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A LITERATURE REVIEW OF ROOT-PARASITISM IN SCROPHULARIACEAE, OROBANCHACEAE, AND SANTALACEAE, WITH SOME PRELIMINARY IN VITRO STUDIES IN SCROPHULARIACEAE

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Abstract

A literature review is presented on five main headings concerning root-parasitic plants in the Scrophulariaceae, Orobanchaceae and Santalaceae. The areas reviewed are *in vitro* experimentation on root parasites, seed germination, parasite roots and root systems, interaction with hosts, and initiation, development and attachment of the haustorium (the parasitic organ). The concept of advanced versus primitive species is developed. Santalaceae and most Scropulariaceae appear to be unspecialized while Orobanchaceae and the genera *Alectra* and *Striga* of Scrophulariaceae seem to show varying degrees of specialization. Trends in specialization appear to be development of and increasing reliance on a primary haustorium, necessity of a host root exudate for seed germination, reduction in root systems and root anatomy and reduction in host range. The genus *Lathraea* of Scrophulariaceae may present different considerations in specialization. Early results of preliminary *in vitro* research on several species of parasitic Scrophulariaceae are also presented. Areas touched on are germination, growth *in vitro* and initiation and self-initiation of haustoria. Finally, an appendix listing known host ranges for many root parasites is included.

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I. Introduction

The roots of Scrophulariaceae, Orobanchaceae and Santalaceae form connections to the roots of neighboring plants by means of haustoria of two origins. Primary haustoria are formed from the apex of the germinating radicle and secondary haustoria form laterally on the root behind the apex of both primary and lateral roots. Secondary haustoria show the wider taxonomic distribution. The early development of secondary haustoria is poorly understood but they appear to be initiated in cells of the outer cortex and perhaps also the epidermis.

Evidence suggests that haustoria are initiated either by chemicals released by a host root or by contact with the host root or both. Atsatt (1973) has reported a chemical stimulus. Indication that the stimulus might be thigmotropic comes from reports in the literature of haustorial attachment to pebbles and grains of sand (Rao, 1942; Fineran, 1965; Malcolm, 1966).

In this paper it has generally been found convenient to divide root parasites into advanced and primitive forms. The advanced parasites usually require host root exudates for germination and form primary haustoria from the "germ tube" or radicle produced by the germinating seed. From the primary haustorium a swelling (termed a "tubercle" by several authors) is formed and the swelling produces the roots (where present) and the flowering shoots. The presumably advanced parasites also seem to show trends towards reduction in root systems and root anatomy, reduction in host range and perhaps also reduction in numbers of secondary haustoria. Several of these trends may be correlated with the presence of a primary haustorium, which in turn may be correlated with the host root exudate requirement for germination. Presumptive advanced parasites in the Orobanchaceae are generally holoparasites and lack chlorophyll while those in the genera Alectra and Striga of Scrophulariaceae are considered to be hemiparasites since they have chlorophyll and photosynthesize in addition to obtaining some of their nutrition heterotrophically. The parasites considered more primitve in this paper are Santalaceae and most Scrophulariaceae. They generally do not require host root exudates for germination, are hemiparasitic, show little restriction of host range, form only secondary haustoria and have growth forms similar to those of autotrophic plants. The holoparasite Lathraea of Scrophulariaceae may demonstrate a different trend in specialization and is considered separately.

The discussions of germination requirements and early haustorial development in this paper are expanded and modified somewhat over the review of these subjects in Kuijt (1969). Thorough reviews of many of the other headings seem to be lacking, however. The data presented in the research report should be stressed as being strictly preliminary - useful for discussion in the light of what is presented in the literature review but not thorough enough or on a large enough scale to allow any conclusions to be drawn. It may safely be stated, however, that axenic techniques hold great promise for the elucidation of the haustorial initiation mechanism and perhaps also for determination of the nutritional requirements of the less specialized parasites. Further, precise determination of both natural germination requirements and alternative dormancy-breaking techniques may help clarify the derivation of the more specialized germination requirements of parasites considered advanced in this paper.

