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Parasitic Plants as Vectors for Pathogens

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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 phyto-plasmas. 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 biotechnological advances, such as metagenomics and high throughput 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, parasitism, 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:Potassium) 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 *Orobanchae*, *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 *Orobanchae*, 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].

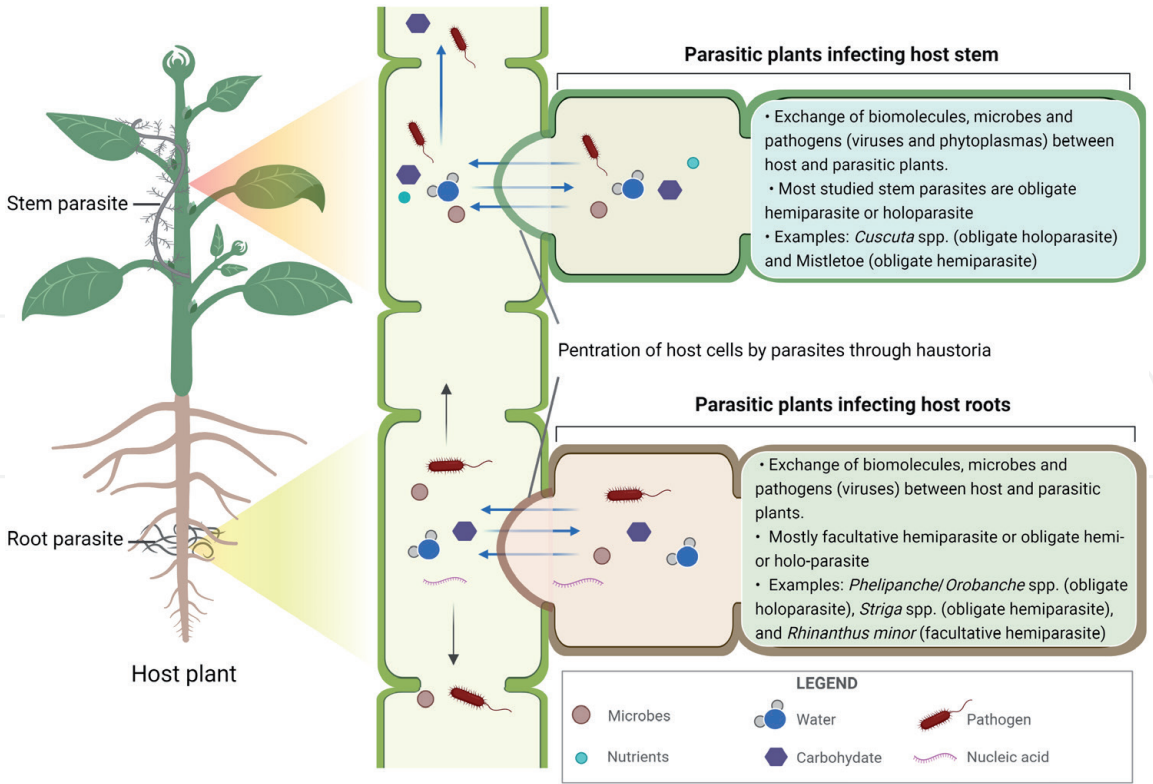


Figure 1.
Schematic representation of parasitic plant-host interaction and pathogen transmission. Bidirectional movement of biomolecules such as water, carbohydrate (e.g., sucrose), nutrients (e.g., phosphorus and nitrogen) and nucleic acids (mRNAs and small RNAs), as well as microbes, may occur through 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	<i>Cuscuta europea</i>	Tobacco	[60]
Apple mosaic virus	<i>Cuscuta</i> spp.	Apple	[57]
Tobacco etch virus	<i>Cuscuta subinclusa</i> & <i>Cuscuta</i> spp.	Tobacco	[57]
Mesta leaf curl virus	<i>Cuscuta</i> sp.	Mesta	[61]
Tomato ringspot virus	<i>Cuscuta</i> sp.	Tomato	[60]
Potato virus Y	<i>Cuscuta reflexa</i>	Tobacco	[55]
Dodder Latent Virus	<i>Cuscuta californica</i>	Sugar beet	[56]
Cucumber mosaic virus	<i>Cuscuta</i> sp.	<i>Nicotiana glutinosa</i> , Lucerne, cucurbits	[16]
Tobacco mosaic virus	<i>Cuscuta</i> sp.	Tobacco	[16]
Potato stem mottle virus	<i>Cuscuta</i> sp.	Tobacco	[16]
Beet curly top virus	<i>Cuscuta</i> sp.	Sugar beets	[16]
Phytoplasma			
Cuscuta Latent MLO	<i>Cuscuta odorata</i>	Periwinkle	[62]
<i>Picris echioides</i> yellows phytoplasma Cal	<i>Cuscuta odorata</i>	Oxtongues (experimental host)	[59]
Cotton phyllody phytoplasma	<i>Cuscuta campestris</i>	Cotton (experimental host)	[59]
Pear decline (<i>Candidatus</i> Phytoplasma pyri)	<i>Cuscuta odorata</i>	Pear (experimental host)	[59]
Rubus stunt (<i>Candidatus</i> Phytoplasma rubi)	<i>Cuscutaeuropea</i>	Different cultivated and wild <i>Rubus</i> spp. (Berries) (experimental host)	[59]
European stone fruit yellows (<i>Candidatus</i> Phytoplasma prunorum)	<i>Cuscuta reflexa</i> & <i>C. campestris</i>	Plum & Apricot (experimental host)	[59]
Proteobacteria			
<i>Candidatus</i> Liberibacter asiaticus	<i>Cuscuta pentagona</i>	Sweet orange (experimental host)	[63]
<i>Candidatus</i> Liberibacter asiaticus	<i>Cuscuta pentagona</i>	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 species: *Tobacco mosaic virus*) are neither persistent nor multiply in dodder, whereas, *Cucumoviruses* (type species: *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 N₂-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, *Orobancha hederaceae*, exhibit strong congruency with the host, *Hedera*; however, the individual bacterial taxa were differentially abundant between *Orobancha* 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 *Orobancha* 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 facilitated 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 *Orobancha crenata* and those of its host *Vicia narbonensis* have been imaged using electron microscopy [82]. Host–parasite connections for *Orobancha* 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.

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