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# Parasitic Plants

*Edited by Ana Maria Gonzalez*
*and Héctor Arnaldo Sato*

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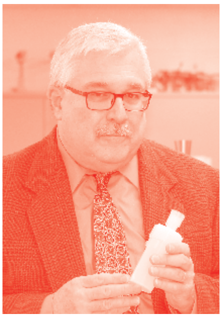

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Contributors
Pervin Erdoğan, Odoligie Imarhiagbe, Khadijeh Ahmadi, Heshmat Omidi, Majid Amini Dehaghi, Basanta Kumar Borah, Anupam Gogoi, Namrata Baruah, Mandeep Paudel, Geetanjali Baruah, Ruby Gupta, Ana Maria Gonzalez, Héctor Arnaldo Sato, Rozafa Fetahaj, Besarta Kabashi, Arben Mehmeti

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# Meet the editors

Ana Maria Gonzalez is the director of the Northeast Botanical Institute, where she is a National Scientific and Technical Research Council (CONICET) researcher. She is also in charge of the Institute's Plant Anatomy Laboratory. Her teaching career includes being a Professor of Vascular Plant Morphology, Faculty of Agriculture, Universidad Nacional del Nordeste, Corrientes, Argentina, and Professor of Biology, Universidad Nacional del Chaco Austral, Saenz Peña, Chaco, Argentina. She is a postgraduate lecturer in master's and doctoral courses in the Faculty of Agricultural Sciences, where she teaches numerous courses on anatomy, histological techniques, and bioimaging. Dr. Gonzalez has published 80 articles and more than 160 abstracts presented at national and international congresses.

Héctor Arnaldo Sato is an agricultural engineer with a Ph.D. from the Universidad Nacional del Nordeste, Argentina. His postdoctoral fellowship was based on the reproductive biology of two holoparasitic plants. He is currently Associate Professor of General Botany and Director of the JUA Herbarium, Faculty of Agricultural Sciences, National University Jujuy, Argentina. He is the author of 11 papers published in peer-reviewed journals and 39 abstracts presented at congresses. His research work focuses on the reproductive anatomy and taxonomy of parasitic plants. Dr. Sato is also the director of a research project on the reproduction of holoparasitic plants.

# Contents

# Preface

Most vascular plants are autotrophic, producing their food through photosynthesis. However, a significant number of plants have adopted a heterotrophic mode of life, obtaining part, or all of their requirements from other organisms. This group of heterotrophic plants includes **parasitic plants**, which grow on other plants and establish an organic union or haustorium through which they obtain food directly from the host. Parasitic plants can be broadly categorized into two groups based on their modes of nutrition: **hemiparasites and holoparasites**. The former possess chlorophyll and are capable of photosynthesis (at least during some phase of their cycle) and they obtain only water and mineral salts through haustoria with the host. The most extreme manifestation of parasitism occurs in holoparasites, which are totally achlorophyllous, obtaining all their nutrients from the host, on which they are totally dependent. Most holoparasites are found parasitizing the roots of their hosts.

Parasitic plants are among the most problematic pests of agricultural crops worldwide. About 4000 parasitic plants exploit another plant vascular system to fulfill their nutrient requirements. In his chapter, "*Parasitic Plants in Agriculture and Management*," Pervin Erdogan reviews these fascinating plants. Parasitic weeds are difficult to control because there are few resources for crop resistance and it is difficult to apply sufficiently selective control methods to kill weeds without physically and biochemically damaging the crop to which they are attached. The author specifically introduces plants such as mistletoe (*Viscum album* L.), *Cuscuta* spp., *Orobanche* spp., and the witchweeds (*Striga* spp.), providing information on their management and control.

"*Parasitic Plants as Vectors for Pathogens*" by Anupam Gogoi et al. discusses the various modes of parasitism and the nutrition of parasitic plants. In addition, the authors describe the mechanism of transmission of various pathogens by parasitic plants (including viruses, phytoplasmas, and proteobacteria) in host plants by *Cuscuta* species.

As mentioned, some of the representatives of these specialized plants represent great losses for agriculture, while others are threatened for various reasons, in addition to having uses and applications for humans. "*Aspects of the Biology and Ethnobotany of Parasitic Angiosperm Species in Nigeria*" by Odoligie Imarhiagbe examines the Nigerian environment, which has heterogeneous vegetation, traversing mangroves, rainforest, and savannah vegetation. It is home to host parasitic plant species, including endemic, native, and exotic species. This chapter gathers and synthesizes available information regarding parasitic plants in Nigeria, particularly their biology and the host species supporting their population.

In "*Anatomy, Embryology and Life Cycle of* Lophophytum*, a Root-Holoparasitic Plant,*" Sato and Gonzalez summarize the entire knowledge of the genus *Lophophytum*, focusing on its life cycle and the anatomy and histology of two species: *L. leandri* and *L. mirabile.* Among the topics discussed are morphology and anatomy of the vegetative body, including the host/parasite interphase; structure, anatomy, and ontogeny of unisexual flowers; description of embryological processes, from gamete formation; morphology and anatomy of fruit and seed; taxonomic value of floral characteristics; observations on dissemination, germination, and the establishment of the parasitic relationship with the host; the evolutionary trend in the gynoecium and embryo sac of the Balanophoraceae; and synchronization of parasite and host life cycles.

Alfalfa (*Medicago sativa* L.) is recognized as one of the most important forage crops in the world. In "*Parasitic Plants in Forage Legumes –* Medicago sativa *L.,*" Rozafa Fetahaj et al. present the problem of parasitic plants for this plant species. Weeds, as the most problematic pests in agriculture, compete with crops for water, nutrients, light, and space, constituting a threat to food production. Weed species such as *Cuscuta* spp. are especially noxious as they also directly extract valuable water and nutrients from the host plant, and in some cases can also be difficult to eradicate.

Finally, in "*A Review on the Botanical, Phytochemical and Pharmacological Characteristics of* Cuscuta *Spp.*," Khadijeh Ahmadi et al. presents a review of the botanical, phytochemical, and pharmacological characteristics for the holoparasite *Cuscuta* spp. in which he mainly states that the active compounds of *Cuscuta* spp. include flavonoids, lignans, quinic acid, and polysaccharides. Pharmacological studies and traditional uses of these plants have proved that they are effective antibacterial, antioxidant, antiosteoporotic, hepatoprotective, anti-inflammatory, antitumor, antipyretic, antihypertensive, analgesic, anti-hair fall, and antistereogenic agents.

**Ana Maria Gonzalez**
Instituto de Botánica del Nordeste (CONICET) -
Universidad Nacional del Nordeste,
Corrientes, Argentina

**Héctor Arnaldo Sato**
Cátedra de Botánica general - Herbario JUA -
Facultad de ciencias Agrarias UNJu,
Jujuy, Argentina

Chapter 1

# Parasitic Plants in Agriculture and Management

*Pervin Erdogan*

## Abstract

Parasitic plants are among the most problematic pests of agricultural crops worldwide. They are found worldwide in all plant communities except aquatic. Parasitic plants are the organisms that settle in the host plant by means of the special organs they have developed and penetrate the vascular tissues of the hosts and meet their nutritional, water and mineral needs from the host plant. This particular body they have is called a haustorium. The discovery and investigation of the haustorium structures led to the evaluation of many heterotrophic plant species previously defined as parasitic plants in different groups. Host organisms are very important in completing the life cycle of parasitic plants. In general, the parasite weakens the host, so it produces fewer flowers and viable seeds or the value of the timber is reduced. However, some parasites, mostly annual root parasites belonging to the Orobanchaceae, can kill the host and cause significant economic damage while attacking monocultures in agriculture, and much effort is put into controlling these harmful parasites. Parasitic weeds are difficult to control because there are few resources for crop resistance and it is difficult to apply sufficiently selective control methods to kill weeds without physically and biochemically damaging the crop to which they are attached.

**Keywords:** Plants, Parasitic, Species, Agriculture

## 1. Introduction

Parasitic plants are among the most problematic pests of agricultural crops worldwide. About 4000 parasitic plants exploit another plant vascular system to fulfill their nutrient requirements. The majority, about 90% of these species are hemiparasites retaining photosynthetic capacity while the rest, 390 species are holoparasites with obligate dependence on the host to obtain all their nutrients [1, 2]. They are extremely morphologically diverse and range from diminutive herbaceous plants to large trees, as well as highly reduced parasites that grow embedded in their host and lack leaves and roots. Parasitic plants can be divided according to whether they are photosynthetically active (hemiparasites) or lack of photosynthetic activity, and whether they are completely attached to a host for carbon (holoparasites), whether they are optional or obligate parasites, and whether they are attached to the roots or stem of the host. In natural ecosystems, parasitic plants form a component of the plant community and contribute to the overall community balance of parasitism. Conversely, when parasitic plants are established in low biodiverse agroecosystems, their persistence causes enormous yield losses and renders agricultural land inoperable. It has been determined that many features from seed germination to haustorium formation, from feeding patterns to host selection are based on the relationships between the host and the parasite [3].

Parasitic plants change in host dependence of and the rate at which they can attach. Facultative hemiparasites complete their life cycle without the need for a host. Also, obligate parasites (can be hemi- or holoparasites) need host to survive and reproduce. Most of facultative parasites have a broad range of hosts. For example, *Rhinanthus* attach to more than fifty species of herbaceous plants and grasses. Obligate parasites (especially holoparasites) more likely to specialize in a single host plant species or a narrow host range, and host shifts can be included speciation. Parasitic plants should synchronize their life cycle with the host for maximum fitness. Tiny seeds of obligate root parasites such as *Striga* germinate only after a conditioning period at the appropriate temperature, then are exposed to host-derived chemical signals such as strigalactones that are extruded by the host's roots to signal symbiotic arbuscular mycorrhiza in the soil [4].

Holoparasities and hemiparasites develop haustoria. There are two types of houstria. Primary haustorium develops directly from the primary root apex. It is the only haustorium to function during the parasite's lifetime. When only the primary haustorium is present, the parasite is considered evolutionarily more advanced. The development of primary haustorim made holoparasitism possible because holoparasites with small seeds usually require water, and nutrients from a host immediately after germination [5].

Parasitism appeared several times independently during angiosperm evolution, and the lifestyles of parasitic plants vary widely between taxa [1]. Some species are optional parasites that can survive in the absence of a host, others are necessarily parasitic and cannot develop independently. A distinction can be made between hemiparasitic herbs containing chlorophyll and can produce some of the essential nutrients through photosynthesis, and holoparasitic plants that do not contain chlorophyll and are completely dependent on host sources, but this distinction is not always clear [6, 7]. They pose a tremendous threat to the world economy because they are virtually uncontrollable at the moment [8, 9]. They belong to a variety of plant families and are attached to host roots, shoots or branches. The mistletoes like *Viscum* and *Arceuthoubium* that parasities trees, climbers like *Cuscuta* that parasitise shoots, and parasites like Striga and *Orobanche* that connect to host roots [3].

## 1.1 Parasitic plants

Weed parasites, usually unique to the host, do their greatest damage before they emerge; therefore, most crop yield loss may occur before infection is diagnosed. Despite intense efforts in the twentieth century, effective ways to selectively control various parasitic weed species are still scary or absent. While all agricultural weeds compete with crops for the field to obtain water, nutrients and light, parasitic weeds are also particularly harmful as they extract valuable water and nutrients directly from the host plant. To extract nutrients from host plants, parasitic weeds have developed a unique multicellular structure called the haustorium that invades the host, connects with the host vascular system and draws the water and nutrients it needs [10, 11]. A successful haustorial connection to the host causes permanent damage to a large part of the crop's life cycle, lowering the harvested yield, lowering the crop value, and contaminating it with parasitic seeds. Parasitic weed infection strongly reduces crop harvest by disrupting crop orchestration of resource allocation by altering dry matter partitioning between crop organs that prioritize those adjacent to the [12].

### *1.1.1 Mistletoe*

Mistletoe (*Viscum album* L.), (Viscaceae) whose distribution areas are widening in the world, is a semi-parasitic plant that lives by sucking the sap of the host plants it lives in, thus harming its host. It has small bushes, leaves and is an evergreen plant. "Zodiac sign" and are also known by the names of "chekem". Rosaceae like apple and pear (Rosaceae) family trees semi parasitic lives on its branches. It can also be found in other trees. The plant can withstand several seasons leathery leaves, narrow and is long. The flowers, the seats of the shoots and yellowish-green is colored. The end of autumn and the beginning of winter the size of a pea. It was white and bright (**Figure 1**). Mistletoe lives as a semi-parasite on nearly 200 plant species, including fruit and forest trees and ornamental plant. This plant can cause losses in many economically important crops. Pear, plum, apricot, apple, almond, pear, walnut, chestnut is some of them. Along with these, the wood quality of trees such as willow, poplar and oak decreases [15].

The way mistletoe spreads are quite interesting, with all leaves, flowers monogamous and sticky, juicy and soft fruit. Thanks to its sticky structure, the seeds that stick to the beaks and feet of the birds or the birds that eat the fruits, especially the junipers, leave their feces on the trees they put on, and the seeds continue to grow by germinating on the tree they are transported. The germinated mistletoe seeds pierce the bark of the tree and reach their suckers down to the wood pipes and share the water and mineral substances of the host. Yield losses of up to 50 percent can be seen in sensitive fruits due to mistletoe Mistletoe provides its food by inserting its

**Figure 1.**
*a) Entry of triple suckers from* Viscum album *seed to plant tissue, b)* Viscum album *L., [13], c) swelling in the branch of the Ankara pear of* V. album*., [14], d) damage of the* V. album *damage (*trwikipedia.org*).*

suckers into the trunks and branches of fruit, park and forest trees. Swelling is seen in these parts. It weakens the host tree, decreases the yield, and sometimes causes the old trees to dry. The fruits are spherical and the abundant viscin substance in the fruit flesh provides the stickiness of the fruit and the seed [16]. The stem of the plant lives dependent on the host, if it cannot find a host, it cannot survive. Seed need to attach to the host in germination the duration is known to be 3–5 weeks. By moving the jab body end counterclockwise hugs the host he reaches. Of the held body parasitic plant from the host facing surface, it dips suckers to his host and these suckers connects with its host phloem and xylem. They typically exhibiting broad host ranges, and inflict serious damage to many crops, including forage legumes (alfalfa, clover, lespedeza), potato, carrot, sugar beets, chickpea, onion, cranberry, blueberry, and citrus [17].

### *1.1.2 Cuscuta* spp

*Cuscuta* spp. leafless, thin, threadlike wrapper has the body. The flowers are small and flower collected in cases. Petals (corolla) combined, usually five-piece rarely four or in three parts. Ovary (ovarium) two carpel and two seed pods in each compartment takes place. Fruit, capsule shaped, seed without cotyledons or in traces, embryos are in the form of threads (**Figure 2**) [17]. This plant is taxonomically the most difficult parasitic is one of the groups. *Cuscuta* breed diagnosis

***Figure 2.***
*Cuscuta* spp. *a, b,) damage of Cuscuta* spp.*, c) damage of Cuscuta* spp. *of in tomato d) damage of Cuscuta* spp. *of in potato (niscole.com; projectnoah.org; Cittaslav botanic; iriss.ca, Erdogan, P.).*

mostly is carried out according to flower and fruit characteristics. These features; stigma shapes, staminal braces shape and condition of filaments, capsules. Whether it is turned on or not depends on features such as [6]. In China, several *Cuscuta* species inflict severe damage on soybeans [18].

Seeds of *Cuscuta* spp. have been spread worldwide in contaminated shipments of crop plant seeds. *Cuscuta pentagona* is a major weed of tomatoes in California, causing yield losses of 50–75% [19]. Nemli and Ongen [20] reported that cayenne in alfalfa causes yield losses up to 91%. It was determined that *Cuscuta* species caused 60–70% decrease in the yield of alfalfa in India [21]. It has been reported that poisoning cases are encountered in animals fed with plants contaminated with coals [22]. In Turkey, species of *Cuscuta campestris* Yunck. and *Cuscuta approximata* Bab. are very common [23].

### *1.1.3 Orobanche* spp

*Orobanche* spp. and *Phelipanche* spp. the most damaging weedy root parasites belong to the Orobanchaceae. One of the most important experts in the Orobanche taxonomy, Prof. Dr. Edward S. Teryokhin divided the genus Orobanche into two important parts, *Orobanche* and *Phelipanche. Phelipanche* was first given to *P. ramosa* by Auguste Pomel (1821–1898), and with the support of increasing molecular studies in recent years, *Orobanche* genus *Orobanche* and *Phelipanche.* It was accepted to be divided into two generals and *P. ramosa* (L.) Pomel and *P. aegyptiaca* (Pers.) Pomel started to be used instead of *O. ramosa* and *O. aegyptiaca* in weed research. The broomrapes (*Orobanche* and *Phelipanche)* are widespread in Mediterranean areas in Asia Southern and Eastern Europe [3, 8].

As a full parasitic weed, *Orobanche* spp. have not green leaves, so they do not contain chlorophyll and cannot perform photosynthesis. Therefore, its life depends on the food and water it receives from the host. In order for the seeds of *Orobanche* spp., which are among the smallest seed plants in the world, to germinate, the host plant they prefer must be planted. When it is a suitable host, the beast seeds under the soil germinate and attach to the root of the host plant by forming a tube, and then it continues its life with ready-made food from the host. An *Orobanche* plant produces between 5,000 and 100,000 seeds, and these seeds can remain in the soil for more than 10 years without losing their viability. Four types of *Orobanche* cause significant damage in agriculture. These species are *O. ramosa* L. and *O. aegyptiaca* Pers. Some vegetables, mainly tobacco and tomatoes, and lentils, *O. crenata* Forsk. mainly broad beans and other legumes and *O. cernua* Loefl. causes significant damage to sunflower. It is possible to see *Orobanche* spp. in many broad-leaved cultivated plants, but it causes significant damage especially in sunflower, tobacco, tomato, eggplant, pea, lentil, broad bean, chickpea, cabbage, oilseed rape, parsley, watermelon, common vetch and carrot [6]. In cases where contamination with this weed is very heavy, yield loss in cultivated plants can reach up to 100%. *Orobanche* spp. may cause loss of yield in the host plant as well as decrease in quality as in tobacco and sunflower. The yield loss they cause in *Orobanche* spp. culture plants may vary between 5 and 100% depending on the time and density of this parasite weed to attach to the culture plant. It was revealed that *Orobanche* spp. caused 33% in tobacco, 50–100% of the bean, sunflower at 33%, 24%, carrots, and tomatoes in the United States 21% 29 and 24% in Turkey [24]. It has been established that the seeds completely lose their vitality when *Orobanche* spp. is harvested fresh. It has been reported that the vitality of the seeds decreased only by 10% within the first 5 years of storage, and this rate decreased to 50% after 9 years. It is stated that the vitality will decrease if the seeds are kept at high temperature and humidity (**Figure 3**) [26].

**Figure 3.**
*a) Cuscuta* sp. *in potato (Karahan. A.)., b, c) Cuscuta* spp. *(coms.wikipidi.org., d) eggplant in Cuscuta* sp. *[25].*

### *1.1.4* Striga spp

The witchweeds (*Striga* spp.) plants are herbaceous plants. The genus is characterized with contrasting leaves, irregular bright-colored flowers corolla, divided into a tube that spreads lobes, herbaceous habitat, small seeds and parasitism. *S. hermonthica* has shiny to dark green leaves, erect and often branched stems grow 77 cm or more. Stems are sturdy and rectangular. The leaves are linear, lanceolate or lanceolate and 1–3 inches long, with acuminate or acuminate tips, multi-shell. The inflorescences have 6–10 open flowers, 1–2 cm in diameter. The flowers are pink, red, white, purple or yellow. The spike has occasionally more than 10 open flowers and the corolla normally drops a few days after fertilization [6]. The infection caused by some hemiparasitic weeds such as *Striga* causes more crop biomass depression than the biomass accumulated by the parasite. *Striga,* like other plant herbivores and pathogens, reduces host productivity by lowering crop photosynthesis rates (press). The impact of *Striga* is complicated further by its predilection for attacking crops already under moisture and nutrient stress, the conditions that prevail throughout the semi-arid tropics [27].

**Figure 4.**
*a, b, c, d) Striga* spp. *(photo: Oisat.org.; Africanplants.sckenberg.de; researchgate; tr.Gaz.Wiki).*

In tropical Africa the most damaging parasitic weeds are *Striga* spp. obligate root parasites of grain grasses and legumes, which endanger food supply in many developing countries. The most destructive species on cereals are *S. hermonthica* and *S. asiatica*, followed by *S. aspera* and *S. forbesii*, parasitising important food crops like rice, pearl millet, sorghum and maize in much of Africa and some parts of Asia. *S. gesnerioides* is an important pest of Fabaceae, especially cowpea). Moreover, the *Striga* epidemic is going to increase and the parasite is likely going to become a more serious threat to crop production [9]. The area infested by *Striga* in sub-Saharan Africa is estimated to be more than 50 million hectares of arable farmland under grains [28]. The area infested by the parasite in West Africa is estimated to be about 17.2 million hectares, and sorghum and millet cover about 64% of the total area [29]. The parasite also causes indirect losses, including human migrations in response to changes in production strategies, land abandonment, and severe invasions in extreme cases (**Figure 4**) [30].

## 2. Management

*Viscum album* L.; the way to prevent the spread of mistletoe, which is mostly propagated by birds, is also through birds. At this point, it is very important to create alternative food sources for birds. Mechanical control is the most effective control technique. Mechanical control is done by removing the mistletoe before the seed binds and pruning the infected branches 20–30 cm below. In severe epidemics, the tree should sometimes be removed completely to prevent contamination to other trees. Kotan et al. [31] reported that five bacterial strains (two *Burkholderia cepacia,* one each of *Bacillus megaterium, Bacillus pumilus* and *Pandoraea pulminicola*) were HR and pathogenicity positive when injected but none of them when sprayed on mistletoe. When fungi were injected, 32 isolates were pathogenic but only thirteen when sprayed on mistletoe. *Alternaria alternata* VAS, -202, VAS, -205, VAS, -217 and *Acremonium kiliense* VA-11 fungal isolates were the most effective ones and caused strong disease symptoms on mistletoe (**Figure 5**).

*Orobanche* spp.; prevent contamination is the most important method to control *Orobanche* spp. Clean seeds and seedlings should be used, and firstly should be preferred certified seed. Beast agricultural tool used in the field contaminated with grass, or machines, without using in the dishwasher field make sure that it is very well cleaned first. in the fields contaminated with monster weeds long-term with non-host cultivars alternation should be made. Seen in fields or greenhouses before the beast weeds bloom, pull them separately by hand It must be burned somewhere or buried very deep. Especially resistant in sunflower cultivation attention should be paid to the use of varieties. In the control against monster weeds solarization is a highly effective method especially in greenhouse plants cultivation solarization should be carried out. *Linum usitatissimum* L. (Lineaceae) is used as a trap plant to control *Orobanche* spp. [24].

*Cuscuta* spp.; control dodder is also particularly effective in preventing spreading. Emphasis on measures and methods of cultural practice should be given. Plants that are found to be dull by visiting the areas contaminated with dodder should be cut in a way that does not leave any residue behind and destroyed immediately. In the vineyards, in the spring at the beginning of May, in order to prevent the germination of the seeds that have fallen to the soil or clinging to the grape branches before the grape leaves take off, they should first pour straw 5–10 cm thick, wider than the crown width, under the vines that are found to be dull, and the straw should be burned after the sprouts are formed and wrapped in straw. Sticks should not be taken from dish washed ties and vines for the purpose of production and should avoid contamination of uncontaminated areas with this path and other

**Figure 5.**
*Infected mistletoe plant samples used for isolating of bacteria and fungi [31].*

forms. Similarly, dodder is an important factor in clover. If alfalfa is to be grown, control should be a problem. Clean and certified seeds should be used the weeds in which there is dodder in the area around the clover field are removed and should be burned [32].

*Striga* spp.; Oswald [33] reported that planting nonhost trap crops that induce suicidal germination is perhaps the most effective strategy currently available for *Striga* control. Recent researchers in this field focused on identifying and assessing the effectiveness of potential trap crops [34, 35]. Botanga et al. [36] revealed that the possibility of breeding for increased Parasitic Plants in Agriculture 131 production of germination stimulants.

