

# Angiosperm Root Parasites of Indiana

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## Introduction

There are 14 genera of parasitic angiosperms that occur in Indiana, with potentially more to be included. Mistletoe (*Phoradendron flavescens* (Pursh) Nutt.), of southern Indiana and dodder (*Cuscuta* sp.) are probably the more familiar examples of parasitic angiosperms; parasitism by these species confined to the host stem. This discussion concentrates on a different group that have received less attention, the root parasitic species. All are characterized by a morphological and physiological connection called the haustorium, a term used to describe a functionally similar structure of fungal pathogens. The majority of root parasites are not host specific, i.e., they indiscriminantly parasitize most herbaceous or woody species. Only in the past decade has any root parasite been shown as pathogenic towards arborescent hosts in the United States (i.e., *Seymeria cassioides* on *Pinus elliotii* 17), though species of *Striga*, *Orobanche*, *Aeginetia*, and *Alectra* have devastated such crops as maize, sugarcane, tobacco, and legumes throughout the world in warmer climates (9).

An objective of this paper is to discuss characteristics of some root parasites known to occur throughout Indiana. Haustorium morphology and anatomy will be reviewed. The ecological significance of root parasitism will also be emphasized.

## Parasitic Plants in General

With the lone and debatable exception of a parasitic conifer found in New Caledonia (11) all parasitic vascular plants are dicotyledenous angiosperms. Plant parasitism has arisen in at least eight unrelated groups of dicots distributed worldwide (11):

1. Santalales (mainly the following three families: Olacaceae—25 genera, 150 species; Santalaceae—26 genera, 250 to 600 species; Viscaceae—7 genera; and Loranthaceae—70 genera, with a combined 1000 species)
2. Scrophulariaceae (210 genera, 3000 species) and Orobanchaceae (13 genera, 140 species)
3. Rafflesiaceae (7 genera, 27 species) and Hydnoraceae (2 genera, 10 species)
4. Balanophoraceae (21 genera)
5. *Cuscuta* of the Convolvulaceae (more than 150 species of *Cuscuta*)
6. *Cassytha* of the Lauraceae (less than 20 species of *Cassytha*)
7. Lennoaceae (3 genera)
8. Krameriaceae (1 genus, 15 species)

The Orobanchaceae, Rafflesiaceae, Balanophoraceae, and Lennoaceae are considered holoparasitic, i.e., their members are without chlorophyll, therefore depend totally on their host for nutrients and water. The remaining groups are hemiparasitic, or semiparasites, in that they are chlorophyllous and obtain some, if not all of the energy requirement through photosynthesis. The degree of parasitism varies between and within chlorophyllous parasitic species as some individuals within a parasitic population may even be autotrophic (2). Only the Loranthaceae, Viscaceae, and *Cuscuta* and *Cassytha* species are stem parasites; the other groups parasitize roots. The Orobanchaceae, Santalaceae, and Scrophulariaceae are the only families of root parasites known to occur in Indiana.

### Indiana Parasitic Plants

Genera which belong to the Orobanchaceae, Santalaceae, and Scrophulariaceae native or naturalized in Indiana are listed in Table 1. Those genera known to be root parasites are designated. The remaining genera, e.g., *Verbascum*, *Veronica*, and *Scrophularia* are apparently not root parasitic (24). At least 12 genera of root parasites are found in Indiana, all of which are herbaceous annuals, biennials, or perennials. Shrubby and arborescent root parasites are more prevalent in subtropical and tropical flora (11) and some are common throughout the southern United States (25).

