8 m asl), during the months from October 2022 to June 2023. The coast's weather is hot semi-arid (BSh) with a mean annual temperature of 26 °C and an annual mean precipitation of *ca.* 350 mm (Orellana *et al.* 2009). The plant community is dominated by herbaceous species such as *Agave angustifolia* Haw. (Agavaceae), *Alternanthera microcephala* (Moq.) Schinz (Asteraceae), *Waltheria rotundifolia* Schrank (Malvaceae) and *Melanthera nivea* (L.) Small (Asteraceae) and shrub species such as *Coccoloba uvifera* L. (Polygonaceae), *Scaevola plumieri* (L.) Vahl (Goodeniaceae) and *Suriana maritima* L. (Surianaceae) (Espejel 1987, Angulo *et al.* 2018). In the coastal dune, nearly a third of all plant species are exotic (Parra-Tabla *et al.* 2018). Among these species, *C. filiformis* is the only parasitic species. Though it has been reported that *C. filiformis* is originally from Asia and currently has a pantropical distribution, botanical and phytogeographic studies from the decade of the 70's or before do not register its presence in the Yucatan coastal ecosystems (Miranda 1959, 1964, Moreno-Casasola & Espejel 1986, Espejel 1987, Castillo & Moreno-Casasola 1996, Chiappy *et al.* 2001, GBIF 2022); therefore, it is considered an invasive species of recent arrival (Parra-Tabla *et al.* 2018, 2024).

Cassytha filiformis L. is an herbaceous hemiparasitic vine; filiform stems, measuring 0.4 to 3.0 mm in thickness, are either glabrous or bear trichomes, exhibiting a greenish or orange-yellow coloration. Leaves are alternate, reduced to sessile scales; the inflorescence takes the form of an axillary spike, comprising white or slightly greenish, hermaphroditic, trimerous flowers distributed along the inflorescence axis, the fruit is a whitish drupe (Silva *et al.* 2021). It possesses haustoria, penetrating the host plants' stem tissue (Zhang *et al.* 2022) and absorbing nutrients, water, and photosynthetic products (Li & Yao 1992, Balasubramanian *et al.* 2014). It has been reported that *C. filiformis* occupies a wide range of hosts, with different life forms distributed in various environments such as grasslands, flooded forests, xerophilous scrublands, Mediterranean forests, and coniferous forests (Li & Yao 1992, Buriyo *et al.* 2015, Debabrata 2018, Zhang *et al.* 2022), as well as coastal dune vegetation, where it has been reported to prefer species of the genera *Scaevola* and *Tournefortia* (Nelson 2008, Castillo-Campos *et al.* 2019). In the Yucatan coastal dunes, it is known to preferentially attack species such as *Scaevola plumieri* (Goodeniaceae), *Suriana maritima* (Surianaceae), and *Tournefortia gnaphalodes* (Boraginaceae) (Parra-Tabla *et al.* 2024).

The damage *C. filiformis* causes to host plants is well documented, with effects ranging from reduced sexual reproduction to decreased survival (Zhang *et al.* 2022). Despite this, some physiological aspects of *C. filiformis*, such as its response to different hosts, have been largely overlooked. It is known that *C. filiformis* seedlings are autotrophic

and can survive up to a month before parasitizing a viable host (Furuhashi *et al.* 2016). Like other parasitic vines, they grow in a creeping form, and upon encountering a potential host, they twine around the stem. If the host is viable, haustoria develops to penetrate the host tissue. Once established, *C. filiformis* can cover the host completely as it grows (Nelson 2008, Debabrata 2018). Even though it can establish on a host, *C. filiformis* may still move toward better-quality hosts, where it eventually reproduces sexually (Zhang *et al.* 2022). This hemiparasitic species does not produce leaves, and its stems slightly vary in color, displaying tonalities that range from yellowish or brown to light or dark greenish depending on the stem type (mature holding stems or young growing stems) (Figure 1). However, it is unknown whether variations in stem color are related to functional differences such as photosynthetic activity.

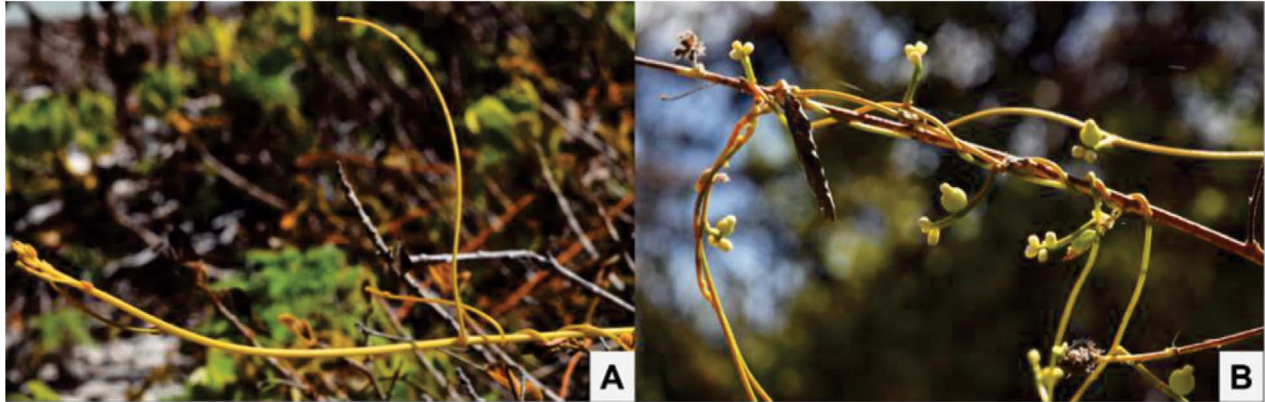


Figure 1. Young stems (A) and mature stems (B) of the hemiparasite *Cassytha filiformis* (Lauraceae) in the coastal scrubland in Telchac, Yucatan, Mexico.

Hosts identification of the hemiparasitic species Cassytha filiformis. A plot of 200 × 50 m (10,000 m²) parallel to the coast was established in a coastal scrubland adjacent to a coastal dune. In this plot, an inventory was made, and all plant species with a height above 30 cm were identified, recording whether they were parasitized or not by *C. filiformis*. The criterion to consider an individual parasitized was the presence of visible haustoria (Parra-Tabla *et al.* 2024). To determine persistent hosts and hosts in which *C. filiformis* produced flowers and fruits, this inventory was performed during the rainy season (October 2022) and during the dry season (May 2023), excluding species that presented only one parasitized individual. Based on these two inventories, the most frequently parasitized persistent species and those in which *C. filiformis* exhibited sexual reproduction were considered the “main” hosts. To confirm parasitism on the primary hosts and to describe haustoria development, histological analysis of transversal sections of host stems was performed in which *C. filiformis* haustorium presence was observed. Fresh samples were processed and embedded in paraffin blocks (Leica®). 5 μ sections of the paraffin-embedded samples were obtained with a semi-automated microtome (Thermo Scientific Microm HM310®) and mounted with resin for observation in a stereoscopic microscope coupled to a monitor (Olympus®).

Physiological parameters of Cassytha filiformis. Water potential.- To evaluate whether differences existed among *C. filiformis* relationships according to host species, water potential (ψ) was measured in young *C. filiformis* stems. As opposed to mature stems, young stems lack lateral growths, and their apical shape allows their handling for such measurement (Figure 1). In the three main host species recorded (see Results), three *C. filiformis* individuals growing on the host species were selected. For each *C. filiformis* individual, three ψ measurements (three stems per host plant) were performed using a Scholander bomb (SOLENS; model 1505D-EXP; USA). Samples consisted of 10 cm *C. filiformis* stem cuts.

Measurements were carried out pre-dawn (*i.e.*, “ ψ_{pd} ”: *ca.* 5:00 a.m.), when there is a water balance between the plant and the atmosphere, and at afternoon (*i.e.*, “ ψ_m ”: *ca.* 13:00 p.m.) when there is higher water deficit (Knipfer *et al.* 2020). To consider initial ψ 's differences among host species, a rate of change between both periods of the day in which measurements were taken was performed applying the following formula: $\Delta\psi = (\psi_{pd} - \psi_m) / \psi_{pd}$. The ψ_{pd} ,

representing the lowest water deficit, was considered the denominator to ensure that the values obtained for each host species were comparable.

Chlorophyll concentration.- To determine photosynthetic activity, the concentrations of chlorophyll *a*, *b*, and total chlorophyll produced in *C. filiformis* were measured in young and mature stems. Both stem types were randomly collected for three *C. filiformis* individuals for each main host species. The method described by Raya-Pérez *et al.* (2014) was used with some modifications. Four grams of plant tissue were measured and macerated in 10 ml of 80 % acetone. Subsequently, 5 ml of 80 % acetone was added, and samples were centrifuged at 3,500 rpm for 30 min (MicroC1 17R centrifuge). Finally, 8 ml of the supernatant was extracted and placed into quartz cells to be read in the spectrophotometer at 647 and 664 nm of visible light.

To calculate chlorophyll concentration, the formula by Leegood (1993) was used, with the chlorophyll extinction coefficients of Graan & Ort (1984) for 80 % acetone solutions: Chlorophyll *a* (μM) $C_a = 13.19 \times A_{664} - 2.57 \times A_{647}$; Chlorophyll *b* (μM) $C_b = 22.10 \times A_{647} - 5.26 \times A_{664}$; Total chlorophyll (μM) $C_a + C_b = 7.93 \times A_{664} + 19.53 \times A_{647}$. Finally, Arnon equations (1949) modified by Graan & Ort (1984) were used: Chlorophyll *a* mg/g of tissue $C_a = (13.19 \times A_{664} - 2.57 \times A_{647}) \times V/1,000 \times \text{weight g}$; Chlorophyll *b* mg/g of tissue $C_b = (22.10 \times A_{647} - 5.26 \times A_{664}) \times V/1,000 \times \text{weight g}$; Total chlorophyll mg/g of tissue $C_a + C_b = (7.93 \times A_{664} + 19.53 \times A_{647}) \times V/1,000 \times \text{weight g}$; where *A* is the specific absorption coefficient at spectrophotometer wavelength in nm, *V* the volume in ml and the weight of the material used in grams. The mean of the samples was used to determine which host species influenced chlorophyll concentration the most, *i.e.*, chlorophyll of young stems and mature stems.

The measurements of water potential and chlorophyll were performed at the beginning of the rainy season (June), which was the moment when *C. filiformis* produced flowers and fruits.

Data analysis. To test whether *C. filiformis* showed host preference according to their life form (herbaceous *vs.* shrub), a χ^2 test of independence (Zar 2010) was performed, which allows for weighting host abundances. After that, a χ^2 test of independence was carried out to test whether *C. filiformis* showed preference among the three main hosts.

To test differences in water potential at each time of the day and the $\Delta\psi$ among the host plant species, a generalized linear mixed model (GLMM) was applied, incorporating the time of the day, the host species, and the stem nested in each host as fixed factors. The stems were incorporated into the model to consider variation due to differences between stems. Each plant was considered a random factor. To test differences in chlorophyll *a* and *b* and the total chlorophyll among the host plant species and stem types (young *vs.* mature), a GLMM was applied with host species and type of stem nested in each host as fixed factors. In this analysis, each plant was also considered as a random factor.

All analyses were performed with the statistical package SAS v. 9.4 (SAS 2002). χ^2 tests of independence were carried out using the *freq* procedure (SAS 2002). GLMMs were evaluated using the *glimix* procedure (Littell *et al.* 2006). When differences were found among fixed factors, the functions *pdiff* and *varcom* were used (Littell *et al.* 2006) to estimate the percentage of variance explained by the nested level (host and stem type) for the chlorophyll concentration.

Results

***Cassytha filiformis* hosts.** The results of the inventory in the rainy season showed that *C. filiformis* developed haustoria in 10 out of 18 plant species recorded. In the dry season, *C. filiformis* developed haustoria in 9 out of 14 species (Figure 2). The total number of parasitized individuals in the rainy season was 129, while 90 were in the dry season. The complete list of parasitized species is shown in the Table S1 and S2. The presence or absence of some species varied depending on the season. The species with the highest percentage of parasitism in both seasons were *Scaevola plumieri* (L.) Vahl (Goodenaceae), *Pithecellobium keyense* Britton (Fabaceae), *Croton punctatus* Jacq. (Euphorbiaceae) and *Agave angustifolia* Haw. (Agavaceae) (Figure 2). However, only in the first three shrubs it was observed that *C. filiformis* frequently exhibited sexual reproduction, and only one individual exhibited sexual reproduction in *A. angustifolia*; therefore, the three shrub species were considered the “main hosts”.

The χ^2 test showed that *C. filiformis* preferred shrub species ($\chi^2_1 = 24.0$, $P < 0.001$). Less than 10 % of herbaceous species were parasitized and among shrub species, this percentage was above 30 % (Figure 3A). Among the main host, the χ^2 test showed significant differences in parasitism preference ($\chi^2_2 = 40.8$, $P < 0.001$). The results suggested a preference by *C. filiformis* for *P. keyense*, in which nearly 90 % of all available individuals were parasitized (Figure 3B).

Histological analysis. The histological analysis corroborated the presence of haustoria penetrating the tissue of the main host species (*C. punctatus*, *S. plumieri* and *P. keyense*), showing observable differences in the morphology of each haustorium depending on the host (Figure 4). Although in all cases the haustoria appear to be in the cortex of the host, in the sample of *C. punctatus* (Figure 4D), a greater degree of penetration is observed, with haustoria closer to the vascular tissue of its host. In contrast, the samples of *S. plumieri* and *P. keyense* (Figure 4E and F) show more superficial penetration, with both *C. punctatus* and *P. keyense* exhibiting secondary growth in the host stem with *S. plumieri* specifically showing a thicker cortex layer.

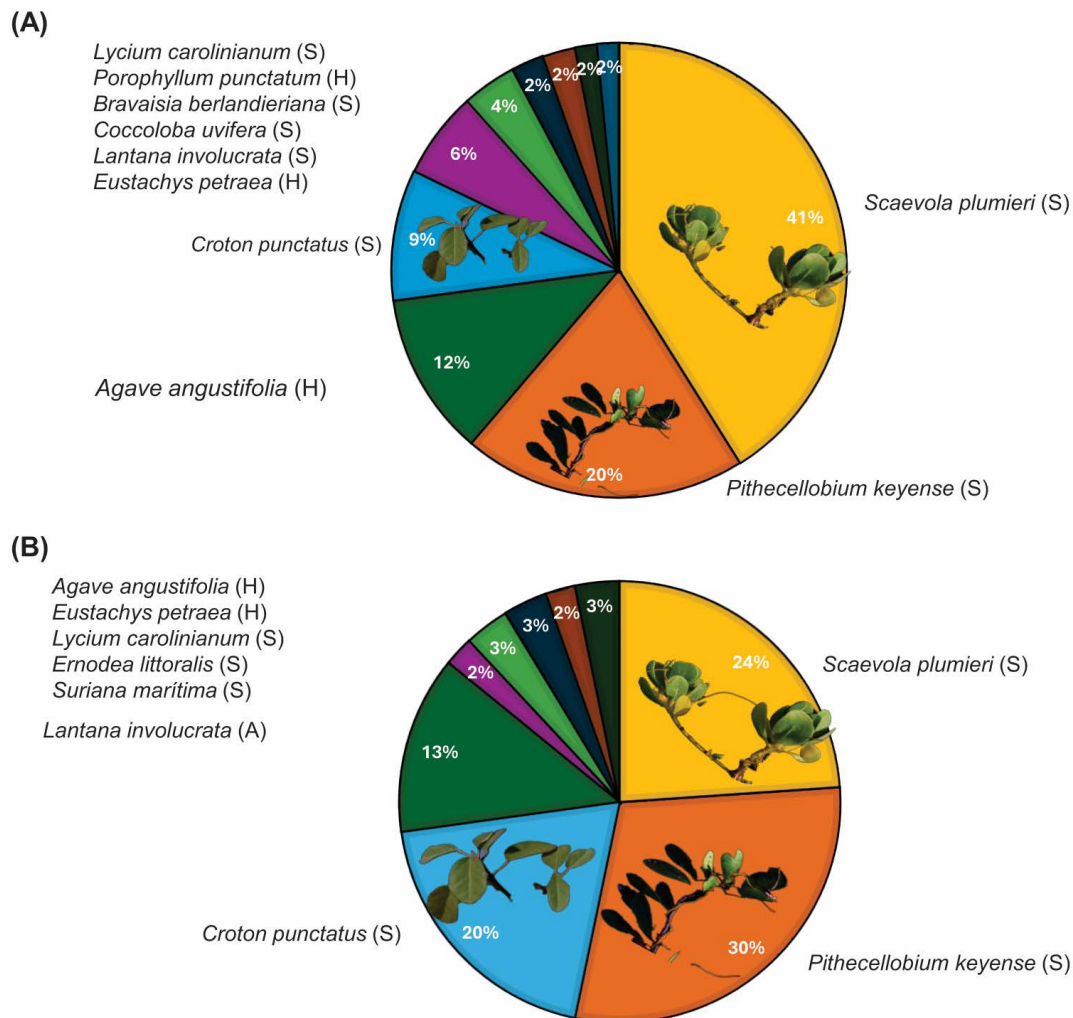


Figure 2. Percentage of individuals parasitized by *Cassytha filiformis* during the rainy season (A) and dry season (B) in a coastal scrubland community of Yucatan. The letter after the name of the parasitized species indicates the life form: herbaceous (H), and shrubs (S). Only species with more than 1 % of individuals parasitized are shown.

Host preference of *Cassytha filiformis*

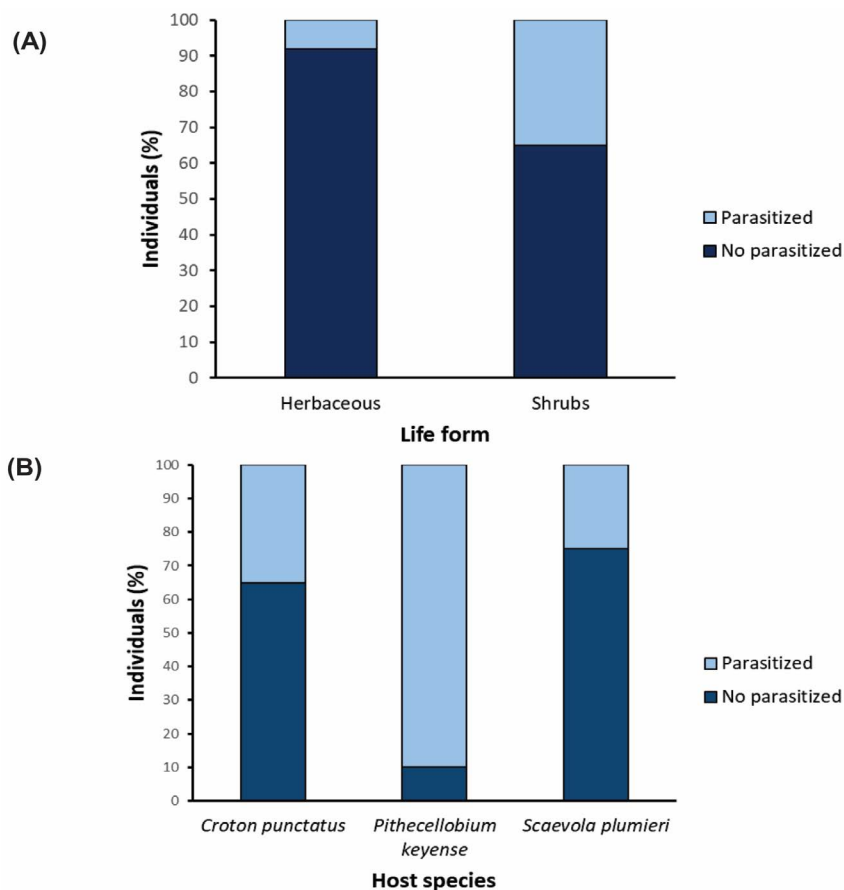


Figure 3. (A) Percentage of parasitized and non-parasitized individuals by life form for *Cassytha filiformis* in a coastal scrubland community of Yucatan. (B) Percentage of parasitized and non-parasitized individuals by *C. filiformis* of the main host species.

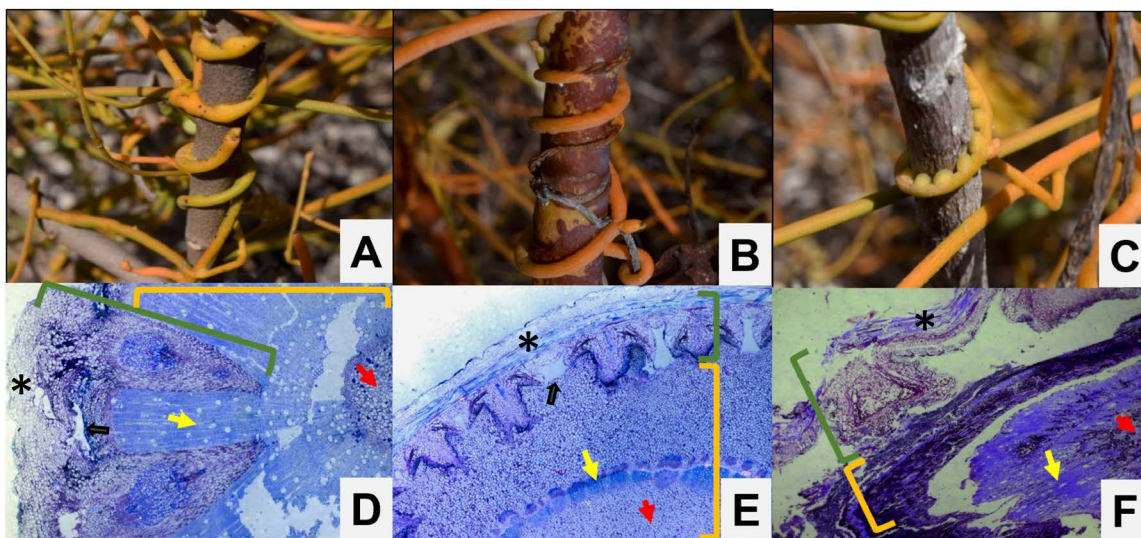


Figure 4. Development of *Cassytha filiformis* haustoria on its main hosts in a coastal scrubland community of Yucatan. (A) *Croton punctatus*, (B) *Scaevola plumieri*, and (C) *Pithecellobium keyense*. The endophyte shows differences in terms of its shape, length, and depth of penetration (D, E, F). Tissue of *C. filiformis* (asterisk), endophyte (green bracket), and host tissue (orange bracket) being observable. Additionally, the host epidermis is indicated (black arrow), with *C. punctatus* (D) and *P. keyense* (F) showing more secondary xylem growth (yellow arrow) than *Scaevola plumieri* (E) with more cortex and pith (red arrow).

Physiological parameters of Cassytha filiformis. Water potential did not significantly vary in any of the two time periods (pre-sunrise and afternoon) due to host identity (Figure 5A and B). However, statistically significant differences were observed in the $\Delta\psi$ ($F_{2,16} = 2.03, P = 0.03$). The highest $\Delta\psi$ occurred in *C. filiformis* individuals growing on *C. punctatus*, and the lowest in individuals growing on *S. plumieri* (Figure 5C). The differences between these two hosts were significant ($t = -2.87, P = 0.01$). On the other hand, individuals growing on *P. keyense* did not show differences compared to *C. punctatus* or *S. plumieri* ($t \leq -1.5, P > 0.05$).

Differences were observed in total chlorophyll concentration (Table 1; Figure 6); the highest concentrations were found when *C. filiformis* was growing on *C. punctatus* or *S. plumieri*, which did not show significant differences between them ($t_{28} = 0.80, P = 0.42$). The lowest chlorophyll concentration was found in *P. keyense*, which showed significant differences with *C. punctatus* and *S. plumieri* ($t \geq 2.6, P \leq 0.01$). Additionally, the analysis showed that chlorophyll *a*, *b*, and total concentration significantly varied according to stem age (young vs. mature) (Table 1).

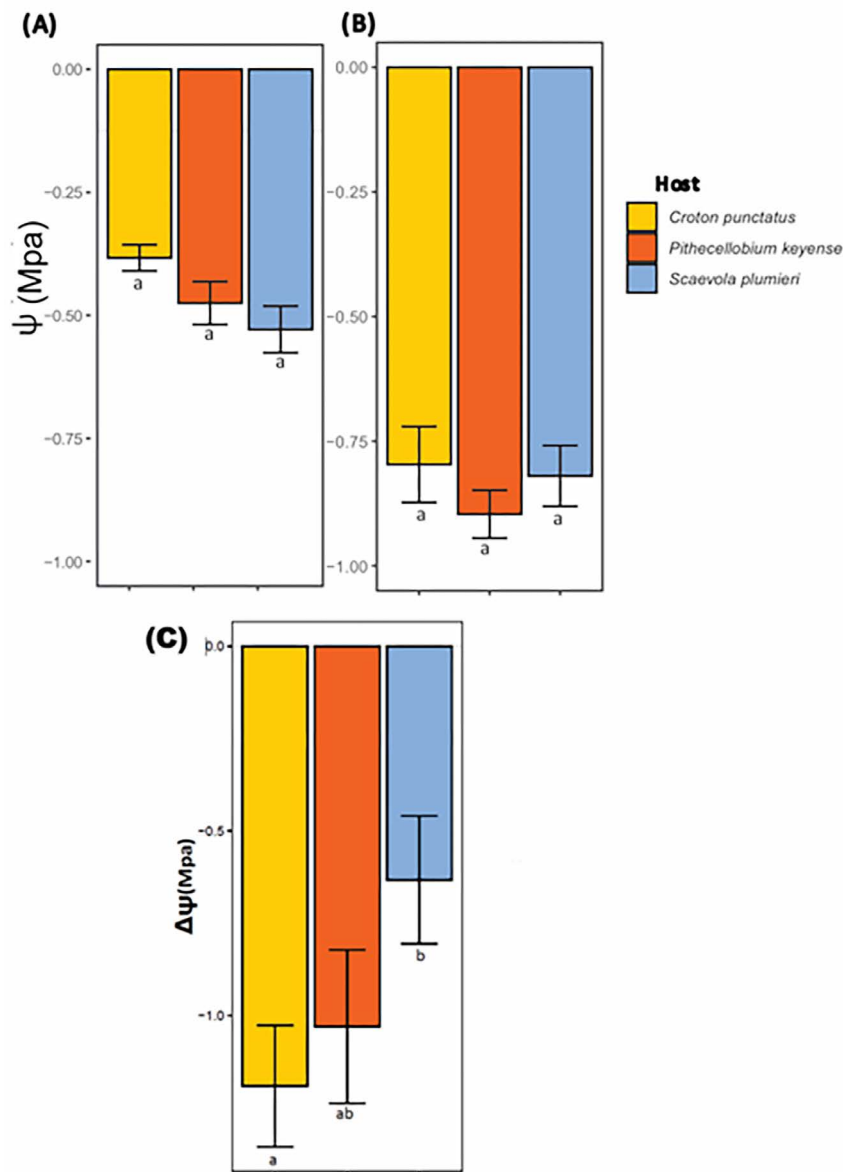


Figure 5. Mean (\pm EE) of the water potential (A: predawn and B: midday) and change in water potential (ψ) (C) of *Cassytha filiformis* according to its host in a coastal scrubland community of Yucatan. Different letters indicate significant differences ($P < 0.05$) between hosts.

In all cases, the highest concentration was observed in young stems (Figure 7). The variance components analysis showed that the type of stem explained a higher percentage of the variance in total chlorophyll, as well as in chlorophyll *a* and *b*, concerning the percentage explained by the host identity (Table 1).

Discussion

The results of this work showed that the invasive hemiparasite *Cassytha filiformis* uses many host plants in the Yucatan coastal scrubland, preferring shrub species on which sexually reproduces. Furthermore, this work revealed differences in *C. filiformis* physiological performance across the main hosts. In general, the results suggest that *C. filiformis*' host selection can be a relevant mechanism in the process of establishment of this species as it colonizes new environments.

Host range and preference of Cassytha filiformis. The results of this and previous work show that *C. filiformis* can parasitize up to 23 different species, including herbaceous and shrub species (Parra-Tabla *et al.* 2024). In particular, the results of the two inventories of this work added up to 8 host plant species, with the shrub species *Pithecellobium keyense* and *Croton punctatus* standing out for their high level of parasitism. Altogether, the results suggested that like several parasitic species (*e.g.*, Gibson & Watkinson 1992, Press 1998, Pennings & Callaway 2002), *C. filiformis* can be considered a generalist. However, the results also suggest that most species are used during short periods. In addition to preferring shrub species, *C. filiformis* selects a lower number of species on which it establishes and reproduces. In the genus *Cassytha*, the temporary use of hosts and the selection of definitive hosts seem common (Zhang *et al.* 2022). Specifically, for *C. filiformis*, it has been suggested that this species temporarily uses several host species as “bridges” that allow them to explore the environment until finding long-lifespan hosts (Zhang *et al.* 2022, Parra-Tabla *et al.* 2024). This has been explained because perennial species can provide long-term resources to parasitic species (Press & Phoenix 2005). However, even within a range of potential host perennial species, many parasitic species select a subset of these (Gibson & Watkinson 1989, Pennings & Callaway 1996). These observations suggest that despite the “generalist” status, several parasitic species have a certain level of specialization, behaving as discriminative consumers that increase the frequency of their parasitism toward “better hosts” (Kelly *et al.* 1988, Press & Phoenix 2005, Liu *et al.* 2023).

Table 1. Results of the nested GLMM model to test the effect of host species and stem type (young *vs.* mature) on the concentration of chlorophyll *a*, *b*, and total, of *Cassytha filiformis* in a coastal community of Yucatan. The percentage of variation explained for each case is shown.

Chlorophyll	Factor	<i>F</i>	<i>P</i>	%
<i>a</i>	Host	3.16	0.057	3.1
	Stem type (Host)	25.9	< 0.001	27.4
<i>b</i>	Host	3.16	0.058	2.0
	Stem type (Host)	16.3	< 0.001	4.1
Total	Host	6.61	0.004	12.3
	Stem type (Host)	17.52	< 0.001	36.4

Specifically, in this work, we observe that *C. filiformis* preferred the shrub species *P. keyense*, *C. punctatus* and *S. plumieri*, regardless of the differences in abundance of these hosts. In these three species, *C. filiformis* showed sexual reproduction, and the histological study confirmed the development of parasitic structures. This evidence suggests that *P. keyense*, *C. punctatus* and *S. plumieri* are adequate long-term *C. filiformis* hosts. Therefore, in addition to the previous study that showed that in the coastal dune, *C. filiformis* prefers the shrubs *Suriana maritima*, *Tournefortia gnaphalodes* and *S. plumieri* (Parra-Tabla *et al.* 2024), this invasive parasite has at least five suitable shrub species

available for establishment and dispersal, considering both the coastal dune and the scrubland. The relevance of *C. filiformis* parasitizing these shrubs is because these species are common or dominant in coastal dune and scrubland communities along the Yucatan Peninsula (Espejel 1987, Torres *et al.* 2010, Angulo *et al.* 2018). Furthermore, these species participate in soil fixation preventing erosion (Espejel 1987, Castillo & Moreno-Casasola 1996), and in the case of *P. keyense*, increase soil nitrogen concentration (Leirana-Alcocer & Bautista-Zuñiga 2014), besides playing the role of nurse plants (Ovando-Hidalgo *et al.* 2020, Hernández-Mendoza *et al.* 2023). Hence, it is possible that in the process of invasion in these coastal ecosystems, *C. filiformis* can provoke cascading effects that affect their functionality.

Different studies have documented that the damage caused by *C. filiformis* ranges from decreasing the sexual reproductive success of its hosts and increasing their mortality to inducing changes in the associations they establish with soil microorganisms (Nelson 2008, Prider *et al.* 2009, Cai *et al.* 2020, Zhang *et al.* 2022). In the coastal dune of Yucatan, parasitized *S. plumieri*, *T. gnaphalodes* and *S. maritima* individuals produce, on average, up to two times fewer flowers and fruits than non-parasitized individuals by *C. filiformis* (Parra-Tabla *et al.* 2024). This result suggests that *C. filiformis* has the potential to significantly decrease the reproductive success of the shrub species they parasitize, thus affecting the recruitment of new individuals via seeds. For this reason, future studies should consider the demographic impact on these species and the facilitation interactions (*e.g.*, nursing) they promote to evaluate the effect of *C. filiformis* on the structure and functionality of the coastal plant communities of Yucatan.

Physiological performance of Cassytha filiformis. Hemiparasitic species such as *C. filiformis* depend highly on their host plants for water and nutrients to complete their life cycle. Therefore, these species must select hosts that give them adequate physiological performance. This performance is largely influenced by the microenvironment in which hosts are found. In semi-arid environments such as the coastal ecosystems of Yucatan, there is low water availability and

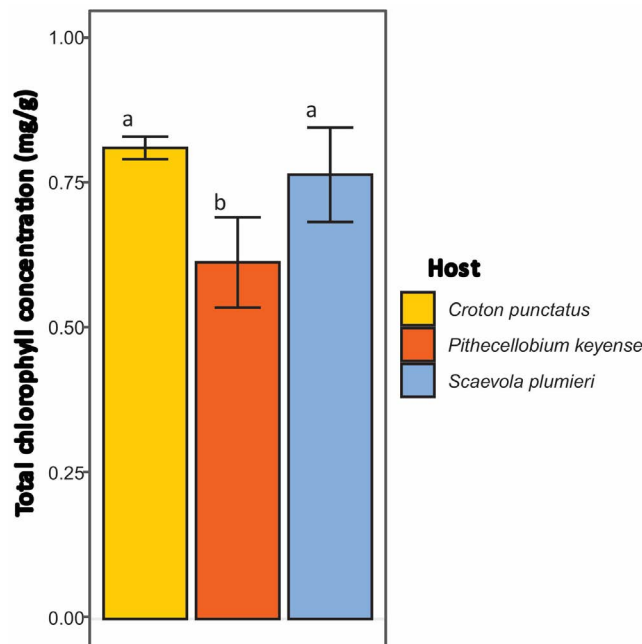


Figure 6. Mean (\pm ES) of total chlorophyll concentration in both stem types of *Cassytha filiformis* according to the host they occupied in a coastal scrubland community of Yucatan. Different letters indicate significant differences ($P < 0.05$) between hosts.

Host preference of *Cassytha filiformis*

variation among plant species in their ability to access this resource (Espejel 1987). In this sense, the host's identity can explain variables such as the water potential of parasitic plants, since in parasitic plants, stress for water deficit is experienced through the host (Zagorchev *et al.* 2021). No statistically significant differences were observed in *C. filiformis* pre-sunrise or noon water potential among the three main hosts in this work. This could indicate that the water status of *C. filiformis* is independent of the host. It is known that parasitic plants present high transpiration rates that cause stronger negative water potentials than the host, facilitating passive water transport (Ehleringer & Marshall 1995).

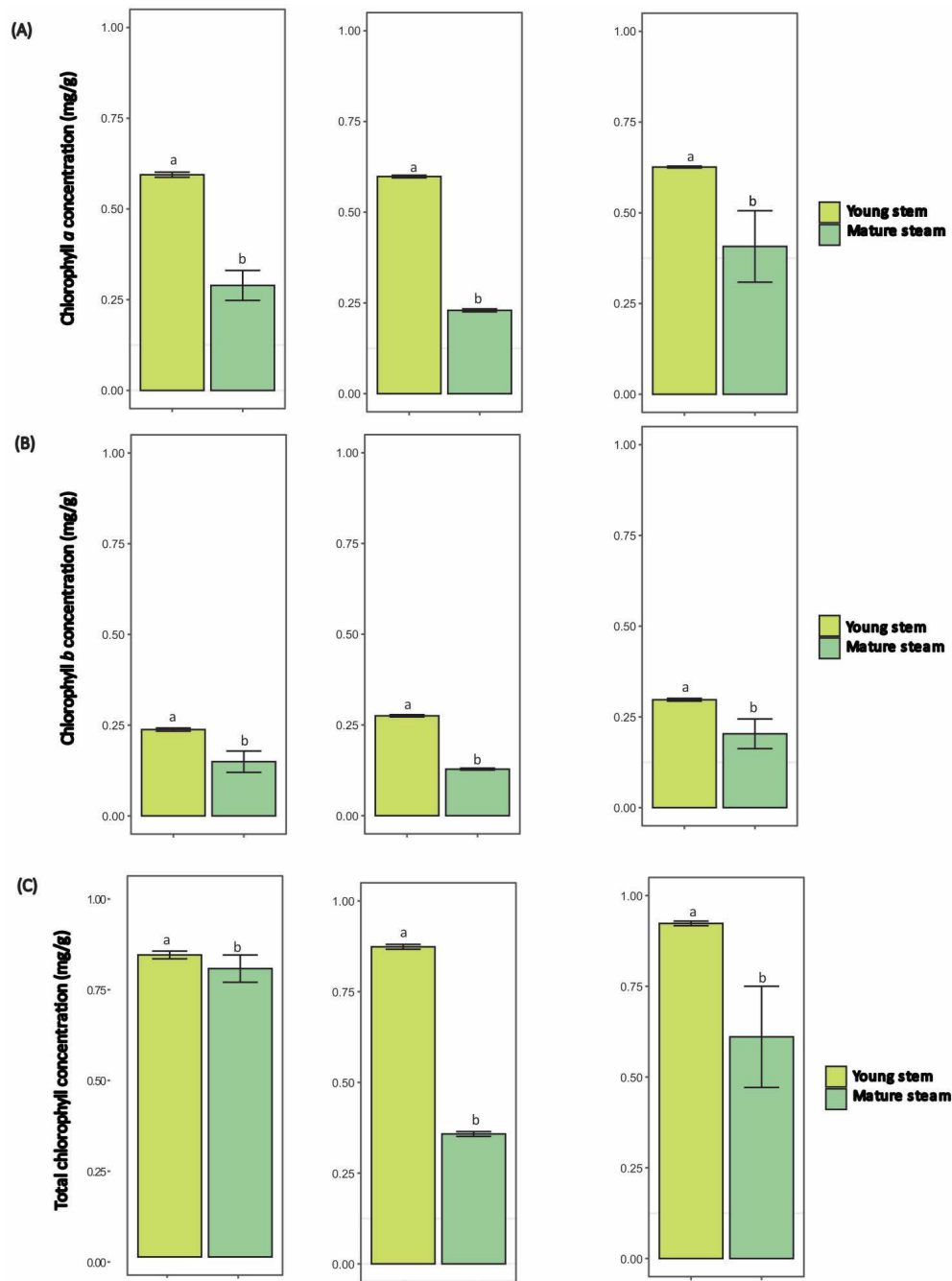


Figure 7. Mean (\pm EE) of *a*, *b*, and total chlorophyll concentrations between young and mature stems of *Cassytha filiformis* according to the host they occupied in a coastal scrubland community of Yucatan. (A) *Croton punctatus*, (B) *Pithecellobium keyense* and (C) *Scaevola plumieri*. Different letters indicate significant differences ($P < 0.05$) between stem types in each host.

However, the analysis of the water potential change ($\Delta\psi$) showed significant differences among hosts, suggesting that the most drastic change throughout the day occurred when *C. filiformis* was established in *C. punctatus* and the lowest in *S. plumieri*. Considering that *C. filiformis* obtains its resources from the hosts, it is likely that the water redistribution of the soil-plant-atmosphere system that occurs naturally between night and pre-sunrise is modified to a soil-plant-parasite-atmosphere system. This result would explain the changes in water potential observed in *C. filiformis* throughout the day. In this context, in drastic temporary changes, water demand can lead to severe effects for both the parasite and the host (Watson *et al.* 2022). In this sense, the host in which haustoria penetrated the deepest was *C. punctatus*, and the most superficial was *S. plumieri*, which could be an indicator of the functional relationship between parasite and host.

In the relationship *C. filiformis*-*C. punctatus*, it is probable that, because of the ability of the parasite to penetrate the host, water exchange between them had been higher than with the other hosts. This can be confirmed by analyzing the water potential change ($\Delta\psi$), which was higher in *C. filiformis*-*C. punctatus* because as *C. punctatus* evaporative demand increases throughout the day, it could have affected the *C. filiformis* hydric status in two ways: by giving preference to the evaporative demand of the leaves or using part of *C. filiformis* water reserve to complement its water demand. In contrast, the relationship *C. filiformis*-*S. plumieri*, $\Delta\psi$ was lower, and this coincided with a lesser penetration of haustoria, suggesting that with deeper haustoria penetration, the relationship between the hydric status of the parasite and host strengthens. Although a follow-up of host plant survival was not carried out in this work, it was evident that *C. punctatus* individuals were the most affected (*e.g.*, dead parasitized branches), which might be related to the degree of haustorium penetration into the host's tissue.

The results of this work also showed differences between hosts and stem types in total chlorophyll concentration, in addition to significant differences in the concentration of chlorophylls *a* and *b* in *C. filiformis*. Although the presence of chlorophyll in hemiparasites indicates some degree of photosynthetic activity (De la Harpe *et al.* 1981), chlorophyll concentration does not necessarily indicate higher or lower photosynthetic activity (Amutenya *et al.* 2023). However, previous studies reported that this is considered functional despite low chlorophyll concentration in *C. filiformis* (De la Harpe *et al.* 1981, Balasubramanian *et al.* 2014). Chlorophyll in hemiparasitic plants allows them to have a nutrient source while searching for hosts or starting to grow on them (Press *et al.* 1988, Zhang *et al.* 2022). At the same time, it permits them to adjust to hosts that show variations in the amount of nutrients they can provide. In *C. filiformis*, the highest chlorophyll concentration was observed on *C. punctatus* and the lowest on *P. keyense*, suggesting that *C. filiformis* has a higher photosynthetic activity on *C. punctatus*. This result is additionally supported by the low concentration of chlorophyll *b* observed, compared to chlorophyll *a*, since the latter is the primary photosynthetic pigment. In contrast, type *b* is an accessory pigment that participates in light absorption at shorter wavelengths (Masuda & Fujita 2008).

In other hemiparasitic species such as *Thesium chinense* (Santalaceae) and *Rhinanthus alectorolophus* (Orobanchaceae), it has also been observed that chlorophyll concentration depends on host plant identity (Luo & Guo 2010, Moncalvillo & Matthies 2023). Differences in the concentration of the chlorophyll produced by hemiparasitic plants in different hosts reflect the complexity of their nutrition process. For example, in several species of mistletoe, resources obtained through the xylem of the host are mostly inorganic solutes and water, while nutritional elements such as carbon or elements for lipid synthesis are produced by the hemiparasite via photosynthesis (Ehleringer *et al.* 1985, Švubová *et al.* 2013). In this sense, the photosynthetic activity of these species might be a path of compensating for resources it does not obtain from the host. For example, carbon assimilation occurs through the host and the parasite in the species *Cassytha pubescens* (De la Harpe *et al.* 1981, Prider *et al.* 2009, Těšitel 2016).

In *C. filiformis*, it has been reported that haustoria can access not only the xylem but also the phloem (Balasubramanian *et al.* 2014, Zhang *et al.* 2022), which in principle allows *C. filiformis* to take carbon directly from its hosts. Thus, *C. filiformis* would not need to perform photosynthetic activity to fix carbon, thus low chlorophyll concentrations would be expected. Nevertheless, the differences observed among hosts suggest differences in *C. filiformis* photosynthetic activity among hosts and differences in host "quality" based on the amount of photosynthates the parasite can obtain. Future studies that associate these differences with the growth, survival and reproductive success of *C. filiformis* will allow us to elucidate the ultimate consequences of host selection by this species.

On the other hand, a noteworthy result of this study was that differences were observed in chlorophyll *a*, *b*, and total concentration between young and mature *C. filiformis* stems. To our knowledge, this has not been reported before in other parasitic species. These differences suggest functional differences where mature stems that serve as support could be taking more resources from the host. In contrast, exploring and growing on the host, young stems would probably need to complete their requirements through a higher photosynthetic activity. This interpretation is consistent with evidence that suggests that in the first stages of its life cycle, *C. filiformis* might have sufficient photosynthetic activity while exploring and finding viable hosts through its growing stems (Furuhashi *et al.* 2016). However, the differences in concentrations and proportions of *a* and *b* chlorophylls might result from other factors and cannot be dismissed. For example, it is known that chlorophyll *b* concentration is related to plant photo-protective mechanisms (Voitsekhovskaja & Tyutereva 2015), which in environments exposed to high radiation, such as tropical coastal environments, could be playing an important role.

We acknowledge the limitations of our results, as we only evaluated the water deficit and chlorophyll content of *C. filiformis* on different hosts. However, as an initial approach to studying its physiological performance on different hosts, we can say that the overall results of this work regarding *C. filiformis*' preference and physiological performance highlight the need for future studies to analyze in detail aspects such as host-parasite water and nutrient flow, and the specific nutrients transferred from host plants to *C. filiformis*. These studies would elucidate the importance of nutritional factors in host selection by *C. filiformis*, helping to explain its success as an invasive species in coastal ecosystems.

In conclusion, this work shows that the coastal invasive hemiparasitic species *C. filiformis* has many available host species, among which selects those whose physiological and reproductive performance is most suitable, probably increasing its invasion success.

Supplementary material

Supplemental data for this article can be accessed here: <https://doi.org/10.17129/botsci.3529>.

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