The use of nitrogen-binding legumes as trap crops has the advantage of increasing soil fertility, which can further assist in *Striga* spp. control because *Striga* spp. thrives in poor soils [6]. Legumes have also proven useful as part of a novel "push-pull" (stimulodeterrent) pest management approach that illustrates the utility of increased plant diversity, simultaneously reducing *Striga* spp. and lepidopteran stemborer infestations [37].

## 3. Conclusions

Parasitic plants are the biggest threats to important crops and can cause crop losses until complete failure of crop productivity. Integrated pest management systems seem to be the best solution to find effective, long-lasting, widely applicable and environmentally friendly methods for parasitic weed control. Considering the life cycle of parasitic weeds, prevention of seed germination and/or host binding would be ideal targets for the successful management of parasites. Recently, some fungal metabolites are in *Striga* spp. and for the first time in *Orobanche* spp. This strategy can be an alternative means of bio-control of parasitic plants and reduce the likelihood of host contact disrupting the fine-tuned process of host recognition.

## Conflict of interest

The authors declare no conflict of interest.

## Author details

Pervin Erdogan
Faculty of Agricultural Sciences and Technology, Sivas University of Science and Technology, Sivas, Turkey

*Address all correspondence to: pervinerdogan@sivas.edu.tr

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## Chapter 2

# Parasitic Plants as Vectors for Pathogens

*Anupam Gogoi, Namrata Baruah, Mandeep Poudel,*
*Ruby Gupta, Geetanjali Baruah and Basanta Kumar Borah*

## Abstract

Parasitic plants obtain their nutrition from their hosts. In addition to this direct damage, they cause indirect damage to their hosts by transmitting various plant pathogens. There are some 4,500 species of parasitic plants known; out of them, nearly 60% are root parasites and the rest of them parasitise on the shoot parts. *Orobanchaceae* and *Convolvulaceae* are the two mostly studied families of parasitic plants; and the parasitic plants are the chief mode for transmission of the phytoplasmas. The parasitic plants have various modes of obtaining nutrition; however, the information about the mechanism(s) involved in the pathogen transmission by the parasitic plants is limited. The latest biotechnolgical advances, such as metagenomics and high througput sequencing, carry immense promise in understanding the host-parasitic plant-pathogen association in deeper details; and initiatives have indeed been taken. Nevertheless, compared to the other pests hindering crop productivity, parasitic plants have not yet been able to gain the needed attention of the plant scientists. In this chapter, we review and present some of the latest advances in the area of these important plant pests.

**Keywords:** parasitic plants, pathogen, parasitisim, transmission

## 1. Introduction

Parasitic plants, like microbes or pathogens, exploit other host plants for water and nutrients. They display a wide range of parasitic lifestyles, from obligate holoparasitism to facultative hemiparasitism [1]. Parasitic flowering plants comprise of 4,500 species distributed in 280 genera in more than 20 plant families and represent roughly 1% of all angiosperm species [1, 2]. Out of total parasitic plants, 60% are root parasites, and the remaining 40% of the parasitic plants are stem parasites [2]. Several well-known and agriculturally important parasitic plant species belong to the families of *Orobanchaceae* and *Convolvulaceae*. Members of *Orobanchaceae* are root parasites, which includes the genera, *Striga* (witchweeds), *Orobanche* (broomrapes) and *Alectra*. Plant species in these genera can cause significant constraints to crop yield and productivity [3]. Species of *Striga* and *Alectra* pose a serious threat to cereal production in sub-Saharan Africa, India, and Southeast Asia. These includes tropical cereals such as corn (*Zea mays*), sorghum (*Sorghum bicolor*), rice (*Oryza sativa*), and millets, as well as sugarcane (*Saccharum officinarum*) [4]. The related species *Phelipanche* and *Orobanche* are destructive plant parasites for broad-leaved crops grown in North Africa, Europe, the Mediterranean and the Middle East [5].

Besides *Orobanchaceae*, the genera, *Cuscuta* (also known as dodder), from the family, *Convolvulaceae*, are known productivity constraints distributed worldwide. The most agronomically important species of *Cuscuta* are *C. pentagona* and *C. campestris* that attack a broad range of host plants, including vegetables, fruits, ornamentals and woody plants [6].

Like fungi and oomycetes, parasitic plants develop specialised feeding structures called haustoria that establish intimate connections with host cells. A haustorium penetrates the vascular tissue of the host plant, forming a bridge between the parasitic plant and its host. The physiological conduit helps in redirecting resources from the host plant into the parasite [5]. These include movement of water, carbohydrates, nutrients, small molecules (e.g., RNA and proteins) and microbes [7–10]. Recent evidence suggested that the movement of biomolecules is bidirectional, which means exchange may occur from the host plant to the parasite and vice versa [11, 12]. Parasitic plants are reservoirs of various microbial groups belonging to bacteria, fungi, viruses and phytoplasmas [9, 13–15]. They can transmit many economically important plant viruses from infected hosts to healthy host plants. Several dodder plants, particularly, *C. campestris* and *C. subinclusa*, are common species that can transmit a range of plant viruses [16]. Besides dodder, *Phelipanche aegyptiaca* (broomrape) has been shown to acquire both RNA and DNA viruses from infected hosts that represent four distinct genera *Cucumovirus*, *Tobamovirus*, *Potyvirus*, and *Begomovirus* [8]. Parasitic plants can also transmit phytoplasmas, which are phloem-limited pleomorphic bacteria that lack a cell wall. Phytoplasma diseases lead to severe yield losses in vegetables, fruit crops, cereals, oilseeds, and woody and ornamental plants [17, 18]. This chapter provides deep insights into the role of parasitic plants in pathogen transmission, their microbiota composition and diversity. In addition, various ecological lifestyles, and management practices of parasitic plants for sustainable crop production is addressed.

## 2. Various modes of parasitism and nutrition of parasitic plants

Plant parasitism is a fascinating plant–plant interaction with the acquisition of at least some essential resources from the host plant. Parasitism exerts a strong impact on host growth, allometry, physiology, and reproduction [19]. Parasitic plants can be broadly categorised into two groups based on their modes of nutrition: hemiparasites and holoparasites. The majority of the parasitic plants are hemiparasites, ca. 4100 species [20], which meet most of their photosynthetic assimilates using own photosynthetic machinery and the nutrients and water from their hosts. Three hundred ninety parasitic plant species are holoparasites that lack chlorophyll and, therefore, photosynthetically inept. They rely entirely on their host plants for nutrients and water [20]. Both groups of parasites either connect to the host shoot (shoot parasites, or stem parasites, or aerial parasites) or to the root system of the host (root parasites). Majority of the parasitic angiosperm are root parasites (approximately 60%), while the rest are stem parasite [21], except the genus *Tripodanthus*, which infects both roots and the stem of the host plant [22].

Hemiparasites are predominantly xylem-feeders absorbing water and mineral nutrients from host plants. To ensure rapid intake of xylem solutes, hemiparasites undergo rapid transpiration to import hosts' nutrients via the transpiration stream [23]. In some cases, flux of organic carbon flow from host plant to the hemiparasite in the form of xylem-mobile organic elements [24]. Hemiparasites can be further classified into two types based on their degree of dependency upon the host plant: facultative and obligate. Facultative hemiparasites can survive without a host and do not strictly require a host plant to complete their life cycle. Most studied root hemiparasites are facultative in nature [20]. This includes parasitic plants from the families, *Krameriaceae*, *Olacaceae*, *Opiliaceae*, *Santalaceae* and *Scrophulariaceae* [25]. A facultative hemiparasite may live independent of the host, although suffer reduction in growth and fecundity [26]. In most cases, plant size and reproductive performances are compromised [27]. However, these parasites opportunistically parasitise the available neighbouring plants and exhibit optimum growth. For example, a root hemiparasite, *Pedicularis cephalantha* showed improved performance in the presence of a suitable host, *P. monspeliensis,* where the host was observed to be essential for proper development rather than survival [26]. Likewise, host-attached *Rhinanthus minor*, a xylem-tapping facultative root hemiparasite, showed substantially better growth performance compared to the host-unattached parasite [28].

On the other hand, obligate hemiparasites need host plants for completion of their life cycles as these depend mainly on their hosts for essential resources. This includes stem parasites belonging to the families, *Loranthaceae*, *Lauraceae*, *Misodendraceae* as well as some members of *Convolvulaceae*, *Santalaceae*, *Scrophulariaceae*, and *Viscaceae* [25]. Obligate parasites require stimulus from the host, specifically xenognosins, to germinate [1, 24, 29]. For example, germination in dust seeded *Orobanchaceae* such as *Alectra* (yellow witchweed) and *Striga* (witchweed) species is induced by a plant hormone strigolactones [1, 30]. Moreover, some host plants promote a lower rate of parasite germination due to reduced production of germination signals. For instance, the germination of *Striga* seeds in response to the root exudates of *Tripsacum dactyloides*, a wild maize, was significantly lower (ca. 38%) than *Z. mays* root exudates [31]. Holoparasites are achlorophyllous and thus are obligate in nature. The majority of the holoparasites are root parasites, while some species of *Cuscuta* (e.g., *C. europaea*) are stem parasites [32]. Unlike hemiparasites, most of the holoparasites spend much of their lives underground and tend to have a lower transpiration rate [33]. They are predominantly phloem feeder and retain soluble carbon, mineral nutrient, and water from the host [34]. Besides macromolecules, RNA-sequencing and proteomic analysis indicated that holoparasite such as *Cuscuta* species (family, *Convolvulaceae*) could perform bidirectional trafficking of phloem-mobile mRNA [35] and proteins [36] between widely divergent species and regulate host gene expression [12]. As the phloem is living tissue, for parasitism, the parasite thus obliges to have biochemical compatibility with its host [37]. Consequently, phloem-feeding holoparasites have complex haustorial structures and are more host-specific than hemiparasites [27, 38]. Apart from their complex haustoria and host preference, phloem-feeding holoparasites have a distinctly lower Ca:K (Calcium:Potasium) ratio because calcium is usually present in very low concentrations in the phloem than in xylem fluid [39]. Phloem-feeding holoparasites also retain features of their xylem-feeding ancestry. However, the xylem bridge form between parasites and their host plants is functionally inactive [40]. On the other hand, some holoparasites show a xylem-only feeding strategy, such as the genera *Lathraea* and *Boschniakia* that acquire host nutrients exclusively through xylem [41]. It shows that all parasites have the universal ability to acquire resources from the host xylem.

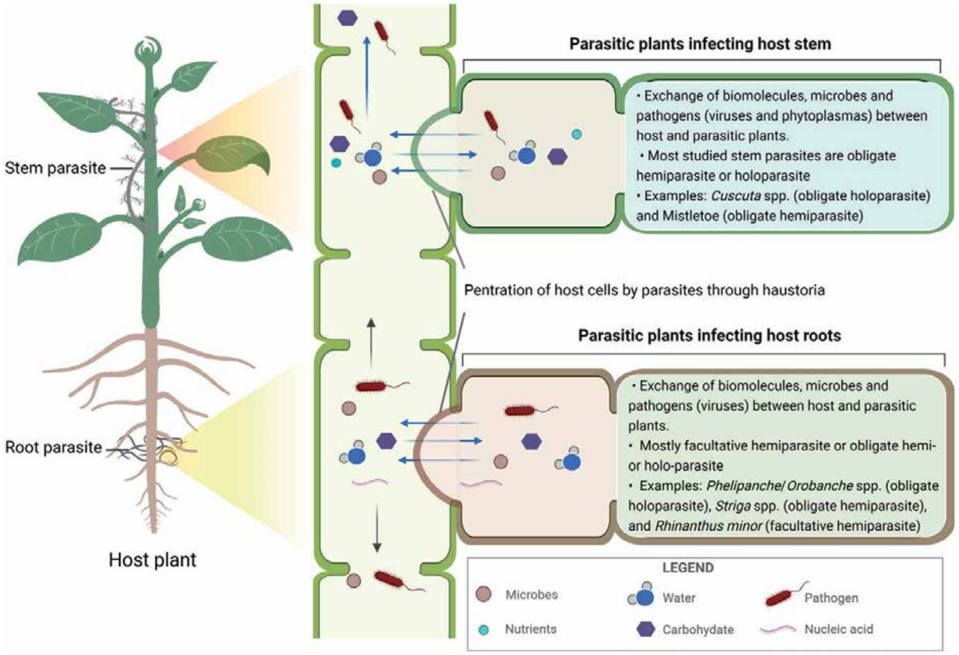
Parasitic plants have a broad host range and attack several co-occurring species, often simultaneously. Host range of parasitic plants is a function of the parasites' feeding mechanisms (xylem- or phloem-feeder), distinct events of the evolutionary history of the species, and the biochemical compatibility with the host cells [40]. However, host specificity is largely determined by the extent of reliance on the host plant and depends on the ability of the haustoria to functionally establish after invading the host. The most common potential hosts are from *Asteraceae*, *Cyperaceae*, *Fabaceae*, *Labiatae*, *Poaceae* and *Rosaceae* families [42, 43]. In general, facultative parasites, specially root hemiparasites, have a broad host range, whereas obligate/shoot parasites tend to be more host-specific [44]. Conversely, holoparasites have a narrow host range compared to hemiparasites due to their greater reliance on host plants. In plant parasitism, host specificity is an exception rather than a rule. A notable exception is a root-parasite *Epifagus virginiana* (beech-drops) which strictly parasitise *Fagus grandifolia* (American beech) [23]. Among shoot parasites, host specificity is particularly seen in mistletoes, for e.g., *Arceuthobium minutissimum* (Himalayan dwarf mistletoe), which only parasitises *Pinus griffithii* (Himalayan blue pine) and *Phoradendrons cabberimum* (Mexican mistletoe) that grow only on other mistletoes [21, 23]. Some species within a genus are found to be in the range of generalist to specialist. For example, among 45 species of the genus, *Arceuthobium* (family: *Viscaceae*), *A. apachecum* parasitise a single host (*Pinus strobiformis*), whereas another parasite, *A. globosum* spp. *Grandicaule*, parasitise 12 different host species [44]. Likewise, tropical rainforest mistletoe *Dendrophthoe falcata* (family: *Loranthaceae*) is known to have at least 343 different host species [20]. Despite their wide host range, parasitic plants prefer host that has readily accessible vascular systems, high nitrogen content (e.g., legumes), lower defence mechanisms and host that provide resources for a longer period (e.g., deep-rooted woody perennials) [19].

## 3. Transmission of various pathogens by parasitic plants

Plant virus and phytoplasma diseases are major threats to modern agriculture and their management can be quite challenging. Different strategies have been developed to reduce the transmission of these pathogens. It is crucial to understand the various sources of contamination or inoculum during cultural practices to restrict the entry and thereby transmission of viruses in fields [45].

For the parasitic infection to initiate, it is important to understand the aetiology behind the transmission process. For infection in the above ground parts of the host, for instances, *Cuscuta* or *Viscum* species, it is mostly coincidental and occurs mainly through dissemination of seeds by wind, rain, or biotic causes [46]. Conversely, the process of infection is different for obligate root parasites, which depends on factors like presence of stimulants, grouped under strigolactones exuding from the host root surfaces instigating the germination of parasitic seeds. The seeds of obligate parasites like *Orobanche, Phelipanche* and *Striga* are also known to lay dormant without the presence of appropriate hosts in soil for years, whereas for some others, germination without a host eventually leads to their death [5]. Upon germination, the radicle tends to sense the host roots in lieu of chemotaxis such as in *Striga* [47, 48]. An example is shown by a time-lapse video of *S. hermonthica* radicle bending towards the host root while it elongates [49]. However, a chemotrophic growth may not be always true in case of some root parasites such as *Orobanche*, where the growth of parasite root towards host occurs without any known factors and only by chance, provided the process of germination take place in close contact to the host plants. One of the essential steps of host-parasitic infection involves the localisation of the hosts, after which their attachment involving the formation of haustoria plays a crucial role in dissemination of viruses and phytoplasma from the infected host to the parasite and thereby initiating the transmission of plant viruses.

The connection between host and the parasite is established with the development of 'prehaustoria' starting from the differentiation of a secondary meristematic tissue from epidermal and parenchymatous tissues of the parasite. Substances, such as pectins, facilitate the adherence and polysaccharides exuded by the prehaustoria and drives the host to produce factors for attachment and penetration [46, 50, 51].



- Exchange of biomolecules, microbes and pathogens (viruses and phytoplasmas) between host and parasitic plants.
- Most studied stem parasites are obligate hemiparasite or holoparasite
- Examples: *Cuscuta* spp. (obligate holoparasite) and Mistletoe (obligate hemiparasite)

- Exchange of biomolecules, microbes and pathogens (viruses) between host and parasitic plants.
- Mostly facultative hemiparasite or obligate hemi- or holo-parasite
- Examples: *Phelipanche/ Orobanche* spp. (obligate holoparasite), *Striga* spp. (obligate hemiparasite), and *Rhinanthus minor* (facultative hemiparasite)

**Figure 1.**
*Schematic representation of parasitic plant-host interaction and pathogen transmission. Bidirectional movement of biomolecules such as water, carbohydrate (e.g., sucrose), nutrients (e.g., phosphorus and nitrogen) and nucleic acids (mRNAs and small RNAs), as well as microbes, may occur through physiological conduit form by the haustorium of the parasite with the conductive tissues (xylem and phloem) of the host plant. Many plant viruses and phytoplasmas are acquired and transmitted by parasitic plants from an infected host to healthy host plants. The figure was created using bioRender.com*

After the process of penetration through a fissure in the host stem, the haustoria invades the epidermal and hypodermal tissue to develop inside the vascular bundle [46]. While growing towards the xylem and the phloem tissues, they develop hyphal structures, similar to finger-like projections, also known as 'absorbing hyphae', which behaves like sieve element or transfer conduits for flow of nutrients between parasite and host [5, 38, 52, 53]. These multicellular haustoria functions with the aid of chemicals, also known as haustoria-inducing factors and some tactile cues [54]. In such an interaction, it has been shown that in transgenic tobacco plants parasitised by *Cuscuta*, there has been wide exchange of molecules through the phloem of tobacco plants until the developing leaf primordia [53]. During such passage of resources between the parasites and the hosts, several fluids including proteins and phloem-mobile RNAs are exchanged, which contributes in transmission of virus and phytoplasmas from infected hosts to healthy plants [11, 35]. A detail schematic representation of host-parasitic plant interactions and exchange of biomolecules, microbes and pathogens between host plant and the parasite is shown in **Figure 1**. The reports from various translocation experiments, specially one using *Cuscuta* bridge between with carbon labelled compounds and *Potato Virus Y* in Pelargonium showed symplastic exchange of solutes between the parasitic species and their corresponding hosts [55].

### 3.1 Transmission of viruses, phytoplasmas and proteobacteria in host plants by dodder

Majority of agriculturally important plant viruses and phytoplasmas are dodder transmissible and among which *Cuscuta* species, *C. campestris* and *C. subinclusa*, are the most common. This is because the *Cuscuta* absorption system for host fluids is directional and has proven to be very effective and has shown rigorous sinking of resources during the host fruit development [46]. Some researchers in their studies with beet curly top virus and cucumber mosaic virus have shown that dodder assimilates virus particles along with nutrients from the host phloem and accumulate in the haustorium of the parasite [56]. While some phytoplasma like Aster yellows move from the phloem of the dodder towards phloem of the healthy host by a 'temporary-reversal' of phloem nutrient flow; others like in mosaic-type viruses like cucumber mosaic virus and beet curly top viruses, that move from the parenchyma of the haustorium to the host occurs through plasmodesmatal connections or from the bare

| Pathogen | Parasitic plant | Main host | Reference |
|---|---|---|---|
| **Virus** | | | |
| Little cherry virus | *Cuscuta europea* | Tobacco | [60] |
| Apple mosaic virus | *Cuscuta* spp. | Apple | [57] |
| Tobacco etch virus | *Cuscuta subinclusa* & *Cuscuta* spp. | Tobacco | [57] |
| Mesta leaf curl virus | *Cuscuta* sp. | Mesta | [61] |
| Tomato ringspot virus | *Cuscuta* sp. | Tomato | [60] |
| Potato virus Y | *Cuscuta reflexa* | Tobacco | [55] |
| Dodder Latent Virus | *Cuscuta californica* | Sugar beet | [56] |
| Cucumber mosaic virus | *Cuscuta* sp. | *Nicotiana glutinosa*, Lucerne, cucurbits | [16] |
| Tobacco mosaic virus | *Cuscuta* sp. | Tobacco | [16] |
| Potato stem mottle virus | *Cuscuta* sp. | Tobacco | [16] |
| Beet curly top virus | *Cuscuta* sp. | Sugar beets | [16] |
| **Phytoplasma** | | | |
| Cuscuta Latent MLO | *Cuscuta odorata* | Periwinkle | [62] |
| *Picris echioides* yellows phytoplasma Cal | *Cuscuta odorata* | Oxtongues (experimental host) | [59] |
| Cotton phyllody phytoplasma | *Cuscuta campestris* | Cotton (experimental host) | [59] |
| Pear decline (*Candidatus* Phytoplasma pyri) | *Cuscuta odorata* | Pear (experimental host) | [59] |
| Rubus stunt (*Candidatus* Phytoplasma rubi) | *Cuscutaeuropea* | Different cultivated and wild *Rubus* spp. (Berries) (experimental host) | [59] |
| European stone fruit yellows (*Candidatus* Phytoplasma prunorum) | *Cuscuta reflexa* & *C. campestris* | Plum & Apricot (experimental host) | [59] |
| **Proteobacteria** | | | |
| *Candidatus* Liberibacter asiaticus | *Cuscuta pentagona* | Sweet orange (experimental host) | [63] |
| *Candidatus* Liberibacter asiaticus | *Cuscuta pentagona* | Tomato (experimental host) | [63] |

**Table 1.**
*Examples of plant viruses, phytoplasmas and proteobacteria transmitted by different dodder species.*

protoplasmic connections of dodder [57]. Regardless of the association between host and the parasite along with the directional movement of nutrients in the phloem, several other factors might play their part. For instance, an inhibitor in the sap of dodder have been proposed as contributing factor for poor transmission of *Tobacco mosaic virus* in some hosts [57, 58]. It is demonstrated that tobamoviruses (type spcies: *Tobacco mosaic virus*) are neither persistent nor multiply in dodder, whereas, *Cucumoviruses* (type spcies: *Cucumber mosaic virus*) persists and multiplies, causing disruption of growth in dodder. Hence, there are around 200 species of dodder, out of which some like *C. campestris* parasitises more than 100 diverse plant species and are capable of transmitting viruses between host species [57]. Moreover, several other parasitic angiosperms such as broomrape (*Phelipanche aegyptica*) can transmit viruses between taxonomically different plant families. However, whether the virus was persistent or developing inside the parasitic plant has not been thoroughly investigated [8].

Although the transmission of phytoplasma is quite similar to plant viruses, they are quite understudied. Most interactions of parasitic plants with phytoplasma necessarily are experimental in laboratory or greenhouse with special reference to dodder mediated transmission. Dodder acquires the phytoplasma cells from the infected plant via haustoria in the direction of the source of inoculum to the healthy host and progresses in the direction of the growing points [9]. However, the efficiency of transmission depends on different combinations of phytoplasma and dodder species. In an experimental trial, it was seen that rubus stunt and cotton phyllody were transmitted in higher frequencies by *C. europea* and *C. campestris*, whereas, other several phytoplasmas causing pear decline, stone fruit yellows and *Picris echioides* yellows by *C. odorata, C. reflexa* and *C. campestris*, respectively were transmitted less effectively [59]. Transmission of plant viruses and phytoplasma to healthy plants via parasitic plants as vectors seems unlikely to cause novel primary virus infection chain, as evidence of parasitic seed-virus/phytoplasma transmission is missing, but can have impact on existing primary or secondary infection [16]. In addition, it should be taken into consideration that in general, parasitic plants are known to have a diverse natural host range, which can provide exceptionally high risk of novel virus or phytoplasma transmission between donors and recipients in natural as well as managed vegetation. During the years 1940 to 1960, many dodder-transmissible viruses or phytoplasmas were found and vividly studied [57]. However, these studies now have rapidly decreased and has just limited to experimental hosts (**Table 1**) to offer possibility of studying the nature of different virus transmission to taxonomically same or varied crop species [64].

## 4. Microbiomes of parasitic plants and their hosts

Microbiomes can expand the genomic potential of plants through efficient nutrients acquisition, promoting growth and development, and tolerance to biotic and abiotic stresses [65]. Endophytic microbial communities of parasitic plants may affect parasitism and influence host microbial composition. Microbiota or microbial communities within a parasite can be divided into core- and transient-microbes. Core microbes are intrinsic to one or more developmental stages of a parasite that can vertically flow from parents to the offspring. Transient microbes are temporarily acquired by the parasite from their interacting hosts or environment [66]. A study on microbial communities of parasitic weed, *P. aegyptiaca*, showed that endophytic bacteria were present at different development stages (pre-haustorium, tubercle, and shoot) of the parasite [13]. It was observed that the presence of alpha- and gamma-proteobacteria (dominant species: *Sphingomonas* and *Acinetobacter*) were abundant during pre-haustorium formation (pre-attachment to the host). In the post-attachment stage, i.e., during attachment of tubercle of the parasite to the host, bacterial communities shifted to flavobacteria and beta-proteobacteria, while during parasite shoot formation, an increase of Bacilli and Actinobacteria have been reported [13]. Besides bacterial communities, endophytic fungi also inhabit the inner tissues of parasitic plants. For instance, the root-parasitic plant *Cynomorium songaricum* parasitise *Nitraria tangutorum*, a flowering shrub from the *Nitrariaceae* family, harbours several fungal species assemblages belonging to the phylum, Ascomycota, Basidiomycota and Zygomycota [67]. Microbial communities play diverse roles during the growth and development and parasitism of parasitic plants on their host plants. For instance, some species of the genus, *Fusarium*, promote parasite seed germination, while symbiosis of arbuscular mycorrhizal fungi (*Glomus mosseae*) and rhizobia can alleviate plant host damage by root hemiparasites [67, 68]. Nitrogen-fixing bacteria associated with host plants may indirectly benefit parasitic plants through efficient $N_2$-fixation and their availability to the parasite during host attachment [69, 70].

Microbial communities of parasitic plants overlapped extensively with their parasitised host while still maintaining taxonomically distinct communities [67, 71]. For instance, bacteria communities of the root holoparasite, *Orobanche hederae*, exhibit strong congruency with the host, *Hedera*; however, the individual bacterial taxa were differentially abundant between *Orobanche* and *Hedera* roots [72]. Transmission of microbiota through xylem tubes or apoplasts (intercellular spaces) may act as a mechanism for the shared microbial communities between the host plant and the parasite [13]. Studies have shown that host-associated microbes induce resistance against parasitic plants in many agriculturally important crop species. The induced resistance is mainly achieved via (i) microbe-mediated activation of the phenylpropanoid/isoflavonoid pathways leading to the production of toxic compounds, including phenolics and phytoalexins in the host plant against the parasite, (ii) reduced activity of host root exudates to inhibit parasite seed germination, and (iii) enhanced production of plant-derived peroxidase that causes tubercles necrosis of parasitic plants [73, 74]. Some *Fusarium* species can directly penetrate *Orobanche* cells leading to disintegration of cytoplasm without apparent damage to the host plant tomato [75]. Root-associated microbes can also modulate root physiology and architecture of host plants to prevent parasite seed germination and infection on hosts [76]. An example is colonisation by an arbuscular mycorrhizal fungus (*Glomus intraradices*) on tomato, which resulted in reduced root exudation of strigolactone (chemo-attractant for parasitic plants) and prevented germination of the *P. ramosa* seeds [77]. In another case study, the release of volatile organic compounds such as sesquiterpenes by ectomycorrhizal fungus, *Laccaria bicolor*, promoted lateral root formation in poplar and *Arabidopsis* plants [78]. Thus, changes in root architecture can potentially affect host infection by parasitic plants [76].

## 5. Mechanism of pathogen transmission

Plant pathogens (mostly, viruses and phytoplasmas) are transmitted by parasitic plants by their twining stems. The parasite stem adheres to the host's stem by exuding cutin as it wraps tightly around the stem of the host plant. Few species of parasitic plants like *Cuscuta californica*, *C. campestris, C. subinclusa*, *C. europaea, C. epilinum* and *C. lupuliformis* are sometimes employed in various research areas for the transmission of viruses [9].

The parasitic plants attach to the host plant through haustoria which originates at the site of association between the parasite stem coil and the host stem or leaf. The haustoria vary among different parasitic plant species, considerably in their anatomy and function, mostly by whether they form connections exclusively to the xylem only or both xylem and phloem [40]. Initially, the haustorium enters the host tissue through the lower haustorium with the help of enzymes that break down cell wall connections. Cells then begin to elongate from the lower haustorium and traverse throughout the host tissue to reach the vascular system of the host which eventually leads to the formation of searching hyphae [79]. These cells, termed searching hyphae, as it grows through the host cells, formation of new host cell wall occurs over the parasite cell wall, which appears to encase the hyphae over their entire surface. This formation of a new host cell wall around the parasite cell wall forms a host–parasite interface similar to that of neighbouring cells of the same species. The searching hyphae may develop as a xylem element when connections are made with the host xylem or it may differentiate into cells that are similar to sieve elements after contacting the host phloem.

The host–parasite cell wall is perforated by both simple and branched plasmodesmata, complete with desmotubules typical of normal plasmodesmata [80]. The plant pathogens, mostly viruses are transmitted to the host plant through these plasmodesmata. The virus transmission through the plasmodesmata is felicitated by non-structural proteins, called movement proteins, which act to facilitate the movement of virus particles from cell to cell through these plasmodesmata [81].

Another mechanism of transmission of the virus from the infected parasite to the host is through the sieve element. The virus after being acquired from the vascular bundles of the infected host plant by the haustoria is transmitted in the food stream of the parasitic plant. After translocation through the parasite phloem, the virus is introduced to the next plant by the new parasite haustoria produced in contact with the vascular bundles of the inoculated plant. The parasitic plant absorbs phloem contents from the host, the searching hyphae of the parasite that contact host sieve elements grow around the element with finger-like projections. The parasite cell then differentiates like a sieve element, but with extensive development of smooth endoplasmic reticulum (ER) near the host cell and grows around the phloem cells of the host [82]. These parasite cells then differentiate in a manner consistent with the development of sieve elements, although they also contain an elaborate network of smooth ER proximal to the host cell, a feature of transfer cells [83]. In contrast to *Cuscuta*, direct connections between sieve elements of *Orobanche crenata* and those of its host *Vicia narbonensis* have been imaged using electron microscopy [82]. Host–parasite connections for *Orobanche* are less controversial in that direct connections between host and parasite sieve elements have been documented by electron microscopy. Plasmodesmata between these species have also been documented and are proposed to lead to the formation of sieve pores between adjacent sieve elements. Because sieve pores are much larger than plasmodesmata openings, the path for pathogens from host to parasite would seem to be relatively unobstructed.

## 6. Management

The management of parasitic plants is difficult because there are few sources of crop resistance and is challenging to selectively kill the parasitic plants without damaging the host, as they are physically and biochemically attached to the host. The efficiency of the management of parasitic plants is also obstructed due to the dispersal efficiency, persistent seed bank, and quick responses to changes in agricultural practices. These qualities of the parasitic plants allow them to adapt to new hosts and manifest aggressively against new resistant cultivars. However, the management strategies of parasitic plants or crop resistance to parasitic plant infection can be classified as pre-attachment or post-attachment resistance according to whether the resistance occurs before or after the haustorium attaches to the host surface [84].

Mostly, the pre-attachment resistance or management includes the mechanisms that can be adopted by a host plant to prevent or avoid parasite attachment, this includes (*i*) prevent germination of the seed by reduced production of germination stimulant(s); (*ii*) production of germination inhibitors; (*iii*) delay, reduction, or complete inhibition of haustorium formation leading to attachment incompetence; and (*iv*) to impede the attachment on the host surface by formation of preformed mechanical or structural barriers which include enhanced cell wall lignification, suberization, or other modifications and structures (hairs or other outgrowths) that retard attachment to the host [5].

Post-attachment resistance occurs when the attached parasite haustorium attempts to penetrate host tissues to make connections with the vascular system. Substantial experimental evidence demonstrates that parasitic plants connect to the endodermis by activating the expression of genes encoding various cell wall degrading/softening enzymes such as pectate lyases, pectin methylesterase, polygalacturonase, endocellulase, β-xylanase, expansins. The expression of these enzymes assists the parasitic plants to penetrate the host endodermis through the epidermis and cortex [85]. During this intrusive process, the host can succumb passively, rely on constitutively expressed general defence responses, or activate specific innate immune response cascades to fend off parasitic progress [86]. Innate immunity can present as (*i*), the synthesis and release of cytotoxic compounds (e.g., phenolic acids, phytoalexins), by the challenged host root cells; (*ii*) rapid formation of physical barriers to prevent possible pathogen progress and growth (e.g., lignification and other forms of cell wall modification at the host–parasite interface); (*iii*) release of reactive oxygen species and activation of programmed cell death in the form of a hypersensitive response at the point of parasite attachment to limit parasite development and retard its penetration; and (*iv*) prevention of the parasite establishing the essential functional vascular continuity (i.e., xylem-to-xylem and/or phloem-to-phloem connections) with the host, delaying parasite growth followed by parasite developmental arrest and eventual death [5, 87].

### 6.1 Use of herbicides as a strategy for parasitic plant control

The use of herbicides for management needs to be specifically designed depending on the target combination of the parasite-crop species and on the information available on the specific herbicide and the optimum herbicidal doses that have been proved to be sub lethal for the crop, on the other hand, it can be applied as lethal doses to the parasite, and the availability of crop varieties with herbicide resistance.

The systemic herbicide is applied to the crop foliage and delivered to the shoot or root parasites either via the haustorium or through exudation to the rhizosphere from the crop roots [88]. The systemic herbicides used for parasitic weeds include inhibitors of aromatic (glyphosate) or branched-chain amino acid synthesis (imidazolinones and sulfonylureas), inhibitors of the vitamin folic acid (asulam), inhibitors of glutamine synthetase (glufosinate), or hormonal herbicides (2,4-D and dicamba) [89, 90].

Rationale and most effective control of parasitic plant disease is possible only if

i. the disease is correctly diagnosed,

ii. the nature of transmission of the disease is known and

iii. life cycle stages of the involved parasite, i.e., its mode of reproduction active structures produced under the favourable condition for repaid and wide dispersal and the structures produced to overcome adverse condition are known.

## 7. Conclusion

Parasitic plants are important hinderance in crop production and productivity, especially for perennial horticultural crops. In addition to their direct influence as a modulator of source to sink balance, they also are known vectors of obnoxious pathogens such as viruses and phytoplasmas. However, there seems not to have been equal, if not more, attention from the plant scientists on these multifaceted pests, as in case of other pests such as the pathogens and the insect-harbivores. Although there are at least 4,500 species of such parasitic plants forming some 1% of the angiosperms, very few of them have been studied in sufficient details. The extent of crop damage and their roles as pathogens vectors of most of them are not well-known. Considering the exploding population and its pressure on the limited resources of the planet, and the increasing demand for food and nutrition, harnessing each and every potential means of crop improvement and tackling all the potential causes of crop loss is the need of the hour. While the genetic potential of the important crops have reached near the maximum, sustainable management of the pests and pathogens is the most important step in this direction. Being a direct and indirect hinderance of crop production, as discussed in this chapter, the parasitic plants, therefore, demand further and deeper future research.

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## Conflict of interest

The authors declare no conflict of interest.

## Author details

Anupam Gogoi[1], Namrata Baruah[2], Mandeep Poudel[1], Ruby Gupta[3], Geetanjali Baruah[4] and Basanta Kumar Borah[5]*

1 Department of Plant Sciences, Faculty of Biosciences (BIOVIT), Norwegian University of Life Sciences, Ås, Norway

2 Ecology and Genetics Research Unit, University of Oulu, Oulu, Finland

3 Tata Memorial Centre, Navi Mumbai, Maharashtra, India

4 Environment Division, Assam Science Technology and Environment Council, Bigyan Bhawan, Guwahati, Assam, India

5 Department of Agricultural Biotechnology, Assam Agricultural University, Jorhat, India

*Address all correspondence to: basanta.k.borah@aau.ac.in

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## Chapter 3

# Aspects of the Biology and Ethnobotany of Parasitic Angiosperm Species in Nigeria

*Odoligie Imarhiagbe*

## Abstract

Parasitic plants continue to gain research attention due to their remarkable lifestyle pattern that clearly cites them as a typical example of a biological oddity. They have defiled the basic characteristics of plants to become dependent on other plants for existence. Aside from their unique heterotrophic mode of feeding, host range and preference, seed germination clues, distribution patterns vary across different parasitic plants, which has partly ensured their presence in virtually every plant community. Among the above-listed factors, host range and preference, in particular, appears to be a major significant factor that shapes their distribution around the world, enabling certain species to thrive in various microclimates. The Nigerian environment has heterogeneous vegetation, traversing mangroves, rainforest, savannah vegetation, and its home to host parasitic plant species, including endemic, natives, and exotic ones. The present chapter gathered and synthesized available information regarding parasitic plants in Nigeria, particularly their biology and the host species supporting their population. Aside from the devastating menace some parasitic plants are known for, this report recognizes their ethnobotanical relevance. Thereby stimulating research interest in these highly specialized plant groups.

**Keywords:** Ethnobotany, Parasitic plants, host species, Nigeria

## 1. Introduction

Parasitic plants are an exceptional group of plants that have defiled plants' basic characteristics of solely synthesizing their own organic nutrient into dependent on other plants for survival [1]. Consequently, they have adapted to an association with a host plant using a physiological bridge known as the haustorium, where water and organic nutrients are transported [2]. This form of association enables the host plant to shape the distribution of the parasite. Based on the degree of host dependence, parasitic plants can exert their impact on an individual or community basis; some parasitic plants, for example, *Striga*, can severely reduce host performance, leading to host death, while others like *Thonningia sanguinea* exert a mild effect on its host. On a community scale, parasitic plants can significantly orchestrate changes in community structure, diversity, vegetation cycling, and zonation by either altering the competitive balance between host and nonhost plants [3] or necessitating an irregular uptake of host solutes which consequently

| Order | Parasitic Evolutionary Linages | Nature of Parasitism | | | Parasitic | | Hemiparasitism | | Holoparasitism | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | R | E | S | Genera | Species | Facultative | obligate | Solely | obligate |
| *Piperales | Hydnoraceae | + | | | 2 | ~18 | | + | | + |
| *Laurales | Lauraceae | + | | | 1 | ~16 | | + | | |
| Zygophyllales | Krameriaceae | + | | | 1 | 18 | + | + | | |
| Cucurbitales | Apodanthaceae | | + | | 3 | 23 | | | | + |
| Malpighiales | Rafflesiaceae | | + | | 3 | ~19 | | | | + |
| Malvales | Cytinaceae | + | | | 2 | ~11 | | | | + |
| *Santalales | Loranthaceae | + | | + | 167 | ~2147 | + | + | | + |
| | Santalaceae | | | | | | | | | |
| Saxifragales | Cynomoriaceae | + | | | 1 | 2 | | | | + |
| *Lamiales | Orobanchaceae | + | | | 90 | 1800 | + | + | | + |
| Boraginales | Boraginaceae | + | | | 2 | ~5 | | | | + |
| *Solanales | Convovolaceae | | | + | 1 | 145 | | + | | |

*R-root, E-endophyte, S-stem.*
**Order having a representative genera in Nigeria.*
*Compiled from: The Angiosperm Phylogeny Website (APG III, & VI); [5], and Christenhusz, and Byng [6]*

**Table 1.**
*Systematic presentation of the diversity of parasitic angiosperm.*

affect other trophic level organisms (such as herbivores and pollinators). These impacts also result in a ripple effect that may extend to the abiotic environment, including impacts on nutrient cycling, soil water relations, local temperature, and atmospheric $CO_2$ concentrations. Importantly, such major impacts can occur even when parasitic plants are minor components of the ecosystem [4].

Despite the uniqueness of plant parasitism, its evolution is polyphyletic [1]. It is reported to have evolved approximately 12 or 13 in the angiosperm phylogeny (**Table 1**). There are approximately 4,500 species in about 280 genera belonging to 20 families [3]. While some angiosperm families, like Balanophoraceae, consist entirely of parasitic members, others have only a few representatives, for example, Lauraceae. Parasitic plants also exist in different life forms, including annuals and perennials, e.g. (*Hydnora* spp. and *Thonningia sangunea*), climbers (e.g., *Cassytha*), shrubs (*Tapinanthus globiferous*), and Tree (e.g., *Okoubaka aubrevillei*). Parasitic plants can be characterized based on the presence or absence of photosynthetic pigments, in which case hemiparasites like *Cassytha filiformis, Agelanthus spp., Globimetula spp.* etc., have the ability to photosynthesize to some extent due to the presence of chlorophyll or holoparasite like *Hydnora* spp., *Thonningia sanguinea*, *Balanophora* sp. *Cuscuta* derived their entire organic nutrient from the host plant due to chlorophyll deficiency. Parasitic plants could also be categorized as stem parasites. For example, *Cassytha filiformis, Agelanthus spp., Globimetula spp.* are attached to the host stem or root parasites, e.g., *Thonningia sanguinea, Hydnora spp.* attached to the host plant's root.

Parasitic plants are virtually present in all plant communities throughout the world. Moreover, a positive relationship between nonparasitic and parasitic plants has been established [4]. By implication, plant-rich ecosystems are also expected to be rich in parasitic plants. The strategic position of Nigeria in West Africa has endowed it with wealthy biodiversity, distributed within different ecological zones, comprising: mangrove, rainforest, montane, and the savanna- Guinea, Sudan, and Sahel [7]. These different eco-geographical zones support a huge diversity of parasitic plants, including endemic ones. Even though some parasitic plant species are important pests of human agriculture and forestry, many are highly valued for food, wood, and medicinal properties [8]. Therefore, the present chapter aims to utilize available literature regarding parasitic plants in Nigeria to document their biology, identified host plants, and their ethnobotanical relevance.

## 2. Materials and methods

The author obtained information on the biology and ethnobotany of parasitic plants in Nigeria from various sources, which include; Published materials in the form of journals from databases, such as Google Scholar, Elsevier, Web of Science, and SCOPUS, and textbooks, particular checklists, monographs, floras (see references). Herbaria visited include Forest Herbarium Ibadan (FHI) and the Edo State University Herbarium (EUH). Also, personal communication with experts about parasitic plants in Nigeria was valuable to completing this report.

## 3. Distribution of parasitic plants in Nigeria

The strategic position of Nigeria in the tropics just above the equator within Latitudes 10 $^0$N and 14$^0$ N has endowed it with very rich yet heterogeneous vegetation. The temperature is high and ranges from 25–34°C. The mean annual rainfall ranges from 500 mm in the north to 2500 mm in the coaster region.

The phytogeography of Nigeria could broadly be categorized into two major regions; the Sudano-Zambezian and the Guineo-Congo [9]. The Northern part of the country falls under the Sudano-Zambezian region, comprising the Sudanian and Sahelian domains. The Guineo-Congo region of Nigeria is made up of Guineo domain to which the west and central part of the country belongs, and the Congo domain has the eastern part of the country. The different domains support various plant species, some of whom are notable host species to the parasitic plants domiciled in the Nigerian environment. For the current discourse on the distribution of parasitic plants, the Nigerian environment will be characterized into two, Northern Nigeria, predominately, savannah, and Southern Nigeria, where the rainforest forest belt is located.

### 3.1 Northern Nigeria

Northern Nigeria has a Savannah ecoregion, comprising the Guinea savanna bordering the rainforests, the Sudan savanna, and the Sahel bordering the desert. The guinea savanna is found in Kaduna, Kwara, Kogi, and Benue states; the Sudan savanna, in Kano and parts of Borno, Sokoto, Niger, and Bauchi states; and the Sahel around the Lake Chad. The savanna ecoregion is renowned for a climate that has a short wet and long dry season. The average monthly temperatures are around 29°C during the hot season and around 18°C during the cool season. The total annual rainfall varies greatly from around 500 mm in regions on the semi-desert fringes to about 1500 mm in regions bordering the rain forests. The savanna rainfall is insufficient to support a rich growth of trees but is mostly dominated by perennial grasses with few tree clumps. In the Guinea savanna, the grasses grow tall during the rainy season. Trees occur quite close together, especially along the rain forest fringe. The grass is shorter in the drier Sudan savanna, and the trees are fewer and more scattered. In the Sahel, which is borders the Sahara desert, the land is quite bear with clumps of short grass and a few isolated shrubs and trees. During the dry season, the grass is usually dry and brown, and bush fires are common occurrences. The underground parts of the grasses survive the dry season and fires and grow again when the rains come. In terms of the parasitic plant distribution, the Nigerian Savanna is home to one of the most devastating parasitic genus, *Striga*. The species are found on cultivated lands, abandoned farmlands, and waste and weed-infested sites, depending on the presence of the host crop. *Striga astiatica*, *S. aspara*, *S. hermonthica*, *S. gesnerioides* are some of the species found in the savanna habitat. The basis for their occurrence only in the savanna part of the country is yet to be fully ascertained. Mohamed et al. [10] reported that the rain forest's high rainfall and moisture levels result in a "wet dormancy" of *Striga* seeds, consequently precluding its occurrence in the zone. Notwithstanding, most host crops, such as Corn, sorghum, and sugar cane, are cultivated majorly in the savanna part. *Hydnora abyssinica,* a root holoparasitic plant, was recently spotted around Nekong, Wusali ward, Kanke Local Government Area, Plateau State, Nigeria [11]. Notable members of the Loranthaceae family like *Agelanthus dodoneifolius, A. heteromorphus, Globimetula cupulata, Tapinanthus cordifolius, T, globiferous, T. pentagonia*, and *T. preussii* are attached to trees and shrubs in this zone. **Table 2** shows potential distribution and host species of common parasitic plants of Nigeria

### 3.2 Southern Nigeria

The Southern part of Nigeria experiences heavy and abundant rainfall due to its proximity to the equatorial belt. It comprises majorly the rainforest and the swarm forest that borders the Southern Atlantic Ocean. The rainforest belt occurs in the regions that lie between the equator and latitude 5° – 10 °N and S. The climate in

| Species | Family | Potential Distribution | Herbarium voucher number | Host species | Literature |
|---|---|---|---|---|---|
| *Agelanthus brunneus* (Engl.) Balle & Halle | Loranthaceae | SN: Edo, Ogun, Ondo | FHI 16684 | *Carissa edulis, Crateva religiosa, Diplorhynchus, Ficus, Funtumia, Gossweilodendron, Ipomaea, Landolphia heudelotii, Ochna sp, Kigelia africana* | [5, 12] |
| *Agelanthus dodoneifolius* (DC.) Polhill &Wiens | Loranthaceae | NN; Kano, Bauchi, Yola<br>SN: Oyo | FHI 16279 | *Acacia* spp., *Afzelia* spp., *Ceiba, Mimosa, Parkia, Piliostigma, Pterocarpus erinaceus, Tamarindus* sp. | [5, 13] |
| *Agelanthus heteromorphus* (A. Rich.) | Loranthaceae | NN: Sokoto, Zamfara, Bauchi, Yola | FHI 15893 | *Anogeissus leiocarpus, Parkia biglobosa, Terminalia avicenioides* | [14] |
| *Alectra sessiliflora var. monticola* | Oronbanchaceae | SN: Oyo | FHI 13735 | parasitic on some members of the poaceae family | [12] |
| *Alectra sessiliflora var. senegalensis* | Oronbanchaceae | NN: Niger, Bauchi SN: Ondo | FHI 24448 | parasitic on some members of the poaceae family | [12] |
| *Alectra vogelii Benth* | Oronbanchaceae | NN: Sokoto, Niger, Kogi, Bauchi, Ilorin | FHI I9265<br>FHI 25638 | Semi parasitic on members of papilionoidae | [12] |
| *Cassytha filiformis* L. | Lauraceae | Widespread | EUI 00018 | *Dodonaea viscosa, Casuarina stricta, Mangifera indica, Myristica fragrans, Persea americana* | [15] |
| *Cuscuta australis* R.Br. | Convolulaceae | widespread | FHI 23459<br>EUH 00015 | *Cassia marginata. Acacia arabica, Azadirachta indica* | [16] |
| *Englerina gabonensis* (Engl.) Balle | Loranthaceae | SN: Ogun, Ondo | FHI 173041 | *Ficus* and *Platysepalum chevalieri* | [17] |
| *Globimetula cupulata* (DC.) Van Tiegh | Loranthaceae | widespread | EUH 00019 | *Dacryodes edulis*, *Ceiba pendandra, Morinda germinata, Neocarya macrophylla* | [18] |
| *Globimetula braunii* (Engl.) Van Tiegh | Loranthaceae | SN: Ogun, Anambra, Lagos, Cross River | FHI 6679 | *Ceiba pendandra* | [18] |
| *Helixanthera mannii* (Oliv.) Danser | Loranthaceae | SN: Cross River | FHI 33216 | Coffea, Citrus, *Ficus* | [5, 13] |
| *Helixanthera spathulata* Wiens & Polh. | Loranthaceae | SN: Cross River | | Coffea, Citrus, *Ficus* | [12] |
| *Hydnora abyssinica* A. Br. | Hydnoraceae | NN: Plateau | | *Acacia hockii* De Wild, *Piliostigma thonningii* (Schum.) Milne-Redh., and *Tamarindus indica* L. | [19] |

| Species | Family | Potential Distribution | Herbarium voucher number | Host species | Literature |
|---|---|---|---|---|---|
| *Okoubaka aubrevillei* Pellegr. & Normand. | Santalaceae | SN: Edo, Cross River and Osun | EUH 00011 | Companion tree plant species | [20, 21] |
| *Phragmanthera capitata* (Spreng.) Balle | Loranthaceae | NN: Niger<br>SS: Oyo, Cross River. | FHI 3420 | *Alchornea, Anacardium occidentale, Annona senegalensis, Bauhinia, Citrus aurantium, Coffea, Cola nitida,* | [12, 13] |
| *Phragmanthera kamerunensis* (Engl.) Balle | Loranthaceae | NN: Niger, Kogi SN: Cross River; | | *Milicia excelsa* and *Isoberlinia doka*. | [22] |
| *Phragmanthera nigritana* (Hook. f. ex Benth.) Balle. | Loranthaceae | NN: Kogi, Adamawa<br>SN: Ogun, Cross River; | | *Morinda lucida* | [23] |
| *Phragmanthera talbotiorum* (Sprague) Balle | Loranthaceae | SN: Akwa Ibom, Cross River; | | *Morinda lucida* | [12, 24] |
| *Striga asiatica* (Linn.) O. Ktze | Oronbanchaceae | NN: Niger, Kaduna, Adamawa | FHI 24389 | Corn, sorghum, and sugar cane | [12] |
| *Striga aspara* (Willd.) Benth | Oronbanchaceae | NN: widespread | FHI 4557 | rice, wild grasses | [5, 25] |
| *Striga gesneriodes* (Willd.) Vatke | Oronbanchaceae | NN: Sokoto, Adamawa | | Cowpea | [5, 25] |
| *Striga hermonthica* (Del.) Benth | Oronbanchaceae | NN: widespread | EUH 00022 | Sorghum roots | [5, 25] |
| *Tapinanthus bangwensis* (Danser. | Loranthaceae | SN: widespread | EUH 00029 | *Cola nitida, Coffea liberica, Terminalia catappa* and *Theobroma cacao*. | [5, 26] |
| *Tapinanthus cordifolius* | Loranthaceae | NN: widespread | FHI 24389 | *Sysygium eucalyptoides; Psidium guajava; Citrus auranthifolia; Citrus medica* | [12] |
| *Tapinanthus globiferous* (A. Rich.) Tiegh. | Loranthaceae | NN: Zamfara, Kano, Bornu | FHI 15683 | *Acacia nilotica, Adansonia, Bauhinia rufescens, Butyrospermum parkii* | [5, 13] |
| *Tapinanthus pentagonia* (DC.) Van Tiegh | Loranthaceae | SN: Oyo | FHI 3442 | *Acacia, Butyrospermum, Ceiba, Ficus, Gardenia, Landolphia heudelotii* | [12, 13] |
| *Tapinanthus preussii* (Engl.) Tiegh. | Loranthaceae | SN: widespread | EUH 00101 | *Parkia biglobosa* | [5, 13] |

| Species | Family | Potential Distribution | Herbarium voucher number | Host species | Literature |
|---|---|---|---|---|---|
| *Thonningia sanguinea* (Vahl.) | Balanophoraceae | SN: Edo, Cross River, Oyo, Ondo, Ogun, Bayelsa | EUH 00055 | *Guarea cedrata Lophira alata*, *Musanga cecropioides*, *Myrianthus arboreus* and *Ricinodendron heudelotii Hevea brasiliensis* and *Theobroma cacao* | [27, 28] |
| *Viscum congolense* De Wild. | Loranthaceae | SN: Akwa Ibom, Cross River | EUH 00121 | *Albizia, Combretodendron africanum, Hevea Funtumia elastica, Polyalthia* | [27] |
| *Viscum decurrens* (Engl.) Bak. & Sprague | Loranthaceae | Rain forest: Akwa Ibom, Cross River | EUH 00122 | *Symphonia globulifera* | [2, 27] |

*NN, Northern Nigeria; SN, Southern Nigeria; FHI, Forest herbarium Ibadan; EUH, Edo university herbarium.*

**Table 2.**
*Potential distribution and host species of common parasitic plants of Nigeria.*

the tropical rainforest region is hot and wet throughout the year. The mean annual temperature is 27°C while the mean total annual rainfall is 2000 mm. The rainforest is characterized by dense and stratified vegetation, comprising various broad-leaved tree species sandwiched by lianas and herbaceous climbers. The rain forest covers Oyo, Edo, Delta, Imo, Cross River, Ogun, Ondo, and Rivers state, while the swarm forest is situated across the Niger Delta region. Parasitic plants are very much represented in the Nigerian rainforest. The largest parasitic tree, *Okoubaka aubrevillei*, is found here. It is believed to parasitize neighboring trees as an adaptive mechanism for creating light spaces in the normally thick rain forest environment. A recent report indicates that the parasitic tree is currently facing a decline in its Population due to forest degradation. Consequently, further isolating the few remnants stands in some forest areas of Edo, Cross River, and Osun States. Another interesting parasitic species found in the Nigerian rain forest is the ground-dwelling, herbaceous plant- *Thonningia sanguinea*, commonly refer to as 'ground pineapple' because they bear morphological similarities. The plant shows a special preference for native host trees such as *Guarea cedrata*, *Lophira alata Musanga cecropioides Myrianthus arboreus*, and *Ricinodendron heudelotii*, and few exotics like *Hevea brasiliensis* and *Theobroma cacao*. It is mostly found growing along forest trails, indicating its preference for disturbed parts of the forest environment. Notable members of the Loranthaceae family like *Agelanthus brunneus*, *A. dodoneifolius, Englerina gabonensis, Globimetula braunii, Helixanthera mannii, Phragmanthera capitata*, *P. kamerunensis, P. talbotiorum,* and *Tapinanthus bangwensis* are present in the luxuriant vegetation of the rain forest, attached on the branches of host trees. Other stem parasites like *Cassytha filiformis* and *Cuscuta australis* have a widespread distribution spanning rainforest and the savanna. Parasitic members of the Orobanchaceae scarcely sighted, only represented in this zone by *Alectra sessiliflora var. monticola.* **Table 2** shows potential distribution and host species of common parasitic plants of Nigeria.

## 4. Systematic presentation of parasitic angiosperm in Nigeria

### 4.1 PIPERALES: *hydnora abyssinica* (Hydnoraceae)

Members of the genus *Hydnora* are subterranean, holoparasitic, and lack leaves or scales [19]. Several species of *Hydnora* have been recognized *H. africana* Thunb., *H. esculenta* Jum. & H. Perrier, *H. johannis* Becc. and *H. triceps* Drege & Meyer as distinct species; however, The family-Hydnoraceae is represented in Nigeria by *Hydnora abyssinica* A. Braun [11]. The first and only report of its existence was around Nekong, Wusali ward, a lowland area in the Sudan-savanna zone in Kanke Local Government Area, Plateau State, Nigeria [11]. *Hydnora abyssinica* is a perennial herb composed entirely of roots with extremely reduced vegetative morphology. It only emerges above ground when fruiting or flowering. *H. abyssinica* grows in a semiarid environment. The adaptation for such an environment might be related to the fact that water availability affects flower growth, including perianth splitting [29]. The flowers of *H. abyssinica* are protogynous; however, both cross and self-pollination can occur. Carrion flies and dermestid beetles carry out pollination. Generally, *Hydnora* species use a system similar to the pitcher traps of Carnivorous plants by trapping insects that fall into the flower tube, ensuring they do not escape [25].

### 4.2 LAURALES: *cassytha filiformis* (Lauraceae)

The genus *Cassytha* consists of about 17 species globally, with *Cassytha filiformis* being the predominant species in Nigeria. *Cassytha filiformis* is a perennial, leafless twining plant with a stem turning clockwise around the support plant [30]. It is less selective in terms of the choice of the host; hence any plant may be used as a host [29]. Stems are green to orange, filiform, and glabrous. Leaves are reduced to minute scales, ca. 1 mm long, easiest seen near tips of stems. Flowers are sessile and few in spicate inflorescences 1(−2) cm long, each subtended by an ovate bract and two ovate bracteoles. The inflorescence is a short raceme or spike. *C. filiformis* produces false fruits enclosed in the accrescent floral tube; dried floral parts persist in the fruiting stage. Information regarding the pollination biology in *Cassytha filiformis* is scanty. However, the floral characteristics point to wind pollination, while on the other, the presence of gland in the flowers point to insect pollination. Birds disperse fruits. Bush fire has been reported to promote the germination of *Cassytha* seeds [29].

### 4.3 SANTALALES: nigerian loranthaceae

Loranthaceae is the largest family in Santalales with about 73 genera and over 900 species [29]. It has a wide distribution particularly in the southern hemisphere, including both subtropical and tropical areas. Members of Loranthaceae have mostly stemmed parasites, with exception of a few root parasites. They possess both primary and secondary haustoria. Loranthaceae leaves are usually evergreen, leathery, and simple with smooth edges but variable forms, from broad flat leaves to cylindrical succulent leaves. Flowers are nearly always bisexual, with 4–7 perianth members who normally are of the same color. Stamens occur in the same number as the perianth parts, but there is only one pistil. Insects and birds, especially sunbirds pollinate flowers. The fruits are berry-like, single-seeded and of different color depending on species. Birds are the main disperser. The family- Loranthaceae is represented in Nigeria by *Agelanthus brunneus* (Engl.) Balle & Halle, *Agelanthus dodoneifolius, Englerina gabonensis* (Engl.) Balle, *Globimetula cupulata* (DC.) Van Tiegh, *Globimetula oreophila* (Oliv.) Danser, *Helixanthera mannii* (Oliv.) Danser, *Helixanthera spathulata* Wiens & Polh. *Phragmanthera capitata* (Spreng.) Balle, *Phragmanthera kamerunensis* (Engl.) Balle, *Phragmanthera nigritana* (Hook. f. ex Benth.) Balle, *Phragmanthera talbotiorum* (Sprague) Balle, *Tapinanthus bangwensis (Engk. & K. Krause) Danser, Tapinanthus cordifolius*, *Tapinanthus globiferous* (A. Rich.) Tiegh, *Tapinanthus pentagonia* (DC.)Van Tiegh, and *Tapinanthus preussii* (**Figure 1**). Generally, these representative species are distributed into two main groups distinguished by the flower bracts, the Tapinanthoid and the Taxilloid group.

The Tapinanthoid group has simple to branched hairs. There are three flower types in this group. Some possess relatively small, non-explosive flowers, which are mostly adapted to pollination by insects. They are considered primitive for example is *Helixanthera mannii*, *H. spathulata.* Others like *Agelanthus* and *Englerina* have explosive flowers, and their corolla is vented. Corolla venting occurs when there is a split in the corolla and the number of splits corresponding to the number of fused petals below the corolla tip. *Agelanthus* is the most species-rich Loranthaceae in Africa. It flowers all year-round depending on the host species and the location, usually much more abundant during the rainy period. *Englerina* is mostly shrubs up to 2 m in size. The flowers are clustered in pedunculate umbels and often standing erect from horizontal branches. The corolla tube is relatively short, adapted to pollination by short-beaked birds. The opening mechanism of the flower with the obvious vents serves as signals to the pollinators that the bud is mature. *Tapinanthus* and *Globimetula.* are non-vented but explosive. The flowers explode without opening first by splits. *Tapinanthus* is a common genus in Nigeria. They are characteristically known to have a swollen tip of the corolla in the bud stage. The tip often has a color

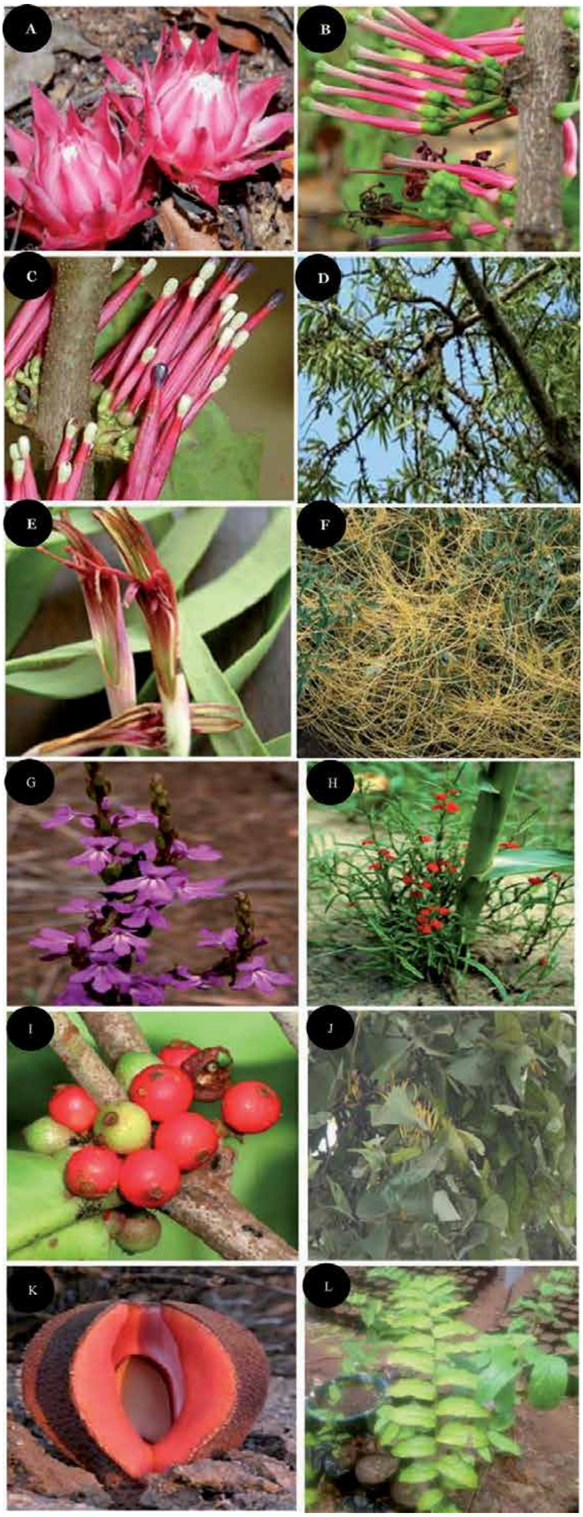

**Figure 1.**
*Some common parasitic plants of Nigeria (A) male inflorescence of* Thonningia sanguinea, *(B) flowers of* Globimetula braunnii *(C) and (D)* Tapinanthus globiferus Syn. Agelanthus dodoneifolius, *(E)* Tapinanthus dodoneifolius, *(F)* Cuscuta camprestris, *(G)* Striga gesnerioides, *(H)* Striga asiatica, *(I) fruits of* Tapinanthus *sp., (J) leaves and inflorescence of* Tapinanthus bangwensis, *(K)* Hydnora *infloresence, (L) a sapling of* Okoubaka aubrevillei.

different from the rest of the corolla and becomes darker as the bud matures. Such a dark color also serves as a signal to the pollinators that the bud is mature. It flowers all year-round depending on the host species and the location, for usually much more abundant during the dry period. *Globimetula* species are known to have just a primary haustorium. The buds have a prominent swelling at the tip like *Tapinanthus*.

The Taxilloid group has stellate hairs and has a flower that is both explosive and vented. Example *Phragmanthera,* which is the largest genus in this group. It has a large single primary haustorium. Several species of this genus are considered pests in plantations.

### 4.4 SANTALALES: *okoubaka aubrevillei* (Santalaceae)

*Okoubaka aubrevillei* is a rare tree endemic to West Africa (**Figure 1**). It is the largest parasitic plant and also produces the largest seeds known for any hemiparasite. It is a monoecious, deciduous tree that grows up to 40 m high [31]. The tree is thought to be useful for various folk medicinal purposes by different ethnic groups in all of its native ranges [21]. *Okoubaka aubrevillei* is perhaps one of the most controversial plants in Africa in terms of taxonomy and ethnobotanical information. It is believed that no tree grows within 80 feet of a 60 feet *Okoubaka* tree, except for *Myrianthus arborea, Musanga cecropoides, Cola attiensis* [31]. Its presence has been confirmed in three state locations in Nigeria: Edo, Cross River, and Osun States [32]. As exercised by *Okoubaka aubrevillei*, parasitism might be for nutritional purposes and as a means of competition for light since it dwells only in a rainforest habitat.

The leaf blade is ovate to oblong, simple and entire in shape, arranged in an alternate to almost opposite. Flowers are green in color and arranged on spines around older branches. Flowers are green in color. Unisexual flowers are present, with the female flowers slightly larger than male flowers [33]. The flowers develop into hard, yellow-colored ellipsoid drupes containing a single large seed that weighs up to 100 g. The tree is monoecious. Hence, it is expected that the plant undergoes self-fertilization (allautogamy), leading to genetic stability. Although little is known about the pollination biology, the pollination type is likely either by ants (myrmecophily) or bats (cheiropterophily) due to the small greenish flowers that preclude its chances of being pollinated by birds [32]. Seeds are speculated to be dispersed by large forest animals such as elephants.

### 4.5 SANTALALES: *viscum* spp. (Santalaceae)

*Viscum congolense* De Wild. And *Viscum decurrens* (Engl.) Bak. & Sprague are two representative species of the family in Nigeria. Reports on these species, particularly, *Viscum decurrens* are scanty. V. *congolense* is a dioecious, globose shrub that grows up to 50 cm tall and is found in humid forests, secondary forests, and plantation forests. Leaves are variable, elliptic-oblong in shape. The fruits are small, smooth and greenish-white in color [12].

### 4.6 Santalales: *thonningia sanguinea* (Balanophoraceae)

*Thonningia sanguinea* Vahl (Balanophoraceae) is a monotypic, rare, cryptic obligate holoparasitic plant endemic to tropical Africa (**Figure 1**). Its distribution is restricted to the forest environment, where it parasitizes forest trees [27, 28]. *Thonningia sanguinea* is a fleshy dioecious herb growing from an underground tuber. It is parasitic on other plants via its tuber. The branching yellow tuber extends horizontally up to 10 or 15 centimeters through the soil. It forms bulb-like swellings at the points where it attaches to the roots of its host plants which could either be exotic or native species. These swellings, or galls, can reach over 18 centimeters wide [34]. The stem is coated with spirals of scale-like leaves. The leaves lack chlorophyll, as the plant obtains nutrients from hosts and does not need to photosynthesize. The flowering stem emerges from the ground to produce a bright red or pink inflorescence containing male and female flowers. The crowded flower heads are covered in scales. The inflorescence is up to 15 to 20 centimeters long [34]. Studies on its reproductive phenology suggest that *T. sanguinea* flowers all year round. The ant *Technomyrmex* species are the most common floral visitors, and it is hypothesized to be the pollinating agent [27, 28].

### 4.7 LAMIALES: *alectra* spp. (Orobanchaceae)

*Alectra* is also known as the yellow witchweed. Representative species in Nigeria include *Alectra sessiliflora var. monticola, Alectra sessiliflora var. senegalensis, and Alectra vogelii Benth.* Generally, *Alectra* grows erect, emerging from a small bulb (haustorium) attached to the root of the root plant. The leaves are lanceolate, simple, subsessile, and arranged in an opposite or alternate pattern. Flowers are borne by a short peduncle and yellow in color. The fruit is a globular dehiscent capsule containing many seeds. At maturity, it opens in 2 valves. The seeds are tiny and ovoid. Seeds are dispersed mainly by wind. *Alectra* species, particularly *Alectra sessiliflora* var. *senegalensis,* are a serious threat to agriculture since they can use members of Papilionoideae such as cowpeas, peanuts, soybeans and other legumes as host.

### 4.8 Lamiales: *striga* spp. (Orobanchaceae)

*Striga*, often refer to as 'witchweed' because several species, despite their beauty, seem to perform "evil magic" like a witch. *Striga* is most common in semi-dry vegetation. *Striga* species are annuals or rarely perennials. Representative species in Nigeria include; *Striga asiatica* (Linn.) O. Ktze, *Striga aspera* (Willd.) *Benth, Striga gesnerioides* (Willd.) Vatke, *Striga hermonthica* (Del.) Benth.

The life-cycle of *Striga* spp. is quite complex [48]. It begins a long period of seed dormancy that could persist for up to after which the seeds then need sufficiently warm and humid conditions for one to two weeks to enter into a condition in which they can germinate (pre-conditioning). Subsequently, they need host-derived signals that stimulate germination [25]. After germination, a special organ, called the haustorium, through which nutrient materials are siphoned from the host [25]. The above-ground part of the parasite emerges after haustorium development and proper attachment to the host. This is accompanied by flower bloom, pollination, and subsequently shedding the seeds as the capsules ripen. Pollination is by insects, probably butterflies; the seeds are tiny, produced in vast numbers and dispersed mainly by wind, but also stick with mud to hoofed and clover-trotted mammals [17].

### 4.9 SOLANALES: *cuscuta australis* R.Br. (Convulvulaceae)

*Cuscuta*, commonly referred to as dodder, is the only parasitic genus in Convolvulaceae, belonging to the order, Solanales. The species is represented in Nigeria by *Cuscuta australis*. *Cuscuta* spp. bear a close similarity to *Cassytha* in appearance. However, some notable differences include that most *Cuscuta* spp. are annuals, unlike *Cassytha*, a perennial herb. Also, while *Cassytha* is a hemiparasite, *Cuscuta* is holoparasitic. Also, *Cuscuta* is a more advanced parasite than *Cassytha* due to the presence of a direct phloem contact [16].

*Cuscuta australis* possess tiny, stalk or sessile flowers that are clustered in dense heads. Flowers are pollinated by insects; however, birds are responsible for seed dispersal [29].

## 5. Ethnobotanical relevance of parasitic plants

The term Ethnobotany was first used by Harshberger [35] to denote the study of plants used by primitive aboriginal people subsequently; different workers have defined the subject, greatly enlarged the scope and accepted it as an interdisciplinary science for a holistic approach to man–plant relationship, hence different definitions of the concept of ethnobotany exist. Allem, [36] defined the concept as the biological, economic and cultural inter-relationship between people and plants in the environment where they exist. Schultes and Raffauf [37] broadly defined the subject as human evaluation and manipulation of plant materials, substances and phenomena in societies. Jain [38] related it to the study of how people make use of plants. According to Pushpangadan and Kumar [39], it is the entire realm of useful relationship between plant and humans. These definitions point out a relationship between people of a given community or society, the environment and the plant diversity in that particular community.

Ethnobotany has now been recognized as an integral part of indigenous/local knowledge of a particular society. Thus, different societies or communities have their own knowledge about plants and their uses. Indigenous knowledge represents an immense valuable database that provides humanity with an insight into how numerous communities have interacted with the changing environment, providing local solutions for local problems and suitable ways for coping with challenges posed by specific conditions. According to Warren and Cashman [40], ethnobotanical knowledge is how most communities survived for centuries by adapting themselves to their environment, using their intrinsic knowledge of associated resource management.

Parasitic plants are keystone species in plant communities, exhibiting a unique and important ecological role [3]. They are common in many natural and seminatural ecosystems, from tropical rain forests to the savanna. Although some parasitic plant species are important pests of human agriculture and forestry, many are highly valued for food and wood as well as for their medicinal and esthetic properties [8].

The study and management of parasites have historically focused on the control, and even elimination, of parasite populations, for example, researchers have intensified efforts to eradicate several mistletoe species, *Cuscuta*: *Striga*, and broomrapes which attack food crops [35]. Despite this ecological and economic importance, parasitic plants have often been overlooked and excluded from most ethnobotanical checklist and flora assessment surveys [8]. Literature survey reveals that only in few instances have parasitic plants been recognized for their ethnobotanical value [41, 42].

The importance of indigenous knowledge is overwhelming especially with regard to parasitic plants. Aiyeloja and Bello [43] valued it as the sum of the experience that forms the basis for decision making for familiar and unfamiliar problems and challenges in a local community. The overall ethnobotanical uses of parasitic plants are quite high. However, the traditional knowledge of these plants have been widely threatened by current trends of economic globalization that promote intensive agriculture, industrialization, and the migration of rural populations to urban areas. Consequently, it is crucial to record this fast-disappearing knowledge before it is lost along with the present generation of elderly persons. **Table 3** shows the ehnobotanical relevance of parasitic plants.

| Species | Geographical location; plant parts use; ethno-uses | References |
|---|---|---|
| *Agelanthus dodoneifolius* (DC.) Polhill & wiens | In West Africa, the leaves of *Agelanthus dodoneifolius* are used by some ethnic groups for headache relief. The leaves and fruit are aphrodisiacs. | [14] |
| *Alectra sessiliflora* var. *monticola* (Engl.) Melch | In Western Kenya, the flowers and leaves of *Alectra sessiliflora* are used to remedy toothache, diarrhea, kwashiorkor, and oral thrush in children, gastrointestinal and sexually transmitted infections. It is also used to hasten childbirth and to treat scars caused by leprosy. | [44, 45] |
| *Cassytha filiformis* L. | Several tribes use the whole plant of *Cassytha filiformis* in Nigeria in the treatment of cancers and gonorrhea. Also, to ease labour pains, quicken labour time, and lubricate the birth canal during childbirth. | [46] |
| *Cuscuta campestris* Yunck. | In Saudi Arabia, the whole plant of *Cuscuta campestris* is used as a purgative and also during constipation. | [47] |
| *Englerina gabonensis* (Engl.) Balle | In Libreville (Gabon), the leaves of *Englerina gabonensis* are used to cure rheumatism. It is also used to heal fractures and scabies, treat mental illness, epilepsy and in performing magic (protection against robbery) | [17] |
| *Globimetula cupulata* (DC.) Van Tiegh | In the Southeast part of Nigeria, the Leaves and fruits of *Globimetula cupulata* are used in the management of high blood pressure and diabetes mellitus | [48, 49] |
| *Helixanthera mannii* (Oliv.) Danser | In West Africa, *Helixanthera mannii* is used for religious ceremonies, superstitions, magic purposes too. | [46] |
| *Hydnora abyssica* A. Br. | In Southern Mozambique, the inflorescence of *Hydnora abyssica* is used to treat diarrhorea, piles, acne, menstrual problems, stomach cramps, and to stop bleeding | [50] |
| *Okoubaka aubrevillei* Pellegr. & Normand. | In Southern Nigeria, the bark and the seeds of *Okoubaka aubrevillei* are used to treat convulsion, for rituals and prevention of miscarriage and as an anaphrodisiac. The bark and leaves are used for reducing swollen testicles (orchitis). The branch is tied on a broken limb along with other plants for the healing of the limbs. Use of the bark infusion or maceration in water to treat skin problems (including those caused by syphilis and leprosy). In contrast, external applications of bark preparations are used to counteract poisoning. | [32, 46, 51] |
| *Phragmanthera capitata* (Spreng.) Balle | **In Logbessou, in the North of Douala (Cameroon),** the leaves and branches of *Phragmanthera capitata* are used for treatments of Nerves attacks, convulsions, chronic muscular pains, diabetes, respiratory dysfunctions, rheumatism related pains, epilepsy, dizziness, uterine hemorrhage, hypertension, hypotension, back pains, kidney pains, menopause, headache, heart palpitations, general purifications, irregular menstruations and nose bleeding. | [22, 24] |
| *Phragmanthera kamerunensis* (Engl.) Balle | In southwest Nigeria, the leaves of *Phragmanthera kamerunensis* is used for the treatment of gastric ulcer. | [23] |
| *Striga asiatica* L. | In South Africa, the stem and leaves of *Striga asiatica* are used for treating hemorrhoids, or smoldering smoke is used to kill off warts, or charred remains are used as a dressing on wounds to dry or rubbed on legs for oedema. | [52] |
| *Striga hermonthica* (Del.) Benth | In Northern Nigeria, the stem and leaves are used to treat dermatosis, leprosy ulcer, pneumonia and jaundice | [53] |
| *Tapinanthus bangwensis* (Engk. & K. Krause) Danser. | Southwest Nigeria leaves; the whole plant is used to treat circulatory and respiratory disease problems, malaria, diabetes, hypertension and sterility in cows. | [54, 55] |

| Species | Geographical location; plant parts use; ethno-uses | References |
|---|---|---|
| *Thonningia sanguinea* (Vahl.) | In Southern Nigeria, the whole plant is used with other materials against anemia, asthma, diarrhea, infant illness, rheumatism, skin infection, sore throat, stomach upset. It is also valuable as (a) an aphrodisiac | [8] |

**Table 3.**
*Ethnobotanical relevance of parasitic plants.*

## 6. Conclusion

Parasitic plants play a vital role in plant communities, and their diversity is quite huge, with various species inhabiting the different ecosystems in Nigeria. The study and management of parasites have historically focused on controlling and even eliminating parasite populations. Although some parasitic plant species are important pests of human agriculture and forestry, many are highly valued for food and wood and their medicinal properties. The current chapter provides an update on the various potential uses of parasitic plants in Nigeria from an ethnobotanical perspective. Therefore it is important to look beyond just their economic implications and approach the conservation of parasitic plants holistically. Next time you walk along nature trails in the forest, look out for some stem parasites on the branches of trees and root parasites at the base of host plants.

## Author details

Odoligie Imarhiagbe
Department of Biological Science, Edo State University Uzairue, Edo State, Nigeria

*Address all correspondence to: imarhiagbe.odoligie@edouniversity.edu.ng

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Chapter 4

# Anatomy, Embryology and Life Cycle of *Lophophytum*, a Root-Holoparasitic Plant

*Hector Arnaldo Sato and Ana Maria Gonzalez*

## Abstract

The most extreme manifestation of parasitism occurs in holoparasites, plants that are totally achlorophyllous. Among them, the genus *Lophophytum* (Balanophoraceae) is characterized by an aberrant vegetative body called a tuber, devoid of stems and leaves. The genus is exclusively South American, comprising five taxa, which parasitize the roots of trees or shrubs. This review focuses on the Argentine species of the genus*: L. leandri* and *L. mirabile* subsp. *bolivianum*. Topics covered include: morphology and anatomy of the vegetative body and host–parasite connection; structure, anatomy and development of the staminate and pistillate flowers; sporogenesis and gametogenesis, embryo sac inversion; endospermogenesis, embryogenesis and fruit development. The evolutionary trend in the gynoecium and embryo sac of the Balanophoraceae is also discussed to reflect the variability. Finally, observations were made on the synchronization of the life cycles of the parasites and hosts to infer possible ways by which parasitism has evolved, until now unknown.

**Keywords:** embryology, embryo sac inversion, holoparasitism, host–parasite connection, legume, tuber

## 1. Introduction

Most vascular plants (Pteridophytes and Spermatophytes) are autotrophic, producing their food through photosynthesis. However, a significant number of plants have adopted a heterotrophic mode of life, obtaining part, or all, of their requirements from other organisms [1–4]. These can be divided into myco-heterotrophs (living in symbiosis with fungi through which they feed on decaying organic matter and the so-called parasitic plants, that grow on other plants and establish an organic union or haustorium by which they derive food directly from the host [4, 5].

There are two basic types of parasitic plants: hemiparasites and holoparasites [6]. The former possess chlorophyll and are capable of photosynthesis (at least during some phase of their cycle) and they obtain only water and mineral salts through haustoria with the host. The most extreme manifestation of parasitism occurs in holoparasites, which are totally achlorophyllous, obtaining all their nutrients from the host, on which they are totally dependent [7]. Most holoparasites are found parasitizing the roots of their hosts.

Worldwide, many of the parasitic plants represent major losses to agriculture, especially in Africa, where root holoparasites cause serious damage to cereals and legumes [8, 9]. Conversely, others are on the red lists of endangered plants, such as the Balanophoraceae [10, 11].

According to Kuijt [1] and Musselman & Press [12] there are about 3,000 species of parasitic plants, representing approximately 1% of flowering plants. Other recent studies put this number at 292 genera and ca. 4750 species [3, 4, 6, 13]. According to Heide-Jørgensen [3] the parasitic plants are distributed in 280 genera and 20 families, 90% (4,100 ssp.) are hemiparasites and only 10% (390 ssp.) are holoparasites. About 60% are root parasites and 40% are stem parasites. Holoparasites are represented in the families Orobanchaceae, Cynomoriaceae, Lennoaceae, Apodanthaceae, Cytinaceae, Raflesiaceae, Hydnoraceae and Balanophoraceae [3, 4]. Parasitism evolved independently in different groups of Angiosperms and there are thirteen lineages where at least one species is parasitic [14, 15].

It is agreed that these modifications respond to a phenomenon of evolutionary convergence [1, 3]. In this sense, Westwood (2010) emphasizes that the study of the structure of parasitic plants provides the conceptual framework for understanding the "specialization" of plants in general.

Among the more specialized holoparasites are the species of the family Balanophoraceae L. C. Richard et A. Richard, which are devoid of chlorophyll and parasitize the roots of trees and shrubs. The best summary of the known characteristics of the family Balanophoraceae can be found in Kuijt & Hansen's work [16]. These plants develop a vegetative body called a tuber, which is partially or totally underground, of variable shape and color, from whitish-yellowish to yellow, orange to reddish-orange or brownish, or even purplish. It lacks the structures of the typical cormophytic organization, as the body is not differentiated into root, stem, and leaves [1, 3, 17–21].

A peculiarity of holoparasites is the tendency to acquire foreign genes from their host plants. It has recently been demonstrated that *L. mirabile* not only harbors in its mitochondria a majority of genes from its host, but also depends on them to carry out cellular respiration. Twenty-three of the 35 protein genes were obtained from Leguminosae. But what is most interesting is that these genes have replaced the native genetic material [22–24].

The family Balanophoraceae is distributed in tropical and subtropical areas. It has 17 genera and 42 species [3, 4, 16]. The genus *Lophophytum*, which is exclusively South American [17, 25–30], comprises five taxa:

- *L. leandri Eichler* from Misiones province (Argentina) and southeastern Brazil
- *L. mirabile* Schott & Endl. subsp. *bolivianum* (Wedd.) B. Hansen, from Jujuy and Salta provinces (Argentina), Bolivia, Brazil
- *L. mirabile* Schott & Endl. subsp. *mirabile*, that grows in Brazil
- *L. weddellii* Hook. f, from Colombia, Peru and Brazil
- *L. rizzoi* Delprete, from Goiás, Brazil

This contribution is based on the results of years of research on the genus *Lophophytum*, focusing on the Argentine species: *L. leandri* and *L. mirabile* subsp. *bolivianum* (hereafter *L. mirabile*). The bibliography used is Sato's doctoral thesis [31] and the numerous papers derived from it [32–35]. The existing bibliography on the other species of the genus *Lophophytum* is scarce, mainly reduced to taxonomic works.

Among the topics included are: i) morphology and anatomy of the vegetative body, including the host/parasite interphase; ii) structure, anatomy and ontogeny of unisexual flowers, iii) description of embryological processes, from gamete formation, iv) morphology and anatomy of fruit and seed, v) taxonomic value of floral characteristics, vi) observations on dissemination, germination and the establishment of the parasitic relationship with the host, vii) the evolutionary trend in the gynoecium and embryo sac of the Balanophoraceae, and viii) synchronization of parasite and host life cycles.

## 2. Morphology and anatomy or vegetative organs

*Lophophytum* plants are formed of an underground vegetative body or tuber, spheroidal or slightly flattened, and 4-(9.5)-15 (38) x 3-(6.5)-12 cm in size [20, 21]. The tubers are connected to the roots of the host tree, close to the trunk. The tubers have no apex and no regions that resemble shoot or root apical meristems; there are no scales, leaves, branches, runners, or roots emerging from the tubers (**Figure 1A**–**C**). The host/parasite interface attachment point is a "woodrose", no larger than 5 cm in diameter; this region has a "coralloid" design in which the host wood is intermingled with the host tissue development (**Figure 1B**). Externally the tubers are dark brown to black and the surface is covered by polygonal or hexagonal "warts" of variable sizes between 0.4 to 1.2 cm.

Anatomically the tuber consists of an outermost black warty surface zone, and an interior body, white in *L. mirabile*, and pink in *L. leandri* (**Figure 1D** and **E**). The warty zone lacks an epidermis, stomata and trichomes. It is composed of a variable number of compact parenchyma cells without any intercellular spaces, with thin, cellulose walls and a completely tanniniferous cytoplasm. The outer cells are progressively detached, as the tuber grows. Solitary or clustered brachysclereids are dispersed between the parenchyma cells of the surface zone (**Figure 1F**).

The interior body is composed of storage parenchyma and abundant collateral bundles that are randomly distributed (**Figure 1F** and **G**). The cells of the peripheral zone showed a positive reaction for tannin by the ferrous sulfate method [36], while the parenchyma cells of the central region have abundant amyloplasts stained with IKI (confirmed by polarized light and the presence of a hilum) and other spherical wax or fat bodies (stained with Sudan IV, not rotated by polarized light, and no hilum) [36–38]. The brachysclereids occur occasionally in the outer region. Vascular bundles are dispersed in the interior body, not organized in a eustele; many of them are continuous from the interior body to the warty zone. The xylem of the vascular bundles is remarkable because the vessel elements have scalariform pitting with ingrowths (**Figure 1H**).

Inflorescences are the only aerial part of the plant and their peculiarity is their endogenous origin (in relation to their own tissues), a characteristic unique to Angiosperms [3, 20, 21, 31–33]. Each tuber usually has one inflorescence, however up to six inflorescences may be produced per plant (**Figure 1A**, **B** and **D**). The inflorescences are monoecious, consisting of one main axis or primary rachis of 2-(21)-40 cm tall, which rises above the soil surface. Short secondary rachises carrying unisexual flowers are inserted in the axil of each bract of the primary rachis; the proximal ones with pistillate flowers and the distal ones with staminate flowers.

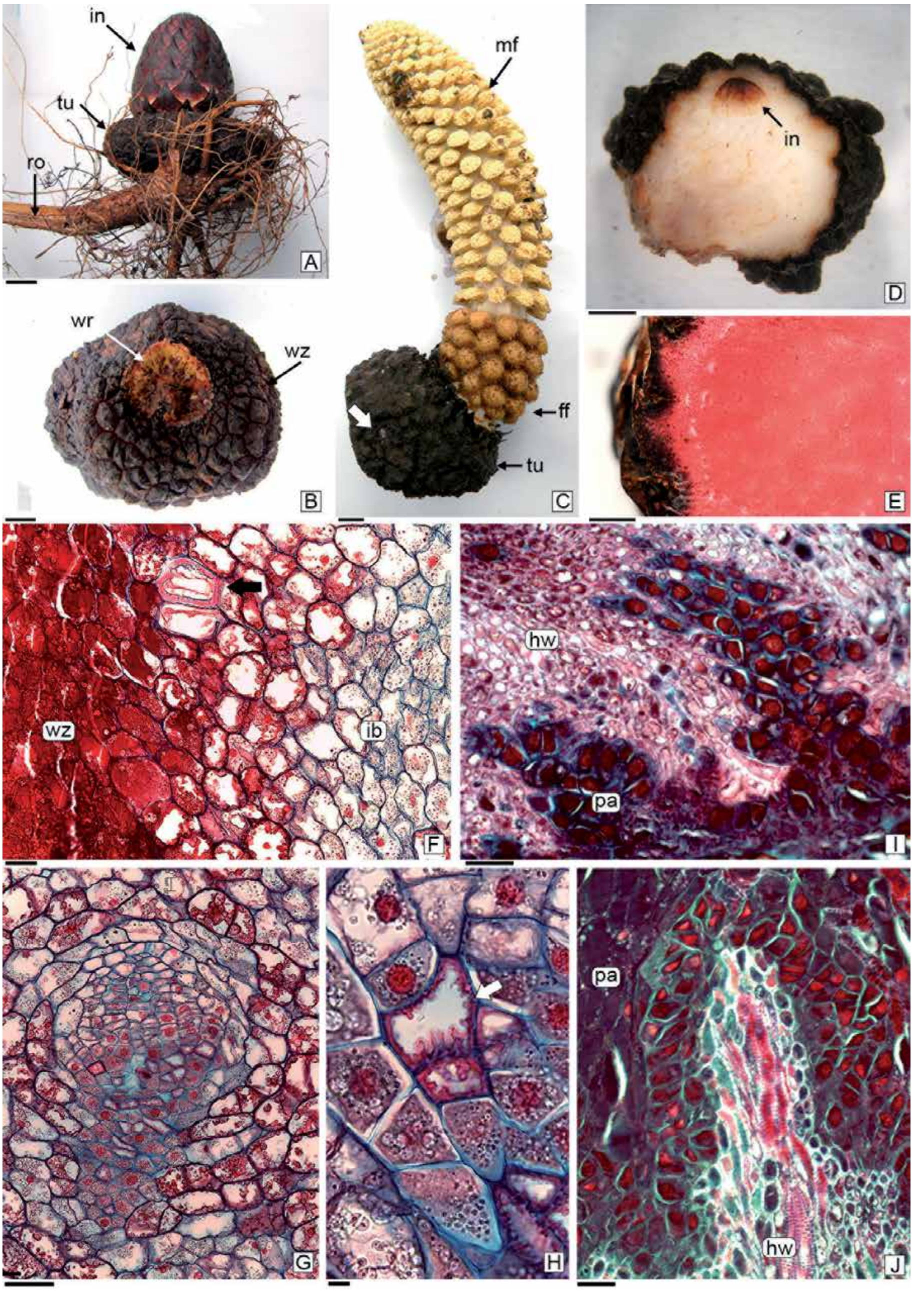

**Figure 1.**
*A, B, E–H: L. leandri; C, D, I, J: L. mirabile. A: Hypertrophied root (ro) of P. rigida with tuber (tu) and immature inflorescence (in) fully covered by scales. B: Tuber showing the warty surface (ws) and the woodrose host/parasite interface (wr). C: Tuber with fully developed inflorescence showing the pistillate (pf) and staminate flowers (sf), the arrow indicates the site where the tuber broke away from the host root. D and E: Longitudinal section through unfixed small tubers showing the warty surface zone, natural color of internal body and the primordium of inflorescence. F: Warty surface zone (wz) showing a group of brachysclereids (arrow) and parenchyma cells of the internal body (ib). G: Transection of vascular bundle. H: Detail of vessels with wall ingrowths (arrow). I and J: Host wood (hw) intermixed with parasite cells (pa). Scales, A,L: 2 cm; B,D: 1 cm; E: 0.5 cm; F-G,I-J: 50 μm; H: 10 μm.*

Immature inflorescences are completely covered by black scales (**Figure 1A**). The scales are shed at flower maturity, starting in the medium region where the staminate flowers are first exposed (**Figure 1C**).

### 2.1 Tubers / host Interface

The root where the parasite is installed stops its growth and elongation after infection, forming a woody gall (**Figure 1A**) [20, 21]. Tuber development is always observed in woody roots, larger than 1 cm in diameter. Infections are focused on the cambium, where the parasite cells divide intensely producing a strong undulation of the cambial zone (**Figure 1I**). One of the main consequences of the infection is the alteration of the axial and radial systems typical of secondary wood (**Figure 1J**).

In the affected xylem, the vessels are narrow and abundant, oriented in concentric rings. The fibers between the vessels are replaced by lignified parenchyma cells, with the same circular distribution of vessels. In the phloem, the tangential bands of the normal wood are almost completely replaced by parenchyma cells, very few fibers, and cells with crystals can be observed, disorganized and dispersed, but no sieve tubes elements are detected. This interaction of the host tissues (both xylem and phloem) with those of the parasite was the origin of the choraloid design of the interphase.

## 3. Structures of flowers

### 3.1 Staminate flower

Each staminate flower is composed of two stamens and 1–2 perianth pieces. *L. mirabile* has a single yellowish-white piece, and there are two deep red pieces in *L. leandri* (**Figure 2A–C**) [31, 32]. In both species, these pieces are fleshy cushion-like organs, formed of tanniniferous parenchyma with vascular supply, and covered with a unistratified epidermis with scattered sclereids. The epidermis lacks stomata and is covered by a thin cuticle (**Figure 2D**).

The stamens are composed of a short filament, and bitechae anthers. In the anther of *L. leandri* the anterior and posterior pollen sacs of each theca are about the same length, but the thecae are inserted at different heights in the connective tissue (**Figure 2E**). This displacement is the result of the adjustment that the thecae must undergo due to the presence of the upper piece of the perianth. In *L. mirabile* the anterior pollen sacs of each theca are 3/4 of the length of the posterior sacs (**Figure 2F**).

Each anther is tetrasporangiate (**Figure 2G**). The mature anther wall consists of the following layers (**Figure 2G–J**): unistratified epidermis with tanniniferous cytoplasm, without any stomata; bi-stratified endothecium with U-shaped fibrous thickening and tanniniferous cytoplasm; one middle layer, which in *L. mirabile* also has fibrous thickenings, forming a tri-stratified endothecium (**Figure 2G**). The tapetum is unistratified, and of secretory type (**Figure 2H**). No orbiculae are observed on the tapetal membrane and/or anther locule. The connective has a single vascular bundle; the surrounding parenchyma cells show the characteristic fibrous thickening of the endothecium, both on the dorsal and ventral sides of the connective. The development of the anther wall can be considered as being within the basic type proposed by Davis [39], although there are variations in the behavior of the middle layers, which develop thickening, constituting a pluristratified endothecium at maturity.

Primary sporogenous cells undergo several mitotic divisions, giving rise to uninucleate microspore mother cells. In meiosis I tetrahedral tetrads are formed by simultaneous cytokinesis, which remain surrounded by a callose wall. Mature pollen grains are released in a bicellular state, they are spheroidal, tricolpate-sincolpate, with a thin exine, and no protruding sculptures (**Figure 2K**).

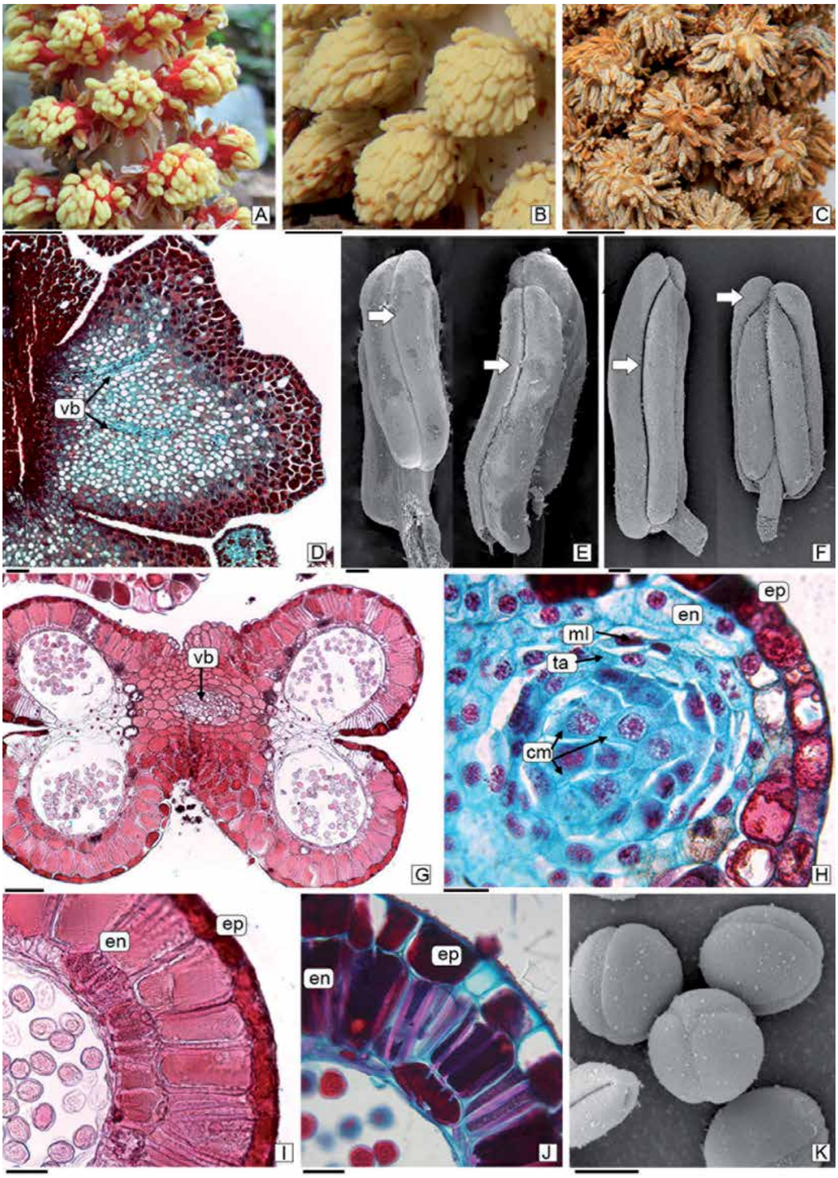

**Figure 2.**
*Staminate flowers. L. leandri: A, D, F, H, J. L. mirabile: B, C, E, G, I, K. A and B: Mature inflorescence without scales, detail of secondary branches showing red perianth pieces and staminate flowers. C: Staminate flowers with dehiscent anthers. D: Stamens, anterior (left) and abaxial (right) views, showing offset in the insertion of thecae. E: Adaxial (left) and lateral (right) view showing different lengths of the pollen sacs. D and E: Arrows mark the lines of dehiscence. F: Longitudinal section of perianth piece with vascular bundles (vb). G: Transection of anther. H: Young pollen sac. I and J: Mature anther walls. K: Pollen grains. Abbreviations: cm: Microspore mother cells; ep: Epidermis; ml: Middle layers; en: endothecium; ta: Tapete. Scales: A–C: 1 cm; D, E: 0,2 mm; F: 0.1 mm; G, H: 0.2 mm; I, J: 20 µm; K: 10 µm.*

### 3.2 Pistillate flower

In both species of *Lophophytum* the pistillate flowers lack a perianth and are reduced to one pistil formed of a superior ovary, two styles and capitated stigmas (**Figure 3A**–**C**) [31–33]. The ovaries of *L. leandri* are arranged compactly in the axil of clavate bracts. These bracts have a thin basal portion and a capitated distal portion, which covers the top of the ovary (**Figure 3A**). *Lophophytum leandri* has

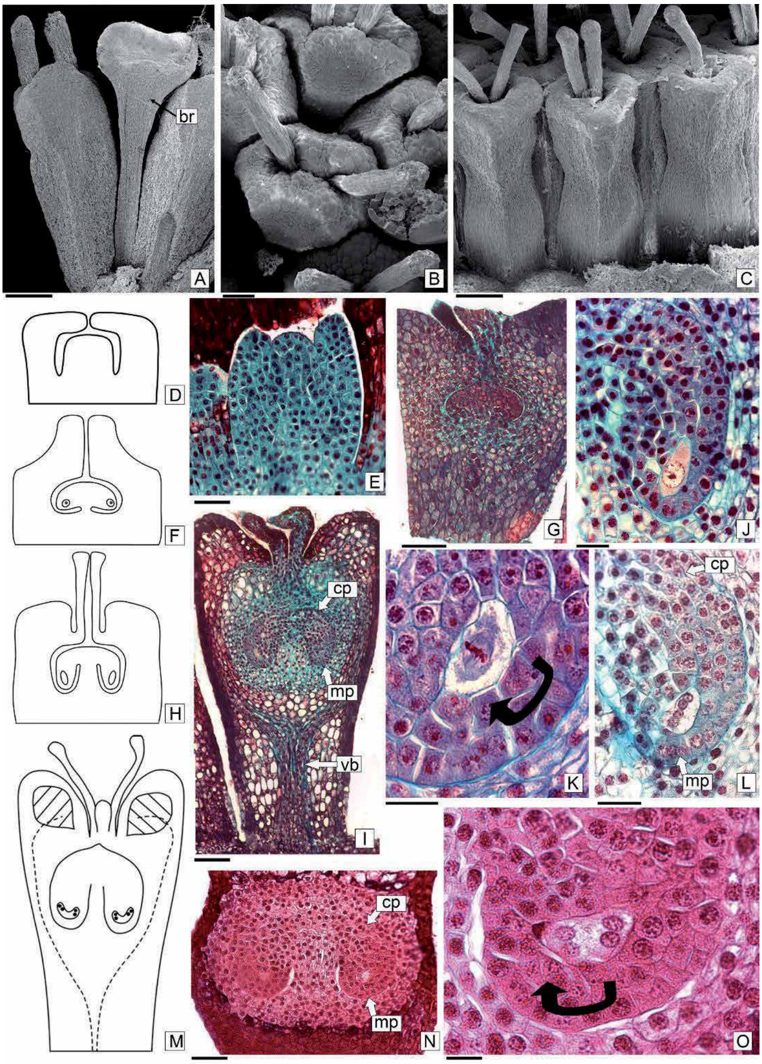

**Figure 3.**
*Pistillate flowers. L. leandri: A, B, E, G, I, K. L. mirabile: C, J, L, N, O. A–C: Scanning electron microscope of pistillate flowers, showing bract (br) and stigma positions. D, F, H, M: Successive stages of ovary and ovule development. D and E: Longitudinal section of ovary at the early stage, cup-shaped with a central placenta. F and G: Ovary with bilobed placenta. H and I: Ovary with two ategmic ovules in stages of megaspore mother cell. J: Megaspore mother cell. K: Metaphase I. L: Linear tetrad of megaspores. M–O: Tetranucleate embryo-sac in horizontal position. O: Details of four megasporic nuclei separated by a central vacuole. Note: All photographs were taken with the ovules in the same position (photo A); arrows indicate the direction of rotation of the megaspore mother cell/embryo-sac. Abbreviations: cp: Chalazal pole; mp: Micropylar pole; vb: Vascular bundles. Scales: A, C: 0,5 mm; 0,2 mm: B; 100 μm: E, G, I, N; 50 μm: J, K, L, O.*

two cavities in the apex of the ovary, on which two separate styles are inserted respectively (**Figure 3B**). *Lophophytum mirabile* lacks bracts, the ovary is cylindrical and is also compactly arranged, acquiring a well-defined hexagonal or square shape. The apex of the ovary has a single cavity where both styles are inserted (**Figure 3C**).

During the development of pistillate flowers, the pistil primordium is initiated from hemispheric meristems on the surface of secondary rachis of a young inflorescence (**Figure 3D** and **E**). In *L. leandri*, the bracts develop first, and then ovarian primordia are formed in their axils. In *L. mirabile* only ovarian primordia are formed. In both species the meristem acquires a cup-shaped form. In the center of the pistil a sub-spherical protrusion corresponding to the placenta is developed. Until the closure of the ovary, the ovarian cavity is unique and almost undetectable; the placenta is located at the base of the ovary and is perfectly distinctive from the tissue of the carpels.

The placenta grows occupying the whole cavity of the single locule, the upper end acquires a sharpened shape and it is united postgenitally to the top of the carpels; therefore the mature ovarian cavity is divided into two locules (**Figure 3F** and **G**). The placenta is laterally enlarged giving rise to two-lobed projections in each locule, which are 90° curved towards the base of the ovary, resulting in two ovule primordia. This primordium of ovules occupies the entire cavity of the locules.

Two ategmic ovules are inserted on the upper portion of a central column placenta. The two locules are almost completely obstructed by the ovules (**Figures 3I** and **4A, B**). As the ovules develop, they are reduced to the nucellus and lack of integuments, but the female gametophyte is developed inside (**Figure 2J–O**). The term micropyle is not applicable in its usual sense, therefore it has been designated as a "micropylar pole" at the apex of the nucellus, which is where the megaspore mother cell develops. Vascular supply is absent in the placenta and the ovule, so the chalaza and the funiculus cannot be defined. Therefore, the basal portion is called the "chalazal pole" where the nucellus is attached to the placenta (**Figure 3D**, **E**, **J**, **L**, **N**, **O**).

The mature ovary wall consists of several layers of parenchyma and two zones are recognized: the outer layers are tanniniferous and the internal layers have starch grains (**Figures 3I**, **N** and **4B**). Different types of sclereids have been differentiated between the two zones: both species present a brachysclereid ring in the apical portion of the ovary (**Figure 4C**). In *L. mirabile* four clusters of macrosclereids are also formed at the base of the ovary, which alternate with the vascular bundles. Vascular bundles show scarce development; elements of the xylem vessels have ingrowths.

The styles are solid and are formed of elongated parenchymal cells with dense tanniniferous cytoplasmic contents. Cells of the center of style are smaller but are not differentiated into transmission tissue. The stigmas are capitate and have depressions on their surfaces, where adhered pollen grains can be observed.

Megasporogenesis [31–33]: In both ovules, a conspicuous cell develops below the nucellar epidermis and acquires archesporial features, this cell gives rise to the megaspores mother cell (MMC) (**Figure 3J**). The MMC meiosis I and II happen normally, resulting in four identical nuclei, which are arranged a linear tetrad or "T" shaped (**Figure 3K**, **L**). These four nuclei migrate in pairs to opposite poles of the cell, all of which participate in the formation of a tetrasporic type of embryo-sac (**Figure 3M–O**). The polarity of the embryo-sac is determined by the displacement of the nuclei and the presence of a central large vacuole. At this stage of the tetranucleated coenocyte the embryo-sac is in a horizontal position relative to the main axis of the gynoecium, this apparent shift is due to the growth of the ovule by increased cell division on the dorsal side of the nucellus.

Megagametogenesis: During the migration of the two pairs of nuclei to opposite poles, the four-nucleate megagametophyte extends and becomes "J" shaped (**Figure 4A**, **D**). Each pair of nuclei undergoes a mitotic division creating an eight-nucleate embryo-sac (ES). Four nuclei remain near to the chalazal pole and the other four move towards the micropylar pole, separated by vacuoles. Three nuclei remain at each end of the ES, and the fourth nucleus moves towards the center of the central cell, where the cytoplasm is gradually increased in density (**Figure 4E**). The three nuclei at the micropylar end of the embryo-sac are compacted and reduced; cytokinesis occurs at this pole and creates three antipodes (**Figure 4F**). At a later stage, when the triad of nuclei at the chalazal pole is

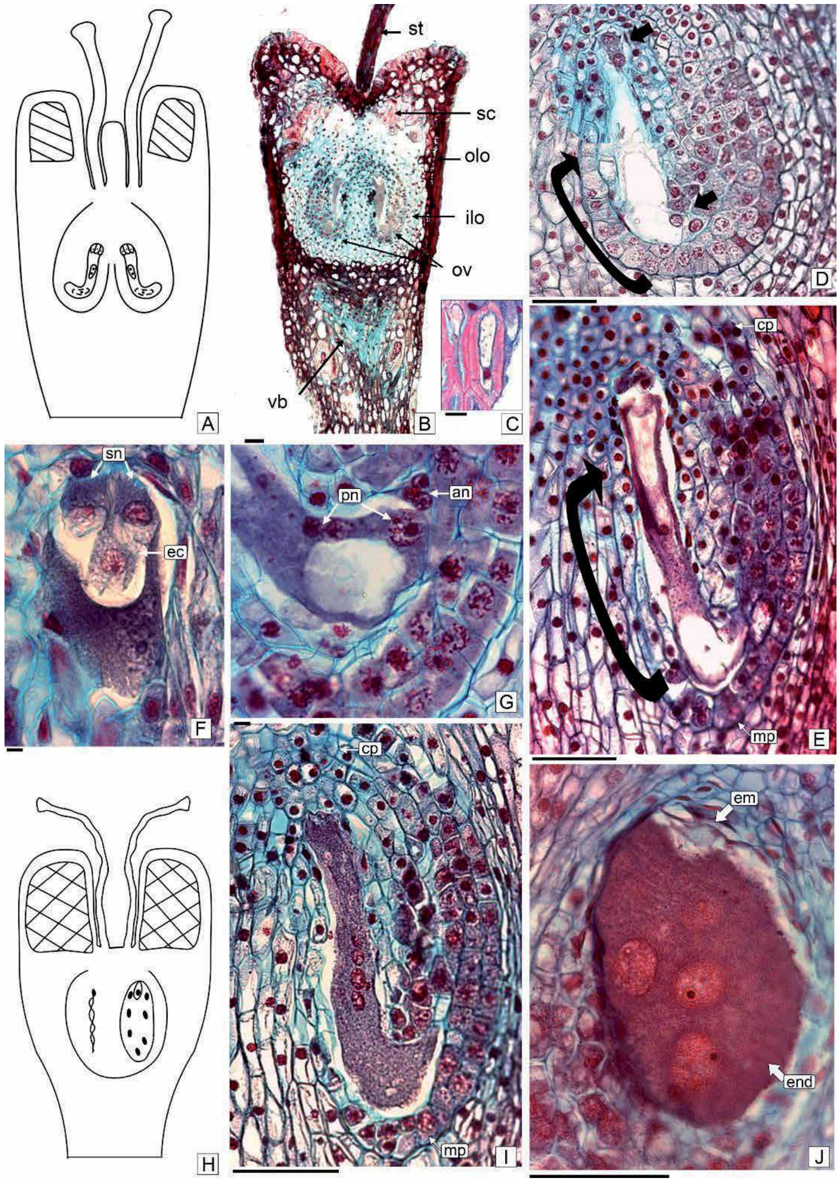

**Figure 4.**

*Embryo sac (ES) development in L. leandri; A and B: Scheme and light microscopy photo of ovary, showing position of ovules and embryo sacs. C: Detail of sclereids. D: Tetranucleate ES. E: Tetrasporic, 8-nuclei ES (arrow indicates the direction of rotation of ES). F: Antipodes (an) and part of the central cell (pn). G: Egg-cell (ec) and the pair of synergids with filiform apparatus (sn). Abbreviations: cp: Chalazal pole; Ilo: Inner layer of ovary; mp: Micropylar pole; olo: Outer layer of ovary; ov: Ovule; sc: Sclereids; st: Stigma. Scales: B, D, E: 100 μm; C, F, G: 10 μm.*

organized as the egg-apparatus, the antipodal cells disappear. At the chalazal pole of the ovule, the typical egg-apparatus is developed, composed of an egg-cell in a central position and two adjacent synergids-cells, all of which determine an inverted embryo-sac (**Figure 4E** and **G**). The synergids-cells are smaller than the egg-cell; their vacuole being oriented towards the center of the megagametophyte, and a prominent filiform apparatus is developed. This tetrasporic, 8-nuclei embryo-sac follows an Adoxa type organization (**Figure 4F**).

## 4. Embryology

Despite the fact that a large number of pollen grains are produced, no pollen tubes or fertilization can be observed [31, 33, 34]. The endosperm and embryo are formed in the absence of double fertilization. The formation of the endosperm occurs in three stages. The fusion of the polar nuclei has not been seen, in contrast, endosperm formation starts with a series of free nuclear divisions that result in a coenocytic structure of up to 12 nuclei, with six being the most frequently recorded (**Figure 5A** and **B**). The second stage in endosperm formation involves nuclei fusion (**Figure 5C**). An interruption occurs in the coenocyte wall and the nucellar cells wall, and then the nuclei of the coenocyte and the nucellar cells are fused. This fusion allows the entrance of both nuclear and maternal cytoplasmic material inside the coenocyte. Once inside the coenocyte, all the fused nuclei become one giant nucleus, reaching 120 x 60 μm in size (**Figure 5C**). The third stage of endosperm formation is the sequence of karyokinesis, producing about 12 nuclei of equal size (50 to 70 μm diameter) (**Figure 5D**). Cytokinesis then takes place, which generates the endosperm cells (**Figure 5E** and **F**). This process only occurs in one embryo-sac as the second embryo-sac is reabsorbed.

The egg cell divides forming a four-cell globular embryo only when the endosperm cytokinesis is complete (**Figure 5E** and **F**). The mature embryo is undifferentiated, globular and it is composed of up to about 24–32 cells; it completely lacks any cotyledons or outline of a radicle (**Figure 5G–I**). No suspensor formation has been verified.

The hypothesis of the existence of parthenogenesis is proposed for the Argentine species of *Lophophytum*, justified by the formation of embryo and endosperm in the absence of fertilization and the beginning of endosperm development is autonomous.

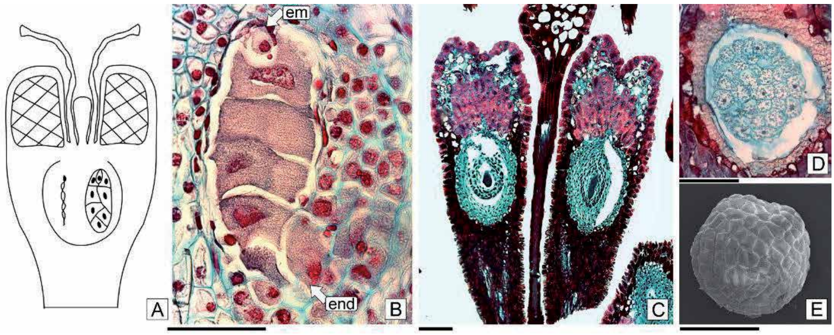

**Figure 5.**
*A, E: scheme of endosperm development. A B: cygote (em) and endosperm cytokinesis. C: fruits. D-E: seeds (light and scanning microscope). Scales: B: 100μm; C: 200μm; D-E: 500 μm.*

## 5. Fruit and seed

In *Lophophytum* the fruits are achenes, reaching an average size of 2.5 x 1.5 mm in *L. mirabile*, and 2 x 1.2 mm in *L. leandri* [31, 34]. As they are indehiscent, they constitute the unit of dissemination or diaspore. The epicarp is derived from the outer epidermis of the ovary, with cells completely occupied by tannins; those in the upper portion of the ovary are differentiated into sclereids (**Figure 5G**). In *L. mirabile* the sclereids occupy the apical and basal portion of the fruit, and in *L. leandri* they spread along its side walls reaching the upper third of the fruit. The mesocarp is made up of parenchyma cells, also with tannins. The endocarp develops from the internal epidermis of the carpel which differentiates into brachysclereids (**Figure 5H**).

The ovule nucellus tissue is digested during endosperm formation, therefore the seed lacks a seed coat. The mature seed is only made up of the endosperm and undifferentiated embryo; its cells completely lack tannins that are omnipresent in the remaining fruit (**Figure 5H** and **I**). The seed is spheroidal with a small wedge towards the upper part of the ovary (**Figure 5I**).

The inflorescence of *Lophophytum* has between 50 and 65 secondary rachises with pistillate flowers, each bearing between 350 and 700 fruits, with each plant producing an average of 25,000 fruits. These may remain aggregated since they are on the secondary rachis and they do not fall until the inflorescence axis becomes decayed. However, in both species of *Lophophytum* the larvae of Oxycorynus consume the parenchymatous axis of the secondary rachis and thus the fruits are separated from the rachis, facilitating their dispersal [35].

It has been recorded that the rodent *Dacyprocta aguti* L. (Rodentia, Agoutidae) digs up the plants of *L. mirabile* to consume the tubers and inflorescence axes, especially the staminate flowers. The female portion, with fruits, remains disintegrated in the ground. In the NW of Argentina, inhabitants have mentioned that the rodent *Agouti paca* L. (Rodentia, Agoutidae) consumes the plants of *L. leandri* very assiduously. However plants gnawed by animals have never been observed in the populations of *L. leandri* under observation in Misiones [31].

## 6. Taxonomic value of floral characteristics

A vegetative body lacking stems and leaves makes it necessary to look for other characters of taxonomic value, such as those related to the floral parts [31]. Several morphological characteristics of the staminate and pistillate flowers allow easy distinction of material from the two Argentine species of *Lophophytum* (**Table 1**).

In flowers of *L. leandri* the perianth pieces have been described by Burkart [25] as reduced ovaries. In the present study it is confirmed that the fleshy excrescences accompanying the stamens do not show any female reproductive structures that could be considered as reduced ovaries, nor any remnants of them. Hansen

| | ***L. leandri*** | ***L. mirabile*** |
|---|---|---|
| PF: clavate bracts | present, the flowers are in the axils of the bracts | absent |
| PF: insertion of styles in top of the ovary | two cavities | one cavity |
| PF: sclereids in ovary | one ring of sclereids at the top of the ovary | four clusters of sclereids in the basal portion of the ovary |
| SF: number and color of the perianth pieces | two deep red pieces | a single yellowish-white piece |
| SF: length of the pollen sacs | the anterior and posterior pollen sacs of each theca are about the same length, but the thecae are inserted at different heights in the connective | the anterior pollen sacs of each theca are 3/4 of the length of the posterior sacs |

**Table 1.**
*Differential morpho-anatomical characteristics of pistillate flowers (PF) and staminate flowers (SF).*

[17, 26] described them as parts of the perianth and used them in the taxonomic delimitation of the species.

In the core Eudicot, the absence of perianth parts is not common, except in wind-pollinated plants and the Balanophoraceae [16, 40]. In the *Lophophytum* species studied, the protective function of flowers is carried out by woody bracts covering the inflorescence. *L. leandri* shows an additional second protective line, represented by the clavate bracts, which accompany each pistillate flower.

## 7. The evolutionary trend in the gynoecium and embryo sac of the Balanophoraceae

The analysis of the anatomy and development of pistillate flowers and the study of the functional architecture of the ovules, carpels and embryo-sac provide embryological data of great importance to complement the phylogenetic studies of the family Balanophoraceae, and even of the order Santalales.

The presence of four vascular bundles in the ovary, two ovules, and two styles and stigmas, suggests the occurrence of two carpels in *Lophophytum*. The bi-carpellated ovary is a widespread condition in the Balanophoraceae s.l., except in *Balanophora* [41], and *Dactylanthus* [42] that have a single carpel and one style.

The reduction of ovules, fusion of the ovules with the carpels, and the number of loculi are variable characteristics in the family (**Table 2**). The complete fusion between the ovules and the carpels determines the absence of a locular cavity in *Balanophora* [41] and Helosis [46–49]. In *Corynaea* [45] and *Rhopalocnemis* [44] they have a single locule due to the absence of postgenital fusion. In *Lophophytum*, the two ovarian cavities are determined by the postgenital fusion of the tip of the placenta with the apex of the ovary.

The ovules of *Lophophytum* are the only ones in the whole family that are still distinguishable from the placenta, although they are ategmic. In *Corynaea*, *Dactylanthus* and *Rhopalocnemis* [42, 44, 49] the term placental-nucellar complex (PNC) has been used instead of ovules, as the boundary between the nucellus and the placenta is blurred. The most extreme reduction occurs in *Helosis* and *Balanophora*, where there are no recognizable ovules; the ovary, placenta and nucellus are completely fused into a compact mass where the embryo sacs develop, there is no ovarian cavity [41, 44, 50]. All genera in the family, except *Balanophora* (with 1 MMC), have two MMCs, but only one ES completes its development and forms an embryo.

| Genera | Locules | MMC | Embryo-sac | | | References |
|---|---|---|---|---|---|---|
| | | | origin | type | shaped | |
| *Lophophytum* | 2 | 2 | 4-sporic | *Adoxa/Polygonum* | J | [18, 31, 32, 43] |
| *Rhopalocnemis* | 1 | 2 | 1? | — | Straight | [44] |
| *Corynaea* | 1 | 2 | 2-sporic | *Allium* | Straight | [45] |
| *Helosis* | absent | 2 | 2-sporic | *Helosis* (four-celled ES) | Straight | [46–49] |
| *Balanophora* | absent | 1 | 1,<br>4-sporic | *Polygonum* | U/J | [50, 51] |

**Table 2.**
*Morpho-embryological features known for pistillate flowers in species of Balanophoraceae s.l.*

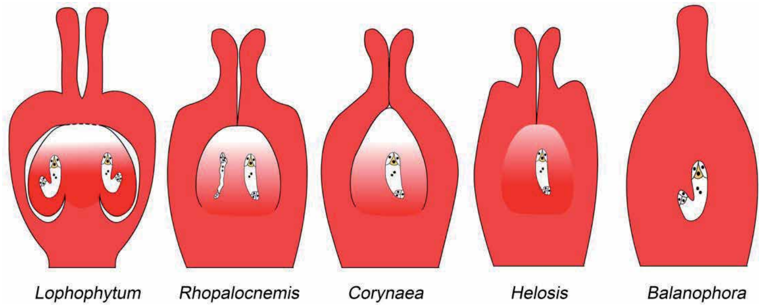

**Figure 6.**
*Hypothetical line of sequences of congenital fusion and reductions within the gynoecium of the Balanophoraceae at the embryo-sac development stage. Without scales bars.*

Among the genera of the family, monosporic, bisporic and tetrasporic ES have been described, with a bisporic ES with Allium-like development being the predominant type (**Table 2**). A new type of embryo sac (bisporic four-celled embryo sac, provided with a typical egg apparatus and a uni-nucleated central cell) has been described for Helosis [49].

In the **Table 2**, a hypothetical line of successive steps that includes several major modifications, such as: a gradual reduction in the integuments; gradual loss of identity of the ovule and placenta, both structures that are still recognized in *Lophophytum*, while in the other genera of the Balanophoraceae it is not possible to discern discrete ovules, presenting a PNC, a consequence of this reduction is the loss of the chalaza, funicle and absence of vascularization; and progressive fusing of the placenta/ovules/carpels, with the consequent reduction of the ovarian cavity, until its complete disappearance, which is found in *Helosis*, *Balanophora* and in some *Loranthaceae* (**Figure 6**).

*Lophophytum* [31] and *Balanophora* [50] studies show the rotation of the ES growing within the nucellus, with the egg- apparatus oriented towards the apex of the ovary, in the region that is more favorable to pollen tube access.

## 8. Synchronization of parasite and host life cycles

### 8.1 Host, environment, and distribution

#### *8.1.1 Lophophytum leandri*

- Host: *Parapiptadenia rigida* (Benth.) Brenan. A leguminous tree, of 10 to 15 m in height, generally associated with the banks of watercourses. Deciduous in the studied areas. Common name "angico colorado".

- Vegetation: humid forest, composed of a compact mass of 20 to 30 m in height, formed of at least four strata: large trees, shrubs, lianas, and epiphytes.

- Distribution: In Argentina *L. leandri* coexists with *P. rigida* in Misiones and to a lesser extent in Corrientes (**Figure 7**). Much of the environment of the species *L. leandri* has been modified by anthropogenic action and the existing and more accessible populations are being decimated by the local people, who commercialize them as medicinal and ornamental plants.

**Figure 7.**
*Map of location of species of Lophophytum and their host in Argentina.*

### 8.1.2 Lophophytum mirabile

- Host: *Anadenathera colubrina* (Vell.) Brenan. A leguminous tree, of 10 to 25 m in height, that grows on riverbanks, generally near watercourses where it is considered a slope fixer due to its rooting type. Characteristic mameloned bark. Deciduous in this area, in August–September it is found defoliated, with dry pods still on the branches. Common name "cebil colorado".

- Vegetation: pedemontane forest up to 600 m, riverbanks in forests with a predominance of A. colubrina.

- Distribution: *L. mirabile* subsp. *bolivianum* and its host were found growing in the provinces of Salta and Jujuy (Argentina), **Figure** 7). In the Calilegua National Park (Jujuy) there are large populations of the parasite and host, representing an important area for their conservation; this species is little known in the northwest and its commercialization has not been recorded as in the case of *L. leandri*. For both species, the areas recorded in the literature and collected in the past are currently being used for agriculture.

## 8.2 Host/parasite relationship

In the study area, *L. leandri* was found parasitizing exclusively on specimens of *Parapiptadenia rigida* and it was found that it carries out its entire cycle connected to it. Likewise, *L. mirabile* was found parasitizing roots of *Anadenanthera colubrina* var. *cebil*, on which it fulfills its entire life cycle [31]. Both are obligate parasites.

Based on the above descriptions, a schematic representation of the reproductive cycle of the Argentine species of *Lophophytum* has been established. The morphological changes of the structures present in both the pistillate and the staminate flowers are correlated with data on their embryology at progressive stages of development. In **Figure 8** it can be seen that the upper part shows anther and microgametophyte formation. In the central region the ontogeny of the pistillate flower and development of the megagametophyte are represented up to fruit formation. The lower region shows the tuber and inflorescence stages. The vertical lines link the developmental stages between the staminate and pistillate flowers on the same inflorescence. The reproductive cycles of both species are completed in 90 days, developing between the months indicated on the timelines for each species.

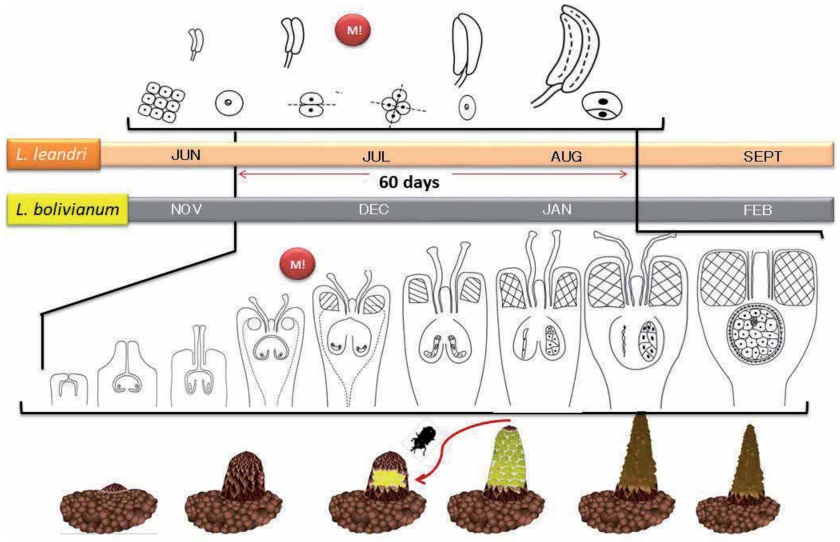

**Figure 8.**
*Schematic representation of the reproductive cycle of species of Lophophytum over time.*

The flowering of *L. leandri* is concentrated between July and August (**Figure 8**). During this period, the host is at the end of its winter dormancy, with practically no foliage and with pods still attached to the branches. These pods open and drop seeds simultaneously with the flowering of *L. leandri*. Seeds of *P. rigida* were found germinating among mature inflorescences already fruiting and with seeds of *L. leandri*, which are generally distributed at the foot of *P. rigida* trees. The seeds of *P. rigida* germinate immediately upon dispersal; they have no dormancy period. In mid-November *P. rigida* resumes vegetative growth, by which time the inflorescences of *L. leandri* are completely disintegrated. The weather throughout this period is humid and conducive to the development of the host seedlings.

In September, specimens of *L. mirabile* have been found with a tuber and the scaly peduncle of the inflorescence still underground, without any developed reproductive structures (**Figure 8**). In November A. colubrina is in full bloom and with regrowth. *L. mirabile* starts flowering at the end of November which may continue until the end of February. Although the seeds of A. colubrina var. cebil are disseminated before the flowering of *L. mirabile*, they have to become scarified in order to germinate, so the appearance of *A. colubrina* var. *cebil* seedlings coincides with the rainy season and with the flowering of *L. mirabile*. In this case, too, the pods and seeds of the host are usually found very close to the plants of *L. mirabile*, and seedlings are even found around the inflorescences of the parasite.

It has been recorded that the seeds of both the host trees (*P. rigida* and *A. colubrina*) fall underneath the canopy of the tree, directly onto the mature infructescences of the parasites. The legume embryo germinates rapidly and it is common to see the young legume seedlings growing directly on the decayed *Lophophytum* infructescences, maximizing the possibility of contact between the roots and the *Lophophytum* embryo. In both pairs of species (*Parapiptadenia*/*L. leandri* and *Anadenanthera*/*L. mirabile*) the time of germination of the legume seeds coincides with the time of the parasite fruit production which would facilitate close contact between the taxa for the establishment of parasitism. It also shows a process of co-evolution of each pair of species in relation to the environment in which they live. Unfortunately, it has not been possible to collect material that shows the morphogenesis of this process, and more collections are needed.

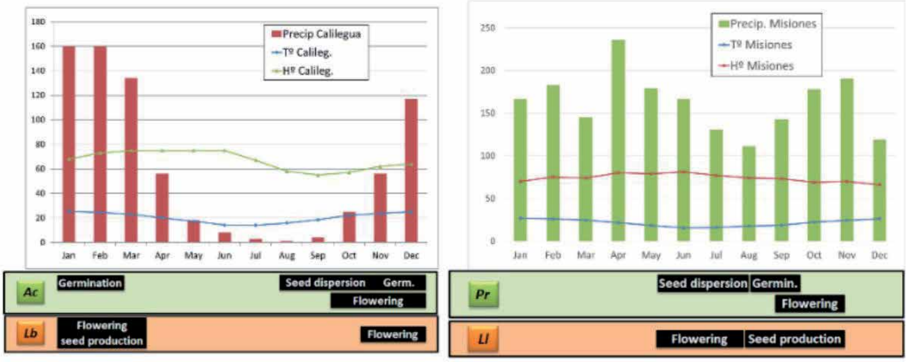

**Figure 9.**
*Phenological stages of the parasites, their hosts and the climatic data of their respective environments over the year (Ll: L. leandri, Lb: L. mirabile, Ac: A. colubrina, Pr: P. rigida; Precip: Precipitation, T°: Temperature, H°: Humidity).*

During the six years of observations [31], phenological data were collected on both the parasitic species and their hosts. Climatic data were also collected for the two regions of Argentina where this parasitic association occurs. Graphs were made comparing the temperature, humidity, and precipitation data with the main phenological stages of each parasite and its host (**Figure 9**). Thus, it was possible to interpret the phenological events of the plants (both parasite and host) better in relation to the climate. In all the years of observations, we have never detected a host tree showing any symptoms of damage caused by the holoparasites. We have collected specimens that were on trees many years old (more than 30 years) and that were vigorous, fulfilling their reproductive cycle with apparently normal flowering and fruiting.

## 9. Conclusions

In the vegetative bodies of *Lophophytum*, like other members of the Balanophoraceae, organs such as leaves, stems or roots are completely absent [1, 3, 20, 21, 31, 52, 53]. The reductions are also extreme when considering the anatomical structures, such as typical meristems or epidermis, and even stomata are absent. The vegetative body is covered by several layers of tanniniferous parenchyma and sclereids, which are progressively detached, similar to a peridermis. The interface between the parasite and the host has a choraloid design, which facilitates the exchange of both water and photosynthates from the vascular tissues of the host legume towards the *Lophophytum*.

In contrast to the strong reductions in the vegetative body, the staminate flowers show reductions only in their sterile floral parts. The development processes of the anthers, microsporogenesis and microgametogenesis occur normally and in correspondence with the antecedents of the majority of the angiosperms studied, and there are no substantial differences between the two species analyzed [32]. The secretory and uninucleate tapetum characteristics are shared with other genera of the family, such as *Helosis* [47–49], and *Corynaea* crassa [45].

The pistillate flowers are another example of the absence of a perianth, but here the reduction of parts also extends to the reproductive structures [31, 33, 34]. The absence of integuments determines the presence of ategmic ovules. The lack of differentiation of the chalaza, funiculus and vascularization makes it very difficult to establish a concrete boundary between the placenta and nucella. The terms anastroph/orthotroph are not applicable in *Lophophytum*. Differentiation of the megaspore mother cell is the feature used to establish the micropylar and chalazal poles. The megagametophyte is of the tetrasporic type, with 8-nucleate nuclei at the maturity of an *Adoxa*-like organization, with the typical egg apparatus. *Lophophytum* is a clear case of megagametophyte inversion, confirmed by ontogenetic studies of numerous flowers and not as isolated cases [34]. The embryo sac develops aggressively within the nucellus and rotates during megasporogenesis and megagametogenesis, finally acquiring a "J" shape with the egg apparatus oriented towards the chalazal pole and the antipodes towards the micropylar pole. This would favor the proximity of the egg cell and the pollen tubes that will eventually enter through the styles. However, double fertilization has not been recorded, suggesting the existence of parthenogenesis.

The development of the endosperm is nuclear in nature, but has particularities, as it is possible to divide it into several stages culminating in a fully cellular endosperm [34]. In *Lophophytum*, similar events to those observed in the apomictic species of *Balanophora* have been recorded, such as the fact that the endosperm develops autonomously without fertilization, that it develops enveloping the zygote, which starts dividing much later than the endosperm. The mature embryo is globular and undifferentiated as in other holoparasites, such as *Pilostyles* and *Orobanche* [54–57]. They lack a seed coat, due to the absence of integuments in the ovule. The term seed in the strict sense could not be applied to the Balanophoraceae, as it has been shown that the structure is derived entirely from the embryo sac and is completely devoid of teguments, as already mentioned by Holzapfel [42].

The dispersal unit of *Lophophytum* is a uniseminated achene [16]. The diaspores of *Lophophytum* are dispersed by rodents that feed on them, separating the achenes from the inflorescence axis. Dispersal is favored by the previous action of Oxycorynus larvae on the axes of the secondary rachis [35].

From the comparative analysis of reductions and fusions in the gynoecium of the Balanophoraceae with the results observed in *Lophophytum*, a line of possible successive steps is proposed which includes several profound modifications: i) gradual loss of identity of the ovule and placenta: both structures are still recognizable in *Lophophytum*, whereas in the other Balanophoraceae they are not distinguishable. ii) gradual reduction of integuments, loss of the chalaza and funiculus and absence of vascular supply in the ovules. iii) progressive fusion of the placenta/ova/carpels, with a consequent reduction of the ovarian cavity until its complete disappearance in *Balanophora*. *Lophophytum* is the only genus of Balanophoraceae in which the ovules are still clearly identifiable from the placenta. In the other genera of the family the boundary between the ovules and placentas is blurred, so the term placental-nucellar complex is still used for these cases.

The family Balanophoraceae is an excellent example of how knowledge of embryological data expands the possibility of establishing their phylogenetic relationships [3, 4, 16, 56, 57]. Given the lack of vegetative characteristics due to the particular structure of these plants, the importance of floral characteristics for taxonomic identification is emphasized. All data acquired from the flower structure and anatomy make species identification possible.

In the family Balanophoraceae, knowledge of the germination process and the initiation of the host relationship (establishment of the initial haustorium) was only achieved in *Balanophora abbreviata* [50]. One of the unfinished points of this review is the germination process and the connection of the haustorium with the host root. Host and host specificity are revalidated, at least for the Argentine species of *Lophophytum*, where *L. leandri* spends its entire life cycle on *Parapiptadenia rigida*, whereas *L. mirabile* spends its entire life cycle on *Anadenanthera colubrina* [31]. There is a direct relationship between the life cycle of the hosts and that of the parasites with respect to the coincidence of their reproductive phases. The seeds of the parasites only mature when the host seeds are ready for germination. The flowering period of the Argentine species is concentrated in contrasting periods, with *L. mirabile* flowering in midsummer, and *L. leandri* in winter.

The studies carried out here are a clear example of the process of co-evolution between a holoparasite and its host. Each species of *Lophophytum* develops its reproductive stages at the time of year when its seeds can come into contact with the seedlings of its host, so the chances of establishing a parasitic relationship are optimized.

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## Author details

Hector Arnaldo Sato[1] and Ana Maria Gonzalez[2*]

1 General Botany, Herbarium, JUA, Faculty of Agrarian Sciences, National University of Jujuy, Jujuy, Argentina

2 Institute of Botany of the Northeast (UNNE-CONICET), Corrientes, Argentina

*Address all correspondence to: anagonzalez.ibone@gmail.com

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## Chapter 5

# Parasitic Plants in Forage Legumes – *Medicago sativa* L.

*Rozafa Fetahaj, Besarta Kabashi*
*and Arben Mehmeti*

## Abstract

*Medicago sativa* L. is one of the main forage crops widely grown throughout the world. The yield quality and quantity of the alfalfa crop are influenced by many factors. Weeds, as the most problematic pests in agriculture, compete with crops obtaining water, nutrients, light, and space, and parasitic weeds are becoming a threat to food production. Weed species, such as *Cuscuta* spp., are particularly noxious since they also directly extract valuable water and nutrients from the host plant, and in some cases can also be difficult to eradicate.

**Keywords:** parasitic plants, forage legume, weeds, *Cuscuta* spp., *Medicago sativa*

## 1. Introduction

Alfalfa (*M. sativa* L.)— as a forage species, is the more important cultivated forage in the world since at least ancient Greek and Roman times [1], as a perennial legume cultivated to provide high-quality forage in the form of hay, silage, and to a lesser extent as a grazing crop, as well as for improving soil fertility [2]. According to Putnam et al. [3], *M. sativa* L. is regarded as the most important forage crop in the world with a global hay market in 2017 of 8.3 million metric tons [4]. It is one of the world's most important forage species, due to its high nutritional quality, yields, and adaptability [1].

As a major forage protein source for livestock, alfalfa is cultivated in over 80 countries with coverage exceeding 30 million hectares [1, 5]. Besides forage quality, alfalfa shows adaptability to different environments, abundant biomass yield, drought tolerance, and more important, capacity to fix nitrogen through symbiosis with rhizobia [1, 3, 6, 7]. After harvesting in late summer or early autumn, different alfalfa varieties show diverse growth speeds, leading to differences in shoot growth height in autumn [8]. Forage quality is also dependent on various factors such as palatability, digestibility, and the final animal performance [9].

Currently, based on food production requirements globally to meet the needs of an increasing population and climate change, the decrease of agricultural lands is crucial to maximizing the yield and nutritive value of forage crops, including alfalfa production [10, 11].

Regarding irrigation and water demand, alfalfa requires significant water annually due to its high yield and long growing season (including border trips, furrows, and corrugations), but it is among the most water-use efficient crops grown under irrigation [12]. Water use by the crop to its production is high when compared to other forage crops such as forage maize, and when economic conditions permit, alfalfa is replaced by maize as a forage crop [13].

One of the current agronomic goals is to improve the performance of alfalfa plants grown at high densities, either as pure stands or as a companion crop with grasses, as this would represent an increase in production resulting from an increase in the number of shoots per unit of the area [14–16].

Given the significant yield decline by weeds in different crops, numerous studies have been carried out on various aspects of weed biology and control. Weeds affect alfalfa stands in different ways during the various stages of alfalfa production: before establishment, in the seedling stage, and established stands. Weeds reduce alfalfa production during establishment by competing with and choking out young alfalfa seedlings. Weeds also invade established alfalfa fields and reduce forage quality and alfalfa yield. *Cuscuta* spp. as a member of Convolvulaceae, plant family, are widespread weeds of parasitic plants, agronomically and economically important in terms of harvest devastation.

## 2. Weeds as a major problem in agriculture

No matter which definition is used, weeds are plants that under certain conditions cause economic and social harm to the farmers. Human activities create weed problems since no plant is a weed in nature. In the agro-ecological context, weeds are a product of the inter-specific selection brought about by humans since they began cropping, which affected the soil and the whole habitat. Weeds are classically defined as plants that spontaneously grow on a land modified by humans [17], while arable weeds are those specifically occurring in regularly cultivated fields.

Weeds are naturally strong competitors for water, space, light, and nutrients, and those weeds that can best compete always tend to dominate. Weeds can produce tens or hundreds of thousands of seeds per plant, while most crop plants only produce several hundred seeds per plant. Most weeds can germinate and become established relatively quickly. They also produce viable seeds even under environmental and soil conditions that are not favorable for most crop plants. In a general aspect, weeds, as a major problem in agriculture, compete with native plants for resources such as moisture, light, and nutrients contributing to reductions in the populations of native species and, in some cases, increasing the risk of species extinctions [18–21]. Weedy plants are considered troublesome because they are prolific and highly adaptable and often persist in large numbers in areas where they are not wanted [22, 23].

Parasitic weeds are becoming a major problem in agriculture, respectively in forage crops. Parasitism among plants is a fascinating phenomenon in which one plant establishes no mutual dependence on another. Parasitic plants have evolved at least 11 times among the angiosperms [24] and are distributed among 17 families [25]. Dodder is an agriculturally destructive weed that causes serious damage by suppressing the growth of its host, in some cases leading to host death [26]. In a general aspect, weeds compete directly and indirectly with crops for the space, water, nutrients, and light, compared to parasitic weeds, particularly noxious since they also directly extract valuable water and nutrients from the host plant. In order to extract nutrients from the host plants, parasitic weeds have evolved a unique multicellular structure termed the haustorium that invades the host, forms connections with the host vascular system, and withdraws its needed water and nutrients [27, 28].

The impact of parasitic weeds species in forage crops is noted in the early stages of germination. *Striga* species, also known as witchweeds, are widely distributed in sub-Saharan Africa, India, and Southeast Asia [29], affecting cereal crops such as maize, rice, millets, sorghum, and the legume cowpea. *Striga* causes yield losses up to 80%, often resulting in field abandonment by local farmers.

The *Phelipanche* and *Orobanche species* are widely distributed, and their hosts are not limited to cereals and legumes, but also comprise *Solanaceae* (e.g., tomato, tobacco), *Asteraceae* (e.g., sunflower), and *Cucurbitaceae* (e.g., watermelon). Geographically distributed, they affect crop production in Western Africa, the Mediterranean area but also occur in Australia, America, and Asia. For *Orobanche* crenata, legume crop losses of up to 100% have been reported in Morocco, Portugal, Spain, and Syria [30].

Weed species, such as *Cuscuta* spp. are particularly noxious since they also directly extract valuable water and nutrients from the host plant, and in some cases can also be difficult to eradicate. In addition, parasitic plants that attack host roots can inflict serious damage to crop plants before the latter emerge from the soil, making it difficult to diagnose infestations before economic losses occur. *Cuscuta* is one of the most economically detrimental groups of parasitic plants worldwide as infestation by some of its species can result in major yield losses in numerous crops [25, 26, 31–33] (**Figures 1** and **2**) (**Table 1**).

**Figure 1.**
*Alfalfa (Medicago sativa L.)—A perennial legume [34].*

**Figure 2.**
*Alfalfa (Medicago sativa L.) (host plant) and dodder (Cuscuta spp.) (parasitic plant) [35].*

| No. | Weed species | Short description |
|---|---|---|
| 1 | *Striga* spp. | Striga species belongs to the family Scrophulariaceae [36]. The genus is now classified in the family of Orobanchaceae although earlier authors placed it in Scrophulariaceae [37].<br>Most Striga-infested areas are characterized by agricultural production systems exhibiting low productivity. Striga germinates close to its hosts in response to specific chemical signals from the root exudates of the host or certain non-hosts plants [38].<br>The major agricultural Striga species are *Striga hermonthica* (Del.) *Benth and S. asiatica* (L.), *Saxifraga forbesii* (Benth.), and *S. aspera* (Willd.) Benth been reported to have sporadic effects on cereal crops in their limited locations [39]. |
| 2 | *Orobanche* spp. | Belonging to the closely related family Orobanchaceae, have no chlorophyll or leaves and are therefore totally dependent on their hosts for all nutrients. Orobanche species, considered serious pests, have the widest host ranges and heavily damage a variety of crops, including tomato, potato, eggplant, faba bean, lentil, peanut, chickpea, cucumber, cabbage, and sunflower [40].<br>Out of the 140 known species of Orobanche [41]. |
| 3 | *Cuscuta* spp. | They are obligate holo-parasites, typically exhibiting broad host ranges, and inflict serious damage to many crops [26].<br>As Cuscuta is the only parasitic genus in the Convolvulaceae family, there is a high similarity among the species within this genus [42].<br>Parasitic plants of the genus Cuscuta have no chlorophyll, or only a reduced amount, and are not usually photosynthetically active.<br>Agriculturally, the most important Cuscuta species are *C. pentagona* and *C. campestris,* which show an almost worldwide distribution and have a wide host spectrum. |

**Table 1.**
*The major parasitic plants in agriculture.*

## 2.1 *Cuscuta* spp. as a parasitic plant: Plant description

| | |
|---|---|
| Genus: | *Cuscuta* |
| Tribe: | *Cuscutaceae* |
| Family: | *Convolvulaceae* |
| Clade: | *Asterids* |

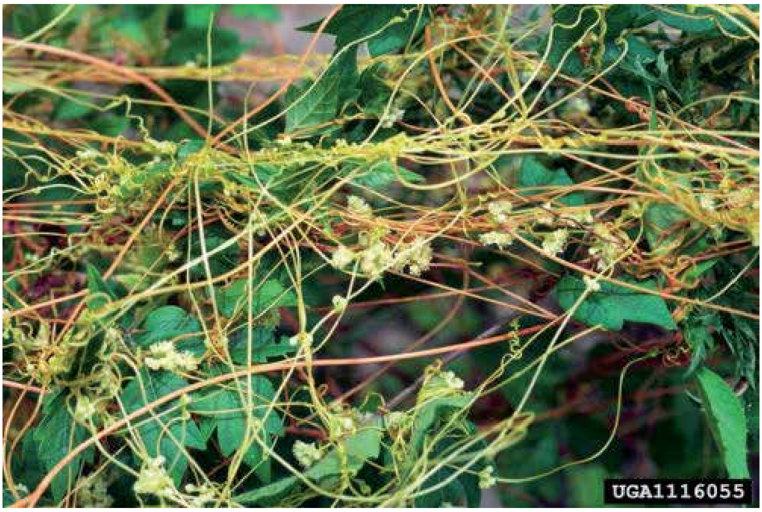

**Figure 3.**
*Cuscuta spp. [50].*

Clade: *Eudicots*
Clade: *Angiosperms*
Clade: *Tracheophytes*
Kingdom: *Plantae.*

*Cuscuta* L. (dodder) is a parasitic weed species belonging to the family Convolvulaceae [43, 44]. The genus *Cuscuta* is distinguished from other Convolvulaceae genera based on the absence of leaves, the presence of haustoria and acotyledonous embryo, arrangement of flowers in clusters, or short racemes and the presence of five-fimbriate scales within the corolla [13]. Although some dodders (15–20 species) cause economic or ecological damage to crop production worldwide as agricultural, horticultural, or exotic pests [26, 32, 45], more species are endangered or even threatened, requiring conservation efforts [46].

Regarding environmental conditions, *Cuscuta* spp. can grow in a wide variety of climates and ecosystems [47]; therefore, are considered as the third-most detrimental group of parasitic plants worldwide following *Striga* and *Orobanche* [47]. *C. chinensis* is a typical native holoparasitic plant that belonged to the *Cuscuta* genus in China, which is also known as the Chinese Dodder [48] or Tu-Si-Zi in Chinese (**Figure 3**) [49].

Dodder is prolific at seed setting and the seeds can remain dormant for 5 years or more, thus making more complex the integrated management as a weed. The seed lacks enough reserves for sustained seedling growth. The seedling contains little chlorophyll and for survival is completely dependent on finding a host within a few days of germination [51]. The germination process of *Cuscuta* is independent of the presence of chemical compounds released by host plants [52].

## 3. Management options

Successful and sustainable weed management of *Cuscuta* spp. requires an integrated approach that includes multiple strategies. There are four general weed management strategies used in alfalfa: preventive, mechanical, cultural, and chemical. To prevent and mitigate the threat of *Cuscuta* as invasive plants and agricultural weeds, quarantine legislation has been enacted worldwide (**Table 2**) [32, 46].

| Weed control type strategy | Short description |
|---|---|
| Preventive | Preventive measures such as crop rotation with non-host plants, delaying planting until fall, use of resistant varieties, and use of herbicides are effective only to an extent [53]. |
| Mechanical | Mechanical weed management offers little help in managing weeds in established alfalfa:<br>Prematurely cut to eliminate the weeds;<br>Plowing or disking before planting alfalfa;<br>Equipment should always be checked and cleaned. |
| Cultural | Planting certified seed and varieties suited for the area;<br>Maintaining proper field fertility and managing any disease or insect problems;<br>Proper irrigation timing strategy;<br>Proper harvest management. |
| Chemical | When using herbicides, pay attention to information such as the timing of application, rates of application, and types of weeds controlled.<br>A shortlist of applied herbicides [54]. For weed management in alfalfa may include the following:<br>• Metribuzin,<br>• Quizalofop-p-ethyl,<br>• Diquat dibromide<br>• Fluazifop-p-butyl |

**Table 2.**
*The integrated weed management of Cuscuta spp. strategies.*

## 4. Conclusions

- According to Putnam et al. [3], *M. sativa* L. is regarded as the most important forage crop in the world with a global hay market in 2017 of 8.3 million metric tons (ITC,2018). It is one of the world's most important forage species, due to its high nutritional quality, yields, and adaptability [1].

- Alfalfa (*M. sativa* L.)—as a forage species is the more important cultivated forage in the world, as a perennial legume cultivated to provide high-quality forage in the form of hay, silage, and to a lesser extent as a grazing crop, as well as for improving soil fertility.

- Parasitic weeds are becoming a major problem in agriculture, respectively in forage crops. Weed species, such as *Cuscuta* spp., are particularly noxious since they also directly extract valuable water and nutrients from the host plant, and in some cases can also be difficult to eradicate.

- Nowadays, in light of the need to increase food production globally to meet the needs of an increasing population and climate change, the decrease of agricultural lands is crucial to maximizing the yield and nutritive value of forage crops, including alfalfa production [10, 11].

- Successful and sustainable weed management of *Cuscuta* spp. requires an integrated approach that includes multiple strategies, including quarantine legislation [32, 46], as a preventive measure.

## Conflict of interest

The authors declare no conflict of interest.

## Author details

Rozafa Fetahaj*, Besarta Kabashi and Arben Mehmeti
Faculty of Agriculture and Veterinary, Department of Plant Protection, Germany and University of Prishtina, Hasan Prishtina, Prishtinë, Republic of Kosovo

*Address all correspondence to: fetahajrozafa@gmail.com

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Chapter 6

# A Review on the Botanical, Phytochemical and Pharmacological Characteristics of *Cuscuta* Spp.

*Khahdijeh Ahmadi, Heshmat Omidi*
*and Majid Amini Dehaghi*

## Abstract

Parasitic life is an example of interaction between two species. The result is positive for one and negative for another. Parasitic plants are more evolved than other species in the same family. *Cuscuta spp*. or dodder is one of the medicinal herbs that belong to the Convolvulaceae plant family. They are annual parasitic plants that reproduce by seed. These parasitic plants do not have any roots, leaves or chlorophyll to produce their own food. Dodders live by attaching to a host plant with small appendages (called "haustoria") and extract its necessary growth elements. The active compounds of *Cuscuta* species include flavonoids, lignans, quinic acid and poly-saccharides. Flavonoids are kinds of effective antioxidants, and polysaccharides are the effective constituents to improve the immune system. *Cuscuta epithymum* is an important herbal medicine that is effective in the treatment of liver and kidney failure, sexual impotence and vision weakness. It also prevents abortion senescence and aging. *C epithymum* possesses anticancer, immuno-stimulatory, anti-oxidant and anti-osteoporotic activities.

**Keywords:** *Cuscuta spp*., flavonoids, lignans, health benefits, medicine

## 1. Introduction

Parasitic life is an example of two-way interactions that result in positive outcomes for one species and negative for the other. Parasites are usually smaller than their host and often do not live independently and freely, and in all or at least one stage of their lives, they act on and feed on another living organism called the host. Parasites do not kill their host because in this case they also die, but in many cases, they disrupt the life of the host [1]. Parasitic angiosperms are found worldwide and in most large ecosystems, from tundra and taiga to temperate deserts and equatorial forests [2]. The effect of the parasite in plant communities is highly variable and unpredictable. Parasitic insects steal water and food from a nearby plant and alter the structure and balance of society. The effect of parasitic plants directly on the amount and volume of biomass, vegetation cycle and interaction with other nutrient levels of pollinators, vegetarians and fungal coexistence is undeniable. The dual effects of parasite can be attributed to the opposite effect of parasite in both living and non-living environments, both of which are key to the structure and function of plant communities. These plants are considered in both positive and negative directions. Many of these plants have industrial, medicinal, food and forage values, and some species can also increase biodiversity [1].

The genus *Cuscuta spp*. commonly known as dodder is one of the essential herbal constituents of pharma foods and curative tonics that are frequently prescribed to nourish various body parts. It is used to enhance the nutritional value of porridge and alcoholic beverages [3]. The genus has a rich history of folk medicinal uses, and numerous phytoconstituents of therapeutic value have been isolated and identified [4]. Various species are indigenously used to cure fits, melancholy, insanity [5], fertility problems [6], tumors [7], scabies, eczema [8], chronic ulcer, jaundice, inflammation [9], chest pain [10], fever, itching [11], osteoporosis [12], diarrhea, oedema, stomach ache, infections, measles, sores, kidney problems [13], sprain [14], alleviation of high blood pressure, leucorrhoea [15], obesity [16], migraine, amnesia, epilepsy and constipation [17].

*Cuscuta* species are among the most successful and common parasitic plants that can be found anywhere on crops and non-crops. The ability to invade different species indicates that these plants have a variety of mechanisms for attaching to host plants. Also, the chemical composition of *cuscuta* will vary depending on the host plant, so cuscuta, which is hosted by medicinal plants, can have more beneficial therapeutic effects. In any case, this article could be an opening on this topic of the *Cuscuta* parasitic species. Undoubtedly, a large number of species in each vegetation and habitat area have medicinal and nutritional values that have often been considered. Parasitic plants such as *Cuscuta* are no exception to this rule, and many parasitic species have medicinal value and have long been traditionally used.

## 2. Materials and methods

The present review covers the literature available from 1956 to 2019. The information was collected from journals, books, theses and electronic search (Google Scholar, PubMed, ScienceDirect, ESBCO, Springerlink and CNKI). Literature abstracts and full-text articles were analyzed and included in the review.

## 3. History

Aftimun is a plant used in traditional medicine of the Middle East, China, India and European countries. In 1652, the use of this plant was recommended for the treatment of Black Bile. The Chinese believe that the sauce plant increases longevity [18]. Among the many species of the genus *Cuscuta*, Aftimun is one of the plants that has the most writing in the authoritative old and new sources of the world. This plant, which lives as a parasite on other plants, has sucking organs on narrow, very thin stems resembling threads, and with these sucking organs, it penetrates into the trunks of nearby plants and uses the sap of those plants [18].

## 4. Botany

*Cuscuta*, a flowering parasitic genus was previously placed in the Convolvulaceae family, but later it was segregated as the separate family Cuscutaceae [19–22]. *Cuscuta* is an annual plant that is propagated by seeds. This plant is leafless, colorless and often without chlorophyll. It is a twisting and parasitic plant. Seeds of this plant grow in the soil and the young stem, which is thread like emerges from the soil and quickly wraps around the host plant, takes root and dips its sucking root into the bark of the stem of the plant. If a piece of the stem of this plant is placed on the host plant, it will start growing immediately. *Cuscuta*, in addition to being a parasite of green plants and feeding on their sap, causes the transmission of various plant diseases and viruses from plant to plant. *Cuscuta* fertilizes in summer and produces seeds in autumn [23].

The number of species of this plant is between 100 and 200. The difference between *cuscuta* species and other species of the family, in addition to being parasitic, is the sticky sepals and scales under the flag. Its complex yellow stem has scaly leaves. The flowers are small and a few millimeters in diameter, including sepals with a 4- or 5-part cover. Although the green color is not seen in the sauce, it has a small amount of chlorophyll and therefore cannot be called a complete parasite. However, photosynthesis is negligible in most species and by default it is parasitic in nature because it is almost entirely dependent on the host from the first days after germination. This species can be identified only through its flowers. Thus, the number and shape of the flower cover parts, the shape and arrangement of the stigma and cream, the shape and the way of opening the capsule and the shape of the scales under the flags are important indicators to identify this species [21].

Medicinally important species are *Cuscuta reflexa* Roxb. [24], *Cuscuta chinesis* Lam. [25], *Cuscuta japonica Choisy* [26], *Cuscuta australis* R. Br. [27], *Cuscuta*

**Figure 1.**
Cuscuta *plant.*

**Figure 2.**
Cuscuta *flower and seed.*

*europaea* Linn. [28], *Cuscuta gigantea* Griff. [29], *Cuscuta hyaline* Roth. [30], *Cuscuta campestris* Yuncker. [31], *Cuscuta racemosa* Mart. [32], *Cuscuta pedicellata* Ledeb. [33], *Cuscuta epithymum* L. [34], *Cuscuta kilimanjari* Oliv. [35], *Crepis kotschyana* Boiss. [36], *Cuscuta mitraeformis* Engelm. [37], *Cuscuta tinctoria* Mart [38] and *Cuscuta capitata* Roxb [39]. The usual growing season is early summer; germination starts in May; parasites invade the host by haustoria and may wither and die in the absence of a suitable host within 2 weeks [40]. Flowering starts in June and seed production in November (**Figures 1** and **2**) [41].

## 5. Medicinal uses

Potentially useful plants have been acknowledged and sequentially conveyed throughout the centuries in all societies. Some of them are used through self-medication, while others are recommended by traditional healers [42]. Plant utilization as medicine ranges from the direct administration of the leaves, seeds, barks, roots, and stems to the extracts and decoctions from different parts of the plants [43]. Many *Cuscuta* species being rich sources of diverse phytochemicals are popular components of various folk medicinal systems. *Cuscuta* species are used in traditional medicine as a purgative, diaphoretic, anthelmintic, diuretic and tonic as well as a treatment for itching and bilious disorders [44, 45]. Seeds, stem and whole plant are utilized as prescription to treat different types of ailments. *Cuscuta epithymum* is a mild diuretic and used to treat sciatica and scurvy. The fresh plant is applied to the skin against scrofula derma and scleroderma. It is associated with the health of liver and kidneys and used in various formulas. It is considered a mild laxative [46, 47].

The whole plant is dried and used as astringent and detersive [34]. Whole plant decoction of *C. campestris* is used as purgative and poultice [48]. The sap of *C. tinctoria* is used to cure ringworm and warts [38]. The juice of *C. gigantea* plant is famous as an anti-poisonous agent [49, 50]. The sap of *C. europaea* is used as a carminative, and the extract is applied to treat psoriasis [51]. Seeds of this vegetative parasitic plant are used as laxative, diuretic and pain reliever and are poisonous. The juice is used for skin treatment [52, 53].

*C. capitata* whole plant reduces the irritation of the bladder and improves urinary function [54, 55]. *C. hyaline* is used to treat chest pain [10, 14]. Its infusion is used as sores washer and to prevent abortion [11, 31]. It is antiulcer and used against culex mosquito. *C. australis* is used as laxative, anthelmintic, astringent, for treatment of sores, measles and as kidney and liver tonic, emollient, sedative and sudorific [13].

## 6. Chemical compounds of Aftimun

In the analysis of essential oil from the stems of Aftimun plant, about 81 species of compounds have been identified; the main components of the essential oil include alpha pinene, beta pinene, limonene and linalool [54, 56]. Of course, some sources have mentioned other compounds such as saponin, tannin, camphor and lignan in the composition of Aftimun essential oil. The main constituents of Aftimun seeds include camphor, resin, aluminum, calcium, sodium and potassium [54].

## 7. Phytochemical and pharmacological properties of aftimun

Aftimun (*Cuscuta* Spp. Or Dodder) is a medicinal plant belonging to the Convolvulaceae family and there are over 150 species of aftimun worldwide. This plant is a parasitic plant and is distributed all over the world except Antarctica [57, 58]. The most common type of aftimun is *C. epithymum*, which has been used in various treatments in traditional medicine [57, 59]. Previous studies have shown that some aftimun species have anti-cancer properties [57]. Studies evaluating the effects of aftimun (*Cuscuta kotschyana* and *Cuscuta chinensis*) in different cell lines including HL60, MCF7, T47D, CCRF-CEM and Jurkat (JM), show the cytotoxic properties of this plant species, although the evidence available is scarce [36, 60].

In a review study, the antiproliferative property of Aftimun (*C. epithymum*) was mentioned [61]. In another study, the effect of methanolic extract of Aftimun (*C. epithymum*) was investigated and its antibacterial and anti-cancer effects were confirmed and further studies were suggested [55]. Some Aftimun species, such as *Cuscuta reflexa*, are known to be anti-cancer and are used to treat prostate cancer, although there is not enough evidence yet [56]. In a recent study that examined the effect of chloroform and hydroalcoholic extracts of *Cuscuta chinensis* and *C. epithymum* on cells of different classes [57], the results showed that the extracts of the shoots of these two types of Aftimun have properties. They are cytotoxic and are the best candidates for further studies to obtain new cytotoxic agents [57].

Numerous studies have shown that the pharmacological effects of different aftimun species are attributed to their active compounds, including flavonoids, polysaccharides and lignans [55, 56]. Flavonoids are a type of antioxidant, and polysaccharides are effective compounds in modulating the immune system. According to studies, the use of special types of polyhydroxyphenols such as flavonoids reduces the risk of colon and breast cancer [62]. The human diet contains a mixture of plant polyphenols. Various studies indicate that these phenols have cytotoxic effects against various tumors and the mechanism of action of these compounds is through the induction of apoptosis [62].

## 8. Economical

*Cuscutas* are plants that are economically one of the most important groups of parasitic plants and can cause great damage to crops by invading by the seeds they produce [63]. For example, *C. campestris* is ubiquitous and is a common species. It attacks at least 25 major crops in 55 countries [64]. Fifteen global species of this genus are known as weeds [63]. However, most species of *cuscuta*, like other parasitic plants, are beneficial [65]. The *cuscuta* species plays a key role in natural ecosystems. *Cuscutas* are able to alter plant community structure and dynamics, nutrient levels, and even modify non-living factors [66].

## 9. Phytochemistry

As *C. epithymum* is a parasitic plant, its chemical constituents are complex and vary in relation with type of the host invaded by the species [67]. In *cuscutas,* different types of chemical compounds such as 18 types of flavonoid compounds, 13 phenolic compounds, two types of steroids, 10 types of volatile oils, 22 types of lignans, nine polysaccharide compounds, 16 types of fatty acids and various types of alkaloids, steroids and so on are identified. Has been [25]. Flavonoids make up 3% of the total phytochemical composition of Cuscuta. The main flavonoid compounds in *cuscuta*, including kaempferol, quercetin, hyperoside, astragaline and ligands, play a very important role in the therapeutic effects of diseases [68].

All species of *cuscuta* have water-soluble phenolic compounds such as hyperoside, quercetin, astragalin, camphorl and so on in different amounts, and Chinese *cuscuta* has a high content of camphor glucoside among all species. So far, mineral elements such as calcium, magnesium, iron, manganese and copper have been identified in this plant through atomic absorption spectroscopy [69]. Also, 16 types of fatty acids, which mostly include linoleic acid, oleic acid and linolenic acid, have been identified from the extract of *cuscuta* by hexane [70].

In general, in the science of classification, the appearance of plant organs is used to identify different species. Because the flowers of different species of *cuscuta* are somewhat similar, Luffer et al. [71] investigated the possibility of accurately identifying *cuscuta* species due to the unique type of phenolic compounds present in their body. In this study, nine different species of *cuscuta* have been studied. First, the last 10 cm of their stem was removed and 15 cm of the remaining stem was collected to analyze the compounds inside. The results showed that there were 10 soluble phenolic compounds, including five hydrocynamic acid-derived compounds and five flavonoid compounds (such as kaempferol, quercetin and their derivatives) in all 9 species of *cuscuta*, each of which had different amounts in different species. These nine species of *cuscuta* were divided into three groups: (1) the group in which the hydrocynamic acid content was higher than flavonoids; (2) the group that had more flavonoids than hydrocynamic acid and (3) the group that had the same amount of hydrocynamic acid and flavonoids. Therefore, based on the results of these researchers, it is possible to identify different species of *cuscuta* according to the number of phenolic compounds present in *cuscuta*.

In addition, in the analysis of the essential oil obtained from the stems of the epithymum plant, about 81 species of compounds were identified, the main composition of the essential oil including Limonene, α-pinene, β-pinene and Linalool [72]. Of course, some sources have mentioned other compounds such as saponin, tannin, kaempferol and lignan as compounds in the essential oil of this plant. The main constituents of epithymum seeds include kaempferol, resin, aluminum, calcium, sodium and potassium [73]. The *C. epithymum* plant contains a significant amount of δ-tocopherol, α-tocopherol and γ-tocopherol as its constituents [74].

## 10. Therapeutic properties of aftimun

This plant has different healing properties. This plant is used to treat diseases of the spleen, liver and gallbladder, including jaundice, has mild laxative and diuretic properties, and is also used to treat scurvy, sciatica and gout. In external and topical use, it has a healing effect and is used to wash wounds and injuries, refreshes cocoons and skin wrinkles, and is effective in treating skin tuberculosis. Another healing property of this plant is its anti-cancer properties [75]. Traditionally it is considered a miracle genus equipped with a broad spectrum of remedial values. Decoctions, extracts, paste, powder, juice and infusions of different parts of the plants are important herbal prescriptions in traditional medicinal systems [76]. In Indian herbal medicine, sauces are used to treat jaundice, muscle and urinary problems. Among the healing properties of other sauces, in addition to the previous cases, we can mention the effect of sexual enhancer, expectorant, antipyretic, diaphoretic and worming. Its effects in the treatment of alopecia, bronchitis, headache, constipation, eczema, epilepsy, muscle pain and urinary problems can also be mentioned. The decoction of the plant with honey is suitable for purifying the blood, and this plant is also used to accelerate the healing of abscesses [77].

## 11. Conclusion

*Cuscuta*, commonly known as dodder, is a genus of the Convolvulaceae family. Approximately 170 species of *Cuscuta* are extensively distributed in the temperate and subtropical areas of the world. Species of this genus are widely used as essential constituents in functional foods and traditional medicinal systems. Various parts of many members of *Cuscuta* have been found efficacious against a variety of diseases. Phytochemical investigations have confirmed the presence of biologically active moieties such as flavonoids, alkaloids, lignans, saponins, phenolics, tannins and fatty acids. Pharmacological studies and traditional uses of these plants have proved that they are effective anti-bacterial, anti-oxidant, anti-osteoporotic, hepatoprotective, anti-inflammatory, anti-tumor, antipyretic, antihypertensive, analgesic, anti-hair fall and anti-stereogenic agents.

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## Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Author details

Khahdijeh Ahmadi*, Heshmat Omidi and Majid Amini Dehaghi
Department of Agronomy and Crop Breeding, Shahed University, Tehran, Iran

*Address all correspondence to: kh.ahmadi612@gmail.com

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Over six chapters, this book deals with different aspects of parasitic plants, from generalities to specific case studies. A large part of the book deals with holoparasites that cause damage in agriculture, such as those of the genus Cuscuta. Their biology, forms of management, interaction with hosts as transmitting vectors, and even their phytochemistry and medicinal uses are analyzed. Cases of parasitic plants approached from the cultural relationship with humans are presented for an area of Africa, as well as a review of the biology of the American genus Lophophytum, a holoparasite that is not harmful to agriculture and is even in danger of conservation.

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