TABLE 1. *Genera of parasitic (\*—references follow) and non-parasitic Orobanchaceae, Santalaceae, and Scrophulariaceae native to or naturalized in Indiana (from 4; names revised according to 8).*

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Orobanchaceae (11, 22, 40)
* <i>Conopholis</i> Wallr. (30)
* <i>Orobanche</i> L. (21)
* <i>Epifagus</i> Nutt. (39)
Santalaceae (11, 23, 37)
* <i>Comandra</i> Nutt. (20, 34)
Scrophulariaceae (11, 24, 26, 29)
* <i>Agalinis</i> Raf. (28)
* <i>Aureolaria</i> Raf. (44)
<i>Bacopa</i> Aubl.
<i>Besseyia</i> Rydb.
* <i>Buchnera</i> L. (25)
* <i>Castilleja</i> Mutis ex L.f. (7, 15)
<i>Chaenorrhinum</i> (D.C.) Reichenb.
<i>Chelone</i> L.
<i>Collinsia</i> Nutt.
* <i>Dasistoma</i> Raf. (32)
<i>Gratiola</i> L.
<i>Kickxia</i> Dumort.
<i>Leucospora</i> Nutt.
<i>Linaria</i> P. Mill
<i>Lindernia</i> All.
* <i>Melampyrum</i> L. (3, 31)
<i>Mimulus</i> L.
* <i>Pedicularis</i> L. (33)
<i>Penstemon</i> Mitchell
<i>Scrophularia</i> L.
* <i>Tomanthera</i> Raf. (24)
<i>Verbascum</i> L.
<i>Veronica</i> L.
<i>Veronicastrum</i> Heister ex. Fabr.

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### The Haustorium

The haustorium is a morphological and physiological bridge, composed at least partly of living tissue, through which materials are transported from host to parasite. Emphasis is placed here on this structure because an understanding of it helps to elucidate the evolutionary origin and function of parasitism (11, 24). There is little chance of distinguishing most species as root parasitic unless the haustorium is evidenced. Root parasitic species appear normal above ground except for *Conopholis americana* (L.) Wallr. (squawroot, cancer-root), *Epifagus virginiana* (L.) Barton (beechdrops), and *Orobanche* sp. all of which are holoparasites.

The following observations are somewhat cursory since the haustoria among the various families and genera in Table 1 may differ in their origin, morphology and anatomy, function, or even mode of attachment (11). More detailed studies on specific genera are referred to in Table 1. An especially thorough, comparative study by Musselman and Dickison (24) included many of the species found in Indiana.

The haustorium varies in size within and between species depending on its age, the species parasitized, and the degree of penetration. It is very small (1.0 mm diameter) in *Pedicularis canadensis* and *Castilleja coccinea* and much larger (to 10 mm diameter) in some genera such as *Aureolaria* and *Dasistoma* (25). Santalaceae, Scrophulariaceae and Orobanchaceae haustoria are whitish to light colored, conical to hemispherical in shape or sometimes flattened. Annual growth of haustoria occurs in some species and also depends on the longevity of the host (annual host vs. perennial). Some haustoria remain for only one year. Only very small host roots are parasitized by some species, e.g., *Epifagus virginiana* (39). Haustoria of *Conopholis americana* are massive and much darker, forming on larger host roots and functioning for many years.

Haustoria occur either sporadically along a host root or clustered in large numbers. Over 2000 haustoria formed within 6 months by various species of *Agalinis* on a single, one year old host (25). In another study, an individual *Aureolaria pedicularia* produced 11,000 haustoria (44). Elliptical scars are sometimes evident on host roots where the haustorium has disappeared (14). Host roots commonly die distal to the point of attachment, or at least decrease in size (24).

A longitudinal section through a typical Santalaceous haustorium (transverse to host root) is illustrated in Figure 1. The two main sections are the outer peripheral