II. Literature Review

The root parasitism of the Scrophulariceae and Santalaceae was first discovered towards the middle of the 19th century. (Bowman, 1933; Decaisne, 1847; Mitten, 1847), while that of the Orobanchaceae had been known for some time. Several genera of the Scrophulariaceae and Santalaceae have not been shown to be parasitic. Little has been learned about haustorial initiation and early development because observation and experimentation have largely been undertaken in nature or in pot culture. The denseness and opacity of soil makes the observation of these phenomena and the manipulation of host and parasite roots difficult. Growth and experimentation in agar overcomes these problems.

A. In vitro Experimentation on Root Parasites

Though agar would appear a convenient medium for work on the root relations of parasitic plants little use of it has been made. Previous *in vitro* work has largely been confined to culture of seeds on complex media and to growth of intact plants. The seed cultures have generally resulted in callus, from which shoot or root apices or accessory embryos may be differentiated. Growth of intact plants has frequently been unsuccessful but in several cases has demonstrated the unspecialized nutritional requirements of some of these parasites.

1. Seed and Callus Culture

Ranga Swamy and his co-workers have induced callusing of embryos of intact seeds in members of all three major taxa of parasitic plants under consideration here (see Table 1.). The basal medium is a modified White's medium. Kinetin is generally present in media on which callusing is induced. In plants in the Scrophulariaceae and Orobanchaceae casein hydrolysate and coconut milk are generally also present in the callus-induction medium though a basal medium with kinetin as the only additive is also capable of inducing callusing in *Striga angustifolia* (Ranga Swamy and Rangan, 1969). Purine derivatives will also induce callusing in *Striga asiatica* embryos (Worsham, Moreland and Klingman, 1964). Since kinetin or purine derivatives are capable of inducing callusing in the parasites mentioned above casein hydrolysate and coconut milk may not be necessary.

Callus growth can generally be maintained on a basal White's medium supplemented with casein hydrolysate and coconut milk. Adenosine sulphate has been shown to substitute for these additives in *Striga angustifolia* (Ranga Swamy and Rangan, 1969).

In several cases cellular organization has occurred in callus; resulting in the formation of root or shoot apices or accessory embryos (see Table 1.). The root apices have formed in callus maintained on media of two different compositions and the complex substances potentially available in coconut milk are apparently not necessary for the induction of root apices. Since only 40% of callus cultures on White's plus casein hydrolysate and coconut milk and only 55% of cultures on White's plus adenosine sulphate form roots (Ranga Swamy and Rangan, 1969) the initiatory stimulus may come from the cells of the culture rather

Table 1. Seed Culture

Species	Manipulation		Basal Medium	Hormone	Other	Results	Reference
Striga angustifolia	1	Seeds placed in culture	Unmodified agar	10ppm Kinetin		Germination and callusing of the cotyledons	Ranga Swamy and Rangan, 1969
	2	Callus from 1 transferred	Modified White's		400ppm casein hydrolysate + 15% coconut milk	Indefinite maintenance of callus and frequent formation of roots	
					10ppm adenosine sulphate		
Striga asiatica		Seeds placed in culture	Distilled water		Purine derivatives at over threshold germination concs.	Embryo callusing with subsequent formation of hypocotyl and cotyledons	Worsham, Moreland and Klingman, 1959
Striga euphrasioides		Seeds placed in culture	Modified White's	1ppm IAA + 10ppm Kinetin	400ppm casein hydrolysate	Germination and callusing of the cotyledons	Ranga Swamy and Rangan, 1966
					15% coconut milk		
					400ppm casein hydrolysate + 15% coconut milk		
Cistanche tubulosa	1	Seeds placed in culture	Modified White's	5ppm Kinetin	Light + 400ppm casein hydrolysate + 15% coconut milk	Germination and radicular proliferation	Rangan and Ranga Swamy 1968
	2	Seeds placed in culture	Tepfer's H_1		Light		
	3	Callus from 1 or 2 transferred	Tepfer's H_1		Dark	Formation of shoot apices from the callus	

Table 1. (Cont.)

Species		Manipulation	Basal Medium	Hormone	Other	Results	Reference
Orobanche aegyptiaca	1	Seeds placed in culture	Modified White's		400ppm casein hydrolysate	Callusing of the radicular end of the embryo	Ranga Swamy, 1963
					10% coconut milk		
				10ppm gibberellic acid			
	2	Callus from 1 transferred	Modified White's		15% watermelon juice	Formation of shoot apices	
Santalum album		Seeds placed in culture	Modified White's	2ppm 2,4-D + 5ppm Kinetin	0.25% yeast extract	Embryo callusing	Ranga Swamy and Rao, 1963
	1	Seeds placed in culture	Modified White's	2ppm 2,4-D + 5ppm Kinetin	0.25% yeast extract	15% proliferated embryo tissue and formed accessory embryos	Rao, 1965
	2	Callus from 1 transferred	Modified White's		500ppm casein hydrolysate + 20% coconut milk	Maintenance of callus growth and production of accessory embryos	

than from substances present in the media. In *Cistanche tubulosa* Tepfer's H_1 medium seems necessary for the induction of shoot apices and the induction is apparently inhibited by light (Rangan and Ranga Swamy, 1968). No such light inhibition is active in *Orobanche aegyptiaca*, in which a substance apparently present in watermelon juice is active in causing the formation of shoot apices (Ranga Swamy, 1963). *Santalum album* callus formed accessory embryos on two media containing various complex additives (Rao, 1965).

2. Intact Culture

Only a few root-parasites have been grown intact *in vitro* (see Table 2.). Of these only *Melampyrum lineare* (Curtis, Cantlon and Malcolm, 1963) and *Striga senegalensis* (Okonkwo 1964, 1966b, c.) have flowered. The requirements necessary for the completion of growth of *Castilleja coccinea*, on the other hand, could not be determined (Malcolm, 1962a). The other parasites which have been grown *in vitro* have merely been noted by their respective authors. Haustoria have been reported as forming *in vitro* in *Melampyrum lineare* (Curtis, Cantlon and Malcolm, 1963), *Orthocarpus purpurescens* (Thurman, 1966) and *Orthocarpus* sp. (Atsatt, 1973).

3. Other

Attempts have been made to grow excised embryos and root tips of two parasites but with no success (see Table 2.).

4. Discussion

Callus culture is of considerable importance in future work on parasitic plants as it offers uniform genetic material such as root tips or undifferentiated cells. At present one of the problems involved

Table 2. *Culture of Intact Plants and Excised Parts*

Species	Manipulation	Basal Medium	Additives	Results	Reference
Castilleja coccinea	Plants grown in culture	Various media containing mineral nutrients and the commoner vitamins,hormones and respiratory substrates		Plants grew slowly and remained alive for months but never reached maturity	Malcolm, 1962a
Melampyrum lineare	Plants grown in culture	Unspecified mineral nutrients	None	Growth to flowering including some self-attachments	Cantlon, Curtis and Malcolm,1963
			2.0% sucrose		
			2.0% sucrose + 0.25% yeast extract + 0.02% DL-asparagine	Rapid growth but flowering never occurred	
			0.5% oak root extract + 2.0% sucrose		
			1.29% oak root extract	Slow growth	
	Embryo excised and placed in culture in the cold	Unmodified agar	1% potato starch	No growth	Curtis and Cantlon,1965
			1% glucose	Slow growth for 8 to 10 weeks	
			400ppm gibberellic acid + 1% potato starch	No growth	
			400ppm gibberellic acid + 1% glucose	Slow growth for 8 to 10 weeks	

Table 2.(Cont.)

Species	Manipulation	Basal Medium	Additives	Results	Reference
Melampyrum lineare (cont.)	Embryo excised and placed in culture in the cold	Unmodified agar	1% sucrose	Slow growth	Curtis and Cantlon,1968
			5% sucrose		
			1% unextracted, milled dormant *Melampyrum* seeds		
			1% benzene-extracted seeds		
			1% benzene-and ethanol-extracted seeds	No growth	
Orthocarpus sp.	Plants grown and haustoria initiated in various ways	Unspecified	Unspecified	Growth apparently normal;haustoria induced in several ways	Atsatt,1973
Orthocarpus purpurascens	Plants grown in culture with host	Unspecified	Unspecified	Growth apparently normal:all potential host plants with which grown parasitized	Thurman,1966
Santalum album	Root tips 4-5mm.long excised and placed in culture	White's	None	10% grew to 7-8mm.long	Srimathi and Sreenivasaya, 1963
	Root tips of *S. album* cultured with root tips of host plants	White's	None	Little growth and no haustorial initiation	

Table 2. (Cont.)

Species	Manipulation	Basal Medium	Additives	Results	Reference
Santalum album (Cont.)	Seeds placed in culture	Modified White's	400ppm casein hydrolysate + 20% coconut milk	Germination and formation of a normal seedling	Ranga Swamy and Rao, 1963
Striga senegalensis	Seeds placed in culture	Murashige and Skoog's	2% sucrose + Sorghum vulgare root exudate	Germination and seedling growth	Okonkwo, 1964, 1966b, c
	Seedlings transferred to fresh medium after 30 days in culture	Murashige and Skoog's	2% sucrose	Growth to flowering	
	Plants grown in culture	Murashige and Skoog's	Various sugars to replace sucrose. Various concentrations	Growth to flowering with several sugars. Most effective conc. was 0.06M.	
	Plants grown in culture	Murashige and Skoog's less inorganic nitrates	100-200 mg/l glutamine + 0.06M sucrose	Growth to flowering	
	Plants grown in culture	Murashige and Skoog's	Various concs. of glutamine + 2% sucrose	Growth rate increases as conc. of nitrogen increases to max. conc. used	
	Shoot buds form on the roots of plants grown to maturity on the above media. Bud formation might be preceded by callusing or could form from differentiation of an initial in the epidermis or hypodermal layer of the cortex				

in performing research on plants obtained from seeds is that they have widely disparate abilities to grow on certain nutrient media and probably also show great variation in their ability to form haustoria. These genetic variations (see Atsatt, 1970) complicate the interpretation of data obtained from an experiment.

Since the media used to induce callusing have normally included complex additives such as coconut milk and yeast extract and since requirements for organogenesis and callusing frequently vary from species to species no general conclusions can be drawn at present.

Work with excised root tips would allow easier manipulation of material than is possible with whole plants in performing haustorial initiation experiments, but so far no success has been obtained with excised root culture. I have made attempts to grow the roots of *Aureolaria pedicularia, Castilleja coccinea* and *Orthocarpus purpurescens* in liquid White's medium with 4% sucrose. I was able to obtain slow growth and lateral root production with about 50% of the *Castilleja* roots, but it still appeared that a factor (or factors) necessary for vigorous growth was missing.

B. Germination

The seeds of most root parasites require vernalization in order to germinate. Some, considered more advanced, require a stimulant found in the root exudates of host plants in order for dormancy to be broken. These more advanced parasites may also require periods of after-ripening and of pretreatment in order to become receptive to the stimulant. A wide variety of chemicals has been found able to substitute for the host root exudate requirement. None of these synthetic chemicals, however, have been established as a natural stimulant. Several natural stimulatory substances are present within host root exudates. The structure of one of them has been published. These parasites may be stimulated to germinate by root exudates of plants not known to be their hosts in nature as well as by known hosts. Most species of parasites requiring a root exudate in order to germinate show a certain amount of "spontaneous" germination when placed under moist conditions without the host root exudate being present.

1. Parasites Not Requiring a Host Root Exudate

Most of the Scrophulariaceae and Santalaceae have germination mechanisms adapted only to environmental variables (see Table 3.). A few such as *Castilleja* spp. (Heckard, 1962) and *Orthocarpus faucibarbatus* (Thurman, 1966) require only exposure to light and moisture in order to germinate. *Lathraea clandestina* is particularly interesting. It spends most of its life underground and is holoparasitic but requires only exposure to moist conditions for several months in order to germinate (Chemin, 1925; Renaudin, 1968). Other advanced parasites of the same family have evolved a more highly specialized seed-germination mechanism (see the next section).

Most of the other species in the Scrophulariaceae and Santalaceae whose germination requirements are known require vernalization in order to germinate. *Melampyrum lineare* requires, in addition, a moist

Table 3. Germination Requisites of Parasites Not Requiring a Host Root Exudate

Species	Pretreatment	Vernalization	Other treatment	Germ.Rate	Reference
Aureolaria grandiflora	None	4.5°C for 5 months	None	ca.50%	Musselman, 1969
Aureolaria pedicularia	None	4.5°C for 5 months	None	ca.50%	Musselman, 1969
Castilleja, several spp.	None	None	Moisture	Significant	Heckard,1962
Castilleja coccