

Article

Diverse Host Spectrum and the Parasitic Process in the Pantropical Hemiparasite *Cassytha filiformis* L. (Lauraceae) in China

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Abstract: Many hemiparasites attach to a range of different host species, resulting in complex parasite–host interactions. Comprehensive molecular phylogenies allow the investigation of evolutionary relationships between these host plants. We surveyed the hosts of the laurel dodder (*Cassytha filiformis*, Lauraceae) in China, representing 184 species from 146 genera, 67 families, and spanning flowering plants, conifers, and ferns, using host phylogenetic relationships to investigate the susceptibility to attack by this hemiparasitic plant among the vascular plants. The process of produced well-formed haustoria by *C. filiformis* was also observed in detail for six different hosts. Our results show that *C. filiformis* grows mainly on trees and shrubs from phylogenetically divergent members of the rosoid and asterid eudicot clades, often attacking multiple adjacent hosts simultaneously, and forming extensive colonies. However, whether and to what extent transitions between *C. filiformis* and host plants occur remain unclear. Physiological evidence for the complex parasite–host species interactions need to be studied in the future.

Keywords: hemiparasite–host species; phylogenetic; *Cassytha*; Lauraceae; woody plants



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1. Introduction

Parasitic plants are a diverse group of 292 genera: approximately 4750 species (1% of all flowering plants) with parasitism evolving at least 12 times [1,2]. Parasitic plants negatively influence host growth and development [3]. They have had increased attention by researchers over the past three decades [1]. Parasitic plants can obtain water, mineral nutrients, and carbon from other plants using the haustorium [1,4]. Parasitic plants can either be photosynthetic hemiparasites or achlorophyllous holoparasites [5], but the majority are hemiparasites [2]. They occur in most major ecosystems across the world from subpolar to tropical latitudes, as well as agricultural ecosystems [6].

Generalist hemiparasitic plants as a group are morphologically diverse with a broad range of host interactions [2], often attacking multiple co-occurring plant species [7]. Parasite performance can be influenced by host characteristics, including biomass [8], carbon

content [9], resistance [10], genetic constitution [11], rate of growth [12], host condition [13], secondary compounds [14], etc., complicating research into the evolution of host range [7]. Hemiparasite fitness has often been linked to host functional plant groups such as legumes, grasses, or forbs [15], but is influenced by life history strategies and resource-linked attributes [16]. However, some functional groups are monophyletic, while others have more complex evolutionary relationships and hemiparasite performance may sometimes be predicted better by host phylogenetic relationships [7]. Host identity may be an important factor in determining the success of the parasitic species.

The literature on parasitic plant host biology covers a range of taxa, including the root hemiparasites in Orobanchaceae [17] and Santalaceae [18], mistletoes of Loranthaceae [19] and Viscaceae [20], and the stem holoparasite *Cuscuta* L. (dodder, Convolvulaceae) [21] and hemiparasite *Cassytha* L. (laurel dodder, Lauraceae) [22]. Parasitic plants also interact with other plants, influencing competition, community biodiversity, and nutrient cycling [23–25]. Although molecular phylogenetic methods have been used to address several long-standing issues in parasitic plant taxonomy and evolutionary biology [1], few studies have examined the evolutionary relationships of host species.

There is a long tradition of the human use of parasitic plants for medicinal and cultural purposes worldwide [26]. *Cassytha filiformis* L. (laurel dodder) is a pantropical hemiparasite which has also been used variously for medicine, cosmetics, cushion, and rope-making in many regions [6,27], as well as being regarded as a serious weed in some tropical regions [7,28]. The species has been reported as having a very wide, possibly indiscriminate host range [28–30], although with some apparent host preferences [30,31]. Identifying its host spectrum and phylogenetic relationships may help with the use of this parasite to control invasive weeds by understanding their interactive biology, as has been suggested for *C. pubescens* R.Br. in Australia [32–34]. Parasitic plants develop haustoria for absorbing water and nutrients from the host plant, so understanding the seed germination to host selection and haustorial attachment process is critical [35].

Cassytha is the only parasitic genus Lauraceae, but it is also morphologically similar to *Cuscuta* L. (Convolvulaceae), with both being leafless, haustorial stem parasites [35]. *Cassytha* is hemiparasitic with white or light green flowers borne in spicate, capitate, or racemose inflorescences and 1-seeded drupes included in a dilated, fleshy, free perianth tube. In contrast, *Cuscuta* is holoparasitic, with white, orange, or purplish-red stems; white, yellow, or pink flowers in globular inflorescences; and two–four seeded capsules [36]. *Cassytha* parasitizes a wide range of mainly woody plants, including plants of agricultural and economic value, and although most species occur in Australia, *C. filiformis* occurs across the tropics worldwide [22,28]. According to Nickrent (2002), *C. filiformis* is indiscriminate in host choice, often attacking multiple co-occurring hosts simultaneously [29], and surveys by Li et al. (1992) in Nanning, Tianlin, Yulin, and other places in Guangxi recorded 137 host species from 113 genera and 58 families [37].

In China, *C. filiformis* causes serious damage to crop and forests in some regions, with Huang et al. (1957) finding that the severe parasitism of oil tea by *C. filiformis* caused a massive yield reduction in Shangsi and Luchuan, Guangxi, China [38]. Similarly, Zhang (1988) found that heavy infestation of *Pinus massoniana* Lamb by *C. filiformis* led to acute deciduous needle disease caused by *Lophodermium pinastri* Chev. in Fuzhou, Fujian [39]. These studies show the importance of investigating the host–parasite relationships of *C. filiformis* and their effects, but to date no systematic and comprehensive studies have been undertaken on host species occurring in China.

Accordingly, we here investigate and summarize the hosts of *C. filiformis* in China, with a particular focus on its host phylogenetic relationships and host–parasite species interactions. Our aim is to understand the evolutionary relationships of the diverse range of host species in China and the potential growth responses of the hosts, specifically: (1) to determine the host range and responses to attack for *C. filiformis* in China and analyze the parasitic progress of *C. filiformis*; and (2) examine the evolutionary relationships among the hosts of *C. filiformis*.

2. Materials and Methods

2.1. Plant Materials

Collection sites in China were selected using data from the Chinese Virtual Herbarium (CVH, <https://www.cvh.ac.cn>, accessed on 5 May 2019), Plant Photo Bank of China (PPBC, <http://ppbc.iplant.cn>, accessed on 5 May 2019), and Global Biodiversity Information Facility (GBIF, <https://www.gbif.org>, accessed on 6 May 2019). We conducted a series of targeted field trips to the geographical range areas of particular interest in 2019–2021 (Figure S1). Efforts were made to ensure sampling from localities across most of the known geographical ranges of the species (144 sample sites; for details see Table S1 and Figure S1). Inflorescences and fruits of *C. filiformis* were gathered (with reproductive characters collected where possible) from Guangzhou (Guangdong), Lingshui (Hainan), and Xishuangbanna (Yunnan) (Figure 1), but the Guangzhou locality (Zhongkai University of Agriculture and Engineering) was the only one with ripe fruit, despite repeated site visits. Host plants were recorded for samples from six provinces: Fujian, Guangdong, Guangxi, Hainan, Yunnan, and Zhejiang (Figure S1; Table S1), with hosts defined as plants having direct haustorial connections to *C. filiformis* (Figure 2). Host identification was performed by experts at PE (Herbarium, Institute of Botany, CAS), Bing Liu, XTBG (Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences), Yunhong Tan and CATAS (Chinese Academy of Tropical Agricultural Sciences), and Shengzhuo Huang, using the reproductive or vegetative characters available on the vouchers. All vouchers were stored at the Herbarium of Xishuangbanna Tropical Botanical Garden (HITBC). In addition, we summarized the host plants of the published literature, together with data from our surveys (40 specimens by the previous published literature, 104 specimens by our surveys; details can be seen in Table S1). In total, the Chinese host range assessment was based on 184 specimens of *C. filiformis*.

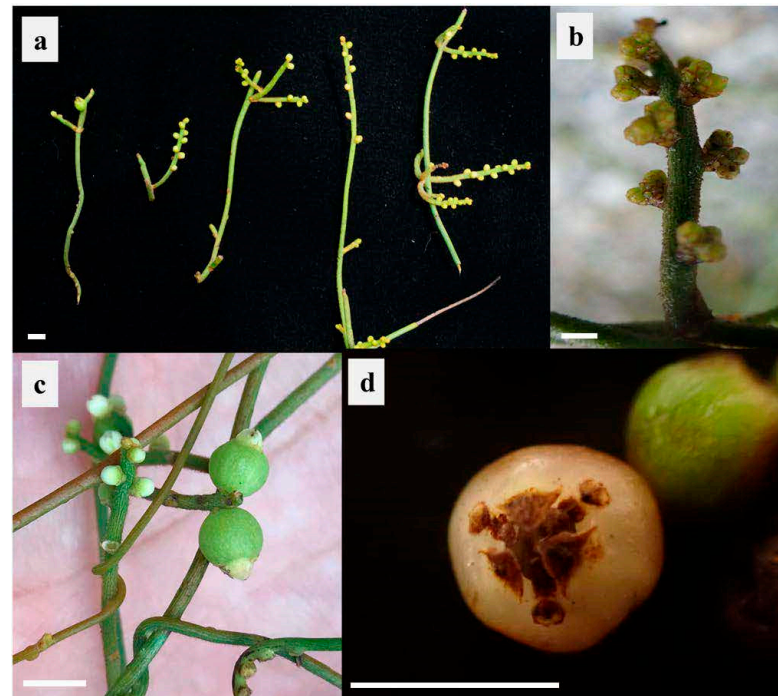


Figure 1. Representative inflorescence and fruits of *Cassytha filiformis*. (a) Inflorescence collected in Guangzhou (Guangdong, longitude: 113°17' E, latitude: 23°0' N, altitude: 10 m). (b) Inflorescence collected in Xishuangbanna (Yunnan, longitude: 100°45' E, latitude: 22°28' N, altitude: 1129 m). (c) Inflorescence and unripe fruits collected in Lingshui (Hainan, longitude: 109°54' E, latitude: 18°34' N, altitude: 76 m). (d) Ripe fruit collected in Guangzhou (Guangdong, longitude: 113°17' E, latitude: 23°0' N, altitude: 10 m). Scale bars = 5 mm.

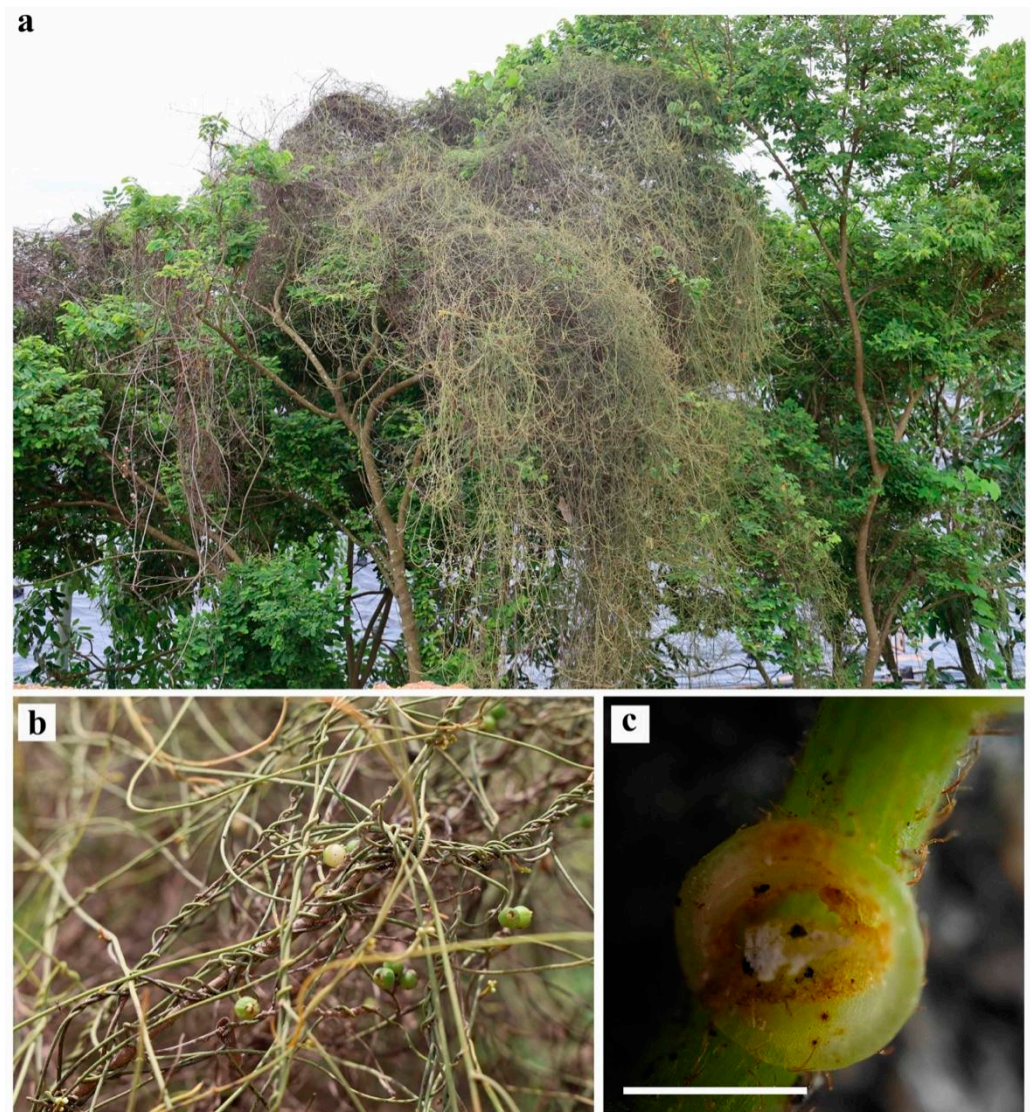


Figure 2. The host *Bridelia balansae* and *Cassytha filiformis* with its haustoria. (a) Host and *C. filiformis* collected in Lingshui, Hainan (longitude: 109°55' E, latitude: 18°33' N, altitude: 42 m). (b) Vines and fruits. (c) The haustorium. Scale bars = 1 mm.

2.2. Growth Conditions of *C. filiformis*

The seeds of *C. filiformis* displayed physical dormancy [40], which was broken by soaking the seeds in warm water at 60 °C for 1 h. The treated seeds were then grown in the soils that collected in Guangzhou (Zhongkai University of Agriculture and Engineering, Guangdong, China) under controlled conditions in a PHCbi CO₂ Incubator (PHC Holdings Corporation, Tokyo, Japan) with a 24–27 °C, 18 h light and 6 h dark cycle. Germination time was measured as the total number of days to seedling emergence after planting. Host seeds (*Bidens pilosa* L. (Asteraceae), herb; *Chromolaena odorata* (L.) R.M.King and H.Rob. (Asteraceae), herb; *Cleome rutidosperma* DC. (Cleomaceae), herb; *Dimocarpus longan* Lour. (Sapindaceae), tree; *Mikania micrantha* Kunth (Asteraceae), liana; and *Scoparia dulcis* L. (Plantaginaceae), herb) were also collected from the sites of *C. filiformis* seed collection, in Guangzhou (Zhongkai University of Agriculture and Engineering, Guangdong, China). These six species were confirmed as hosts of *C. filiformis*, based on field observations of haustorial attachment. We filled pots (18 cm diameter, 16 cm height) with soil collected from these field sites and sowed a minimum of five seeds of a single species per pot, with three replicate pots per host species for a total of eighteen pots. Hosts were observed at the same time each day (10 a.m.) in each pot once germination had commenced.

To investigate the interaction between *C. filiformis* and hosts, we observed and recorded the growth and germination progress. Three replicates were used, each of which was pooled from at least five seeds. To obtain laurel dodder and hosts from host–laurel dodder parasitization systems, we put different host plants with five seeds of *C. filiformis* together to form the host–laurel dodder parasitization system. This system was cultivated under controlled conditions in PHCbi CO₂ Incubator (18 h light, 6 h dark) at 24–27 °C. From germination to growth conditions, *C. filiformis* as well as hosts were observed at the same time each day (10 a.m.) in each pot.

2.3. Phylogenetic Analysis

To examine the host–parasite relationship, a host frequency analysis was determined using two methods of classifying species: (1) life history (woody or herbaceous) and (2) taxonomic levels (family, genus, and species). We recorded the percentage of the number of instances *C. filiformis* was found on each of the hosts from the total host occurrences. The lists of family, genus, and species' hosts were clustered using the R packages APE [41] and V.PhyloMaker2 [42], based on the botanical nomenclature of the World Plants (WP) Database for Pteridophytes and Gymnosperms (<https://www.worldplants.de>, accessed on 20 September 2022), the Angio-sperm Phylogeny Website (<http://www.mobot.org/MOBOT/research/Apweb/>, accessed on 20 September 2022), and the Angiosperm Phylogeny Group IV (APG IV) [43] classification for angiosperms. The percentage of different types was imported into Excel to summarize the hosts' frequency.

3. Results

3.1. Biology of Laurel Dodder and Its Hosts

Cassytha filiformis and the host seeds germinated under the soil surface without light, with *C. filiformis* producing a rudimentary primary root about 0.5 mm long (Figure 3a). This root grows for 2–4 weeks, degenerating when the embryonic axis starts to grow and three–four adventitious roots 2–6 mm long and 0.2–0.4 mm thick develop at the base of the axis (Figure 3a). This free-living phase can last up to two months (Figure 3b,c), but unless a suitable host is found during this period, the seedling dies (Figure 3c).



Figure 3. Images of *Cassytha filiformis* growth and parasitic processes on host species in laboratory conditions. (a) Germinated seed with a rudimentary and short-lived root. (b) Independent growth stage of seedlings. (c) The dead *C. filiformis* seedlings unsuccessfully parasitized a viable host; the red arrow indicates the dead stem of *C. filiformis*. (d) The survived *Cassytha filiformis* seedlings successfully parasitized the viable host *Mikania micrantha* with the haustoria. (e–h) *Cassytha filiformis*–*Cleome rutidosperma* host associations via the haustoria. The thin stem is *C. filiformis*, and the thick stem is *C. rutidosperma*. The red arrows indicate infected parts.

For the laurel dodder as well as the hosts, the percent germination exceeded 80% (Table S2). The average time to germination of *C. filiformis* was 15 days (± 10 –20 SD) and for

the host species: *M. micrantha* (3 ± 3 – 4), *B. pilosa* (5 ± 4 – 6), *C. odorata* (5 ± 4 – 6), *C. rutidosperma* (7 ± 6 – 8), *S. dulcis* (8 ± 7 – 9), and *D. longan* (21 ± 20 – 22). The host species belongs to the family Asteraceae germinated firstly (*M. micrantha*, three days), then *B. pilosa* and *C. odorata* (five days), followed by *C. rutidosperma* (Cleomaceae, seven days), *S. dulcis* (Scrophulariaceae, eight days), and *D. longan* (Sapindaceae, three weeks). It took eight weeks for parasitism to occur following germination of the host liana species *M. micrantha* (Figure 3d). Then, the same *C. filiformis* vine that was attacking *M. micrantha* (Asteraceae) was also connecting to herb species *C. rutidosperma* (Cleomaceae) a month later (Figure 3e–h). When the *C. rutidosperma* (Cleomaceae) plant died, some parts of the host in contact with the haustoria survived for a further two months (Figure 3f–h), apparently deriving water and nutrients from the parasite and even producing new shoots (Figure 3h). The signal transduction mechanism for infection is unclear yet. Except tree species *D. longan* (Sapindaceae), the other host species were all successfully parasitized. Under the controlled conditions, it seemed easier to infect herbs than woody plants.

Flowering and fruiting in wild Chinese *C. filiformis* occur from May to December, with considerable overlap (Figure 1a,c). The inflorescence is arranged into a spicate, capitate, or racemose (Figure 1a,b), and the ripe fruit is a drupe with a white translucent, fleshy pericarp (Figure 1d). The cultivated *C. filiformis* plants did not flower under the laboratory conditions used here, but this may be because at least several Australian *Cassytha* species take >5 years to flower from seed in the wild (J.G. Conran, pers. obs.).

3.2. Host Range of *C. filiformis*

After three years of field investigation, we found *C. filiformis* preferred to grow on trees and shrubs in well-lit, open, well-watered habitats, especially along roadsides. Based on our surveys and the published literature [37,44,45], we found that *C. filiformis* produced well-formed haustoria onto diverse vascular plants, including angiosperms, conifers, and ferns (Figures 4 and 5; Table S1). The overall host range of Chinese *C. filiformis* included 184 species, which belonged to 146 genera, 67 families, and 32 orders (Table S1). In total, 80.80% of the host species in this study, defined by the presence of haustoria, were woody taxa, including trees (82/184, 44.57%), shrubs (58/184, 31.52%), and occasionally lianas (9/184, 4.91%), but herbaceous plants were also affected (35/184, 19.20%) (Figure S2). The most common hosts at order-, family-, genus-, and species levels are summarized in Table S1. Nine preferred orders had hosts with more than ten species (Asterales, Ericales, Fabales, Gentianales, Laurales, Malpighiales, Myrtales, Rosales, and Sapindales. All contain 30 families, 96 genera, and 126 species; Figure 5; Table S1 noted with different colors). To our knowledge, there is currently no comprehensive survey of the host range of laurel dodder for such a broad geographic range of China.

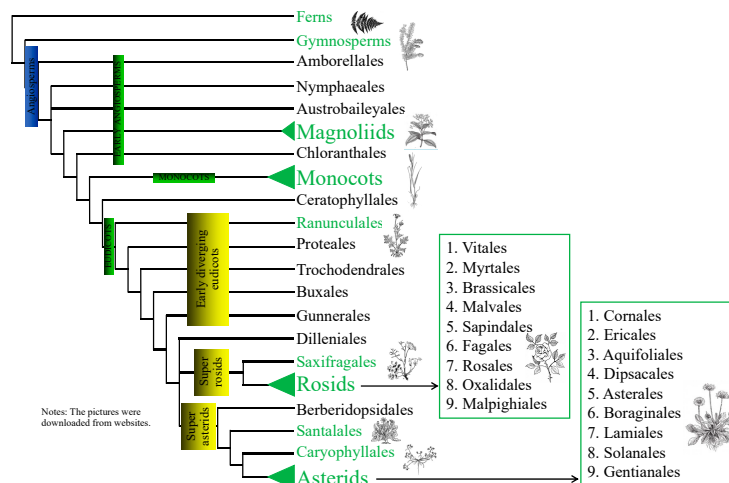


Figure 4. A simplified phylogenetic tree showing major orders that include *Cassytha filiformis* hosts. The green labels indicate the host positions among the vascular phylogenetic relationships.

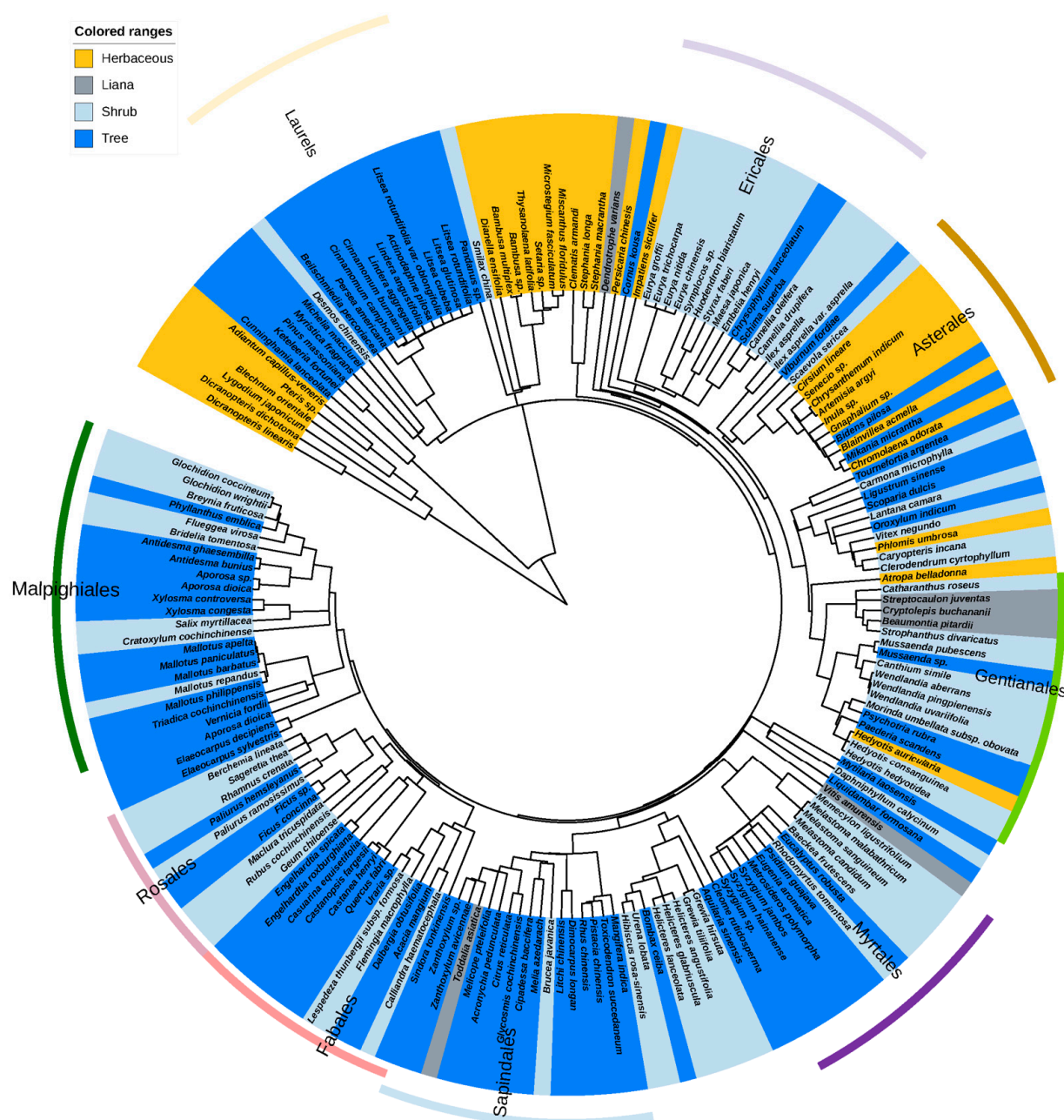


Figure 5. The host plants' phylogenetic tree for *Cassythia filiformis* in China. Yellow notes herbs. Grey notes lianas. Light blue notes shrubs; and darker blue notes trees. Hosts belonging to ferns, gymnosperms, and angiosperms are coded with different colors corresponding to Table S1.

The host range of *C. filiformis* spanned most of the vascular plants (Figure 4), with six ferns (*Adiantum capillus-veneris* L., *Blechnopsis orientalis* C. Presl, *Dicranopteris pedata* (Houttuyn) Nakaike, *D. linearis* (Burm.) Underw., *Lygodium japonicum* (Thunb.) Sw., and *Pteris* sp. L.) and three conifers (*Cunninghamia lanceolata* (Lamb.) Hook., *Keteleeria fortunei* (Murr.) Carr., and *Pinus massoniana* Lamb.) parasitized by *C. filiformis* (Figure 5).

In the flowering plants, rosids were common hosts, with Malpighiales containing the largest number of host species (twenty-two species), and Sapindales containing the largest number of infected genera (fifteen genera), while the asterid order Ericales had the most host families (seven) (Figures 4 and 5; Table S1). Euphorbiaceae was the largest single family with eight genera and thirteen species (Figure 5; Table S1). The order Gentianales represented the widest array of host plant growth forms, including the tree *Psychotria rubra* (Lour.) Poir., shrub *Wendlandia aberrans* Cowan, herb *Hedyotis auricularia* L., and

liana *Cryptolepis buchananii* Roem. et Schult (Figure 5). Four angiosperm families had at least 10 host species (Table S1): Rubiaceae (12), Lauraceae (11), Phyllanthaceae (11), and Asteraceae (10). These results differ from the study by Zhang et al. [6], where they reported seven families at the world level with at least 10 host species: Anacardiaceae, Asteraceae, Euphorbiaceae, Fabaceae, Myrtaceae, Phyllanthaceae, and Rubiaceae. This confirms that *C. filiformis* is a generalist hemiparasite that is associated with many host species. These species are relatively common (Figures 4 and 5), with no obvious evolutionary relationships, as observed by Zhang et al. [6].

4. Discussion

4.1. Laurel Dodder Prefers Woody Hosts

Eighty-one percent of the hosts noted in this study were woody (Figures 5 and S2), but numerous herbaceous plants were also affected, agreeing with the conclusions of previous studies such as those by Zhang et al. [6] and Parra-Tabla et al. [44]. However, the percentage of host life form preferences varies considerably between countries, with trees most widely affected in Tanzania (69.7%), China (44.6%), India (36.1%), and down to Japan (19.2%). Shrub hosts percentages were similar for China (36.9%) and India (36.1%), but lower for Japan and Tanzania (both ca. 20%) (Table 1). In contrast, herbaceous host ratios for the Japanese Ryukyu Islands were much higher than these other three reported regions (46.2%).

Table 1. Host plants' life forms for *Cassytha filiformis* infestation in four countries.

Country	Herb	Shrub	Tree	Liana	Study
China	15.51%	36.90%	44.39%	3.20%	[37,46]; Present study
India	13.89%	36.11%	36.11%	13.89%	
Japan	46.15%	19.23%	19.23%	15.39%	[48]
Tanzania	0.09%	21.21%	69.70%	/	[45]

In addition to *C. filiformis*, the Australian species *C. melantha* and *C. pubescens* also seem to prefer woody hosts [46–48] and this preference for woody hosts may accord with the perennial life form and hemiparasitic nature of *Cassytha*. However, the networks created by a parasitic plant attached simultaneously to multiple hosts may trigger transferring systemic signals between the hosts [26]. Herbaceous species might also act as bridging hosts to allow *Cassytha* seedlings to survive long enough to grow onto nearby shrubs or trees [6]. It may also reflect the speciose nature of many woody host families, combined with the problem that as many herbaceous plants are annuals this could be problematic for their use by perennial *Cassytha* species [6]. The reasons why *Cassytha* seem to prefer certain plant families as hosts are unclear, though there is some evidence from Australia of a preference for nitrogen-fixing taxa [33,49]. However, the factors that might contribute to host susceptibility are currently unknown.

Although unrelated, *Cuscuta* and *Cassytha* are morphologically similar rootless stem parasites that spread by developing haustoria along their stems. Similarly, *Cuscuta* different species can vary in host specificity from a single species to hundreds of taxa covering diverse genera and families [35], with 237 species, 120 genera, and 32 families reported as hosts in one study [49]. *Cassytha* and *Cuscuta* mainly occupy different habitats and have different ecologies, which may indicate that the hemiparasitic *Cassytha* represent a less specialized parasite than the holoparasitic *Cuscuta*. It is not known what factors might contribute to the susceptibility of various hosts in *Cassytha* [50], and the location of hosts in *Cuscuta* occurs by a range of methods, including host chemistry [51,52]. Host choice in these two genera may also be influenced in part by the availability suitable host-derived resources, based on the degree to which the parasites can function independently [6,53]. Long-term host range divergence also helps to drive speciation in these two parasitic genera, but further study is needed.

4.2. The Host Phylogenetic Relationships of Laurel Dodder and Its Potential Application

The mechanisms by which *C. filiformis* selects the suitable hosts are complex. *C. filiformis* parasitizes plants throughout the vascular plant phylogeny. Vascular plants play a major role in global carbon cycling and are of fundamental importance to life on earth. Phylogenetic studies have led to tremendous progress in our understanding of the origin, phylogeny, and evolution of the plants [54]. The wide variability of the host cannot predict hemiparasite performance as the host species is scattered on vascular plant phylogenetic clades (Figure 4). Asterids (more than 80,000 species) and rosids (70,000 species) comprise more than half of the hosts (Figures 4 and 5), as they are the two largest core eudicot clades (>50% of the total angiosperm species diversity) [55,56]. Some hosts' clades do not comprise as many species as the above two clades, such as the ferns (about 10,500 to 15,000), gymnosperms (only 900 living species), and some angiosperm orders (Ranunculales, Saxifragales, and Santalales have about 2000 species, respectively) [43,56–58]. We found these host species have wide ranges and high population densities. So, the parasitism of the hosts seems likely related to the species' richness and distributions. That is different from Parra-Tabla et al. who studied the host of *C. filiformis* distributed in the coastal dunes of Yucatan. They claimed the frequency of parasitized plants by *C. filiformis* was not dependent on host plant abundance [44].

Parasitic plants have been documented repeatedly to play the role of keystone species in the ecosystems [59]. Many parasitic plants also parasitize multiple hosts simultaneously; thus, they may serve as a common network connecting multiple individuals in a plant community [26]. Harmful effects on community dominants, including invasive species, may facilitate species coexistence and thus increase biodiversity [27]. In our experiment, we found *C. filiformis* may act as a trigger transferring systemic signal to connect *M. micrantha* (Asteraceae) and *C. rutidosperma* (Cleomaceae) (Figure 3). Haustorial connections very likely allow the flow or even exchange of various molecules between *C. filiformis* and hosts, and it has been long known that viruses [60] and phytoplasmas [61] can be transmitted between *Cuscuta* and its hosts. The study on *Cassytha* has been relatively neglected, leading to it being less well-characterized compared to its companion *Cuscuta* [62]. We would like to take this opportunity to encourage researchers to explore the detailed relations of *C. filiformis*–host associations because understanding the host associations will likely provide an insight into the transition between laurel dodder and their host plants.

5. Conclusions

This study investigated the host range of *C. filiformis* over major areas of its geographic range in China and reported observations of the germination and parasitism of the selected host species. *Cassytha filiformis* was found to attach to many different host species, displaying complex parasite–host interactions. The results confirm that *C. filiformis* grows mainly on diverse woody species with divergent phylogenetic relationships. However, evidence for more complex parasite–host species interactions is unclear, and the physiological basis for these associations requires further study.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15040492/s1>, Figure S1. The collection geographical range of *Cassytha filiformis* and its hosts in China; Figure S2. The percentage of different host life forms parasitized by *Cassytha filiformis* in China; Table S1. A summary of the hosts of *Cassytha filiformis*; Table S2. The hosts' germination rates and parasitizing situation by laurel dodder.

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