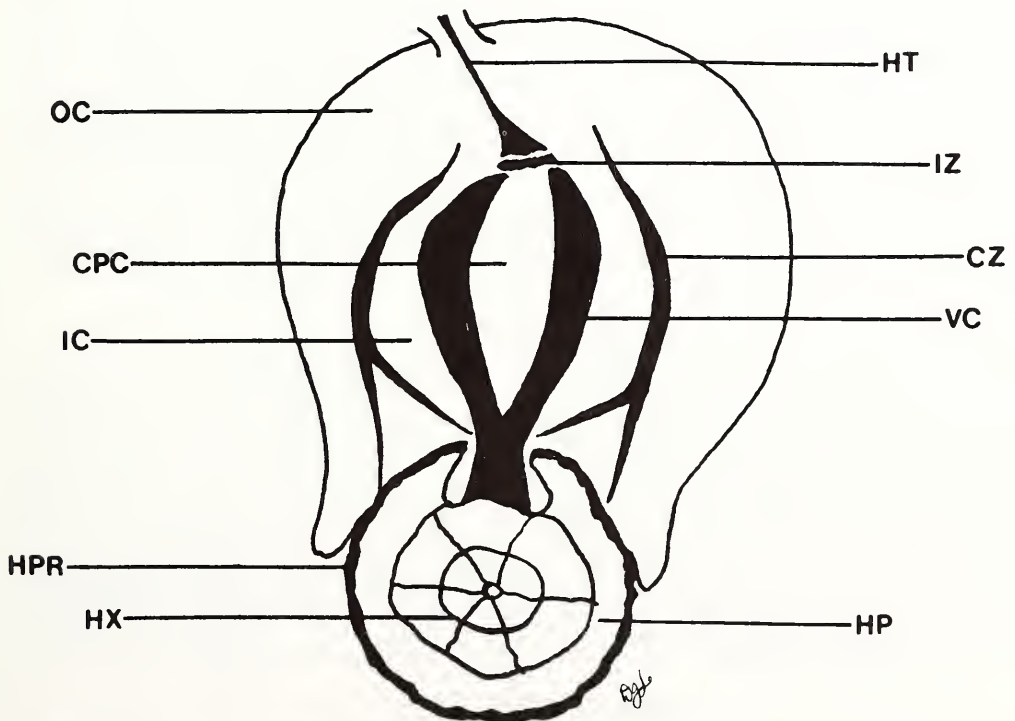


FIGURE 1. Longitudinal section of *Pyricularia* haustorium, transverse to host: CPC—central parenchymatous core; CZ—collapsed zone; HP—host phloem; HPR—host periderm; HT—haustorial tracheids; HX—host xylem; IC—inner cortex; IZ—interrupted zone; OC—outer cortex; VC—vascular core (from 14).

or outer parenchymatous region and the axial region or inner core. The outer peripheral region is primarily parenchyma cells and may be superficially suberized. The main functions of this layer are: (1) to protect the inner haustorium tissue; and (2) to assist in the attachment of the haustorium to the host (6).

Three areas are delineated within this outer layer which are the outer cortex (OC), inner cortex (IC) and at least one layer of collapsed tissues (CZ). The outer cortex consists of closely packed cells with few intercellular spaces and often abundant starch grains. The tissues located between the collapsed layers(s) and the axial tissue constitute the inner cortex. The collapsed zone is a distinction of Santalaceous haustoria and a few other genera of root parasites, excluding the Scrophulariaceae (24).

Cortical or clasping folds are also apparent around the apex of the haustorium where it is affixed to the host root. These folds aid in protecting the internal haustorium tissues and in fastening this structure to the host. Prying folds, possibly with the aid of host tissue reaction, are responsible for the peeling back of host periderm and cortex, and help expose the host xylem.

The vascular tissue within the axial region is shown as an inverted flask-shaped area. Three areas are typical within the axial region: (1) the neck or track of vascular tissue which connects to the xylem of the parent (parasite) root (HT); (2) a hemispherically shaped, fairly homogeneous core of parenchyma in the upper body region (CPC); and (3) a tract of tracheary tissue which converges from the periphery of the vascular core towards the intrusive organ of the parasite (VC). Five cell types constitute the vascular core: vessel elements (about 95% of cells), vascular tracheids, libriform fibers, parenchyma, and phloetracheids (24).

A zone of scattered and disintegrated xylem elements may exist slightly above the widest expansion of the vascular loop. This zone of uniseriate strands of xylem dispersed in parenchyma is known as the interrupted zone (IZ), another characteristic feature of the Santalaceous haustoria (and only a few Scrophulariaceae). Though some observers have not noted this layer (e.g., 20, 37), others have had no difficulty showing its presence in many of the same species (42, 43). Failure to locate the interrupted zone is attributed to improper orientation of the haustorium during the sectioning process (12). The function of this zone poses further speculation since the translocation of various compounds from the host to the parent plant may be rather selective or impeded here (43).

### **Development of Haustoria**

Haustoria result from a simple lateral extension of the primary root as a whole structure. The epidermis, cortex, and endodermis of the parasite root bulges out to form a protuberance which becomes the haustorium (43). Though haustoria are borne laterally along the parent root, this lateral root often senesces distal to the haustorium, making the haustorium appear as if it was terminal. There are five stages in haustorial development (taken directly from 24): (1) hypertrophy of the cortical parenchyma of the haustorial root; (2) attachment to the host root; (3) periclinal divisions in haustorium pericycle (development of vascular core); (4) penetration of host tissue; and (5) establishment of xylem continuity between host and parasite.

### **Host Parasite Contact**

The contact between host and parasite xylem by the intrusive organ (endophyte), can be a fairly uniform line, or bluntly pointed, wedge-shaped structure. Both types are depicted in Figure 2.

The lack of crushed xylem tissue in the host in the zone of host-parasite contact



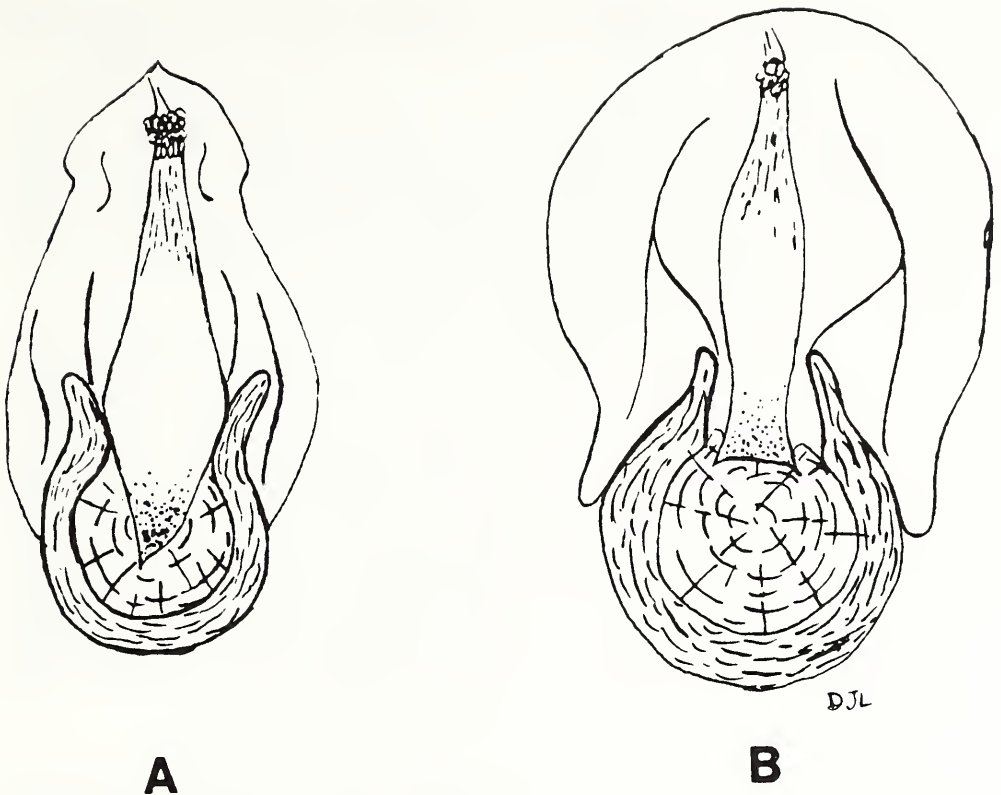


FIGURE 2. Two paths of intrusion by haustorial xylem: A, wedge-shaped; B, uniform line of penetration (redrawn from 43).

demonstrates that mechanical pressure has little or no role in the penetration process. Instead, enzymes allow penetration for the growing intrusive cells. A darkened area of cells between the host tissue and the intrusive organ results from the release of digestive enzymes in this region. Enzymes digest the host periderm and cortex but may be resisted by the lignified tissue of the host xylem (38).

Some investigators attribute these enzymes to the presence of a gland. The gland may be the only true diagnostic structure of the Santalaceous haustoria. However, some have never observed this structure, possibly because it exists only at an early stage in haustoria formation (12).

The actual connection of xylem between parasite and host is afforded by an apposition of the pit apertures of the vessel elements in both members. The xylem of the parasite does not appear to directly penetrate the host xylem.

Though phloem has been located only in *Castilleja* (13), phloetracheids occur within the area of xylem vessel members in the vascular core of Santalaceae and Scrophulariaceae (12). The importance of phloetracheids is obscure, though these structures seem to further obstruct the intake of materials into the haustorium (12).

#### Function of Parasitism

The function of parasitism is perplexing. Musselman and Mann (26) suspect that water is an important factor between parasite and host, based on the occurrence of pronounced wilting taking place in hosts under water stress. Thurmann (41) also noted that host plants wilt first when both the parasite and host are subjected to moisture stress. Various *Cordylanthus* (Scrophulariaceae) species could grow in dry chaparral

and woodland savanna presumably because parasitism allowed these species to use water from their host (36). Parasitic plants in general are known to have high transpiration rates (11).

Many plants have developed a particular means for tolerating an inadequate moisture supply, such as thicker cuticles, bulliform cells, microphylls, sunken stomata, strong palisade development, stem and branch photosynthesis, deep rooting and adventitious roots (5, 10). Haustoria may be yet another adaptive structure which enables a species to survive under moisture stress. Increased haustorial frequency on more xeric sites has been noted for *Aureolaria pedicularia* (44).

Mann and Musselman (19) demonstrated that many species of root parasites in the Scrophulariaceae could grow to maturity from seed, without any host, as long as the parasites were fertilized regularly with nitrogen, phosphorous, and potassium. However, parasites without a host and no fertilizer died within two to three months after germination. The number of haustoria and the height growth of the root parasites increased when the parasite was grown with a host and fertilizer.

Either a micro-metabolite or mineral nutrients may be required by the root parasite, *Castilleja coccinea* (16). Though minerals are undoubtedly sequestered by parasitic plants, it is not known which are essential for a parasite's continued existence. Atsatt (2) surmises that potassium and phosphorous are perhaps the key nutrients. Parasitism arose in tropical and subtropical regions, possibly as a adaptive response to mineral-poor soils typical of these regions (9).

Movement of materials through the haustorium is unidirectional, from host to parasite (16). Though the movement of various substances (minerals, carbohydrates, water, hormones, organic acids, etc.) through this structure has been shown (2) the actual materials required are left up to speculation.

### Host Specificity

Phanerogamic root parasites in natural plant communities have been mostly ignored until Mann *et. al.* (17) reported on the herbaceous *Seymeria cassioides* (Scrophulariaceae), senna seymeria, killing slash pine (*Pinus elliotii*) in northern Florida. Because of the forestry profession's past lack of concern regarding root parasites, Musselman and Mann (25) studied the ecology and potential host range of nineteen root parasites native to the southeastern U.S. and the potential damage to commercial forest tree species by such parasitism. They discovered actual connections between the root parasite and host tree roots in nearly all of the species tested. None of the 19 root parasites (the majority of which were of the Scrophulariaceae) were host specific.

Host specificity may have important ecological implications, as host species may react differently to the additional demands of the parasite. Most root parasites are nonselective in attaching to a host (e.g., 3, 11, 15, 17, 26, 32, 33, 34); exceptions include *Epifagus virginiana* on *Fagus grandifolia* and *Conopholis americana* on *Quercus*, subgenera *Erythrobalanus*.

Some root parasites have been considered host specific only because they would occur in nature with a certain species, genera, or family. While Pennell was preparing his monograph of the Scrophulariaceae (29) he noticed that the range of *Dasistoma macrophylla* did not agree totally with that of *Aesculus glabra* in Indiana (32). Pennell informed Deam of this inconsistency, convinced that *Aesculus glabra* had to occur wherever *Dasistoma macrophylla* did. Apparently Pennell was persuasive as Deam eventually modified his range map of *A. glabra* to include the range of *D. macrophylla*.

Over 30 years later, the host specificity of *D. macrophylla* on *A. glabra* was disproven as haustoria were found on various other species (32).

*Buckleya distichophylla*, a rare parasitic shrub endemic to the southern Appalachian mountains, presumably was limited to sites that were dominated by *Tsuga caroliniana*, Carolina hemlock. Piehl (35) however, has demonstrated that *Buckleya* is not host specific to hemlock but rather that it occurs naturally with it because both species have similar site requirements. Musselman and Mann (27) have also shown, in a controlled environment, that *Buckleya* parasitized nineteen different tree host species within five months after germination. Since *Buckleya* and most root parasites can potentially parasitize numerous hosts, these species are most likely restricted in distribution for reasons of site characteristics, such as soil, moisture, exposure, disturbance, etc; or due to a lack of dispersal.

Greenhouse culture of root parasites with potential hosts facilitates the study of haustorial connections. Since haustoria usually are formed on the delicate roots of the parasitic species, Piehl (33) notes that excavating the host and parasite roots virtually always severs the parasitic root leading to the haustoria. In these circumstances, the haustoria are usually left affixed to the host root and have to be located. A disadvantage of pot culture in establishing host specificity is that this technique only shows what the potential hosts may be (25). It does not account for the competition, the increased microbial activity and the much higher concentration of root exudates more typical of natural plant communities.

### Pathogenicity

The demand for host nutrients and water by mistletoe (*Arceuthobium* sp.) induces host stem dieback and eventually death of the host (1). Pathogenicity has also been established for other stem parasites, e.g. dodder, and many root parasites have caused significant losses of agricultural crops, particularly in the tropics. Only *Seymeria cassioides* has been determined as pathogenic to any tree species in the United States. However, other temperate genera, e.g. *Agalinis* and *Orobanche*, are potentially pathogenic (18, 25).

Pathogenicity may be manifested by the parasite inducing a detrimental imbalance of hormones (particularly cytokinins), carbohydrates, inorganic ions (P, K, S, Mg), and nitrogen in the host (9). Host responses include elevated or suppressed levels of respiration, transpiration and photosynthesis; and increased cell division. Perhaps the critical host reaction to parasitism is the deregulation of a sucrose-amino acid cycle in the host (9) which causes a carbohydrate and nitrogen deficiency in the host.

It is essential to study the life history of these parasitic species and to determine which species are pathogenic, since many parasitic plants function as weeds. These opportunistic species are adapted to perturbed environments (25) and respond positively to cultural practices such as site preparation and fertilization (19). Research is needed in this area so that resource managers can make intelligent decisions regarding the treatment of sites occupied by both parasitic and commercial species.

### Conclusion

Root parasitism is a form of plant interference given little attention thus far in the literature. However, the effect that a root parasitic species may have on the growth and reproductive potential, and spatial distribution of its associated vegetation, may be important in the dynamics of vegetation change. How the host responds to an additional and continuous moisture and mineral demand depends on many factors within the parasitic species, the hosts, and the environment. The actual loss of growth to



an individual species due to insects or pathogenic organisms is often difficult to quantify. Root parasites may cause no conspicuous pathogenicity in their hosts. However, the loss in host net primary production may be significant due to the demands for its water or nutrients on sites where parasitic plants are common. The assessment of site productivity and the spatial distribution of the vegetation should consider yet another factor, that of root parasitism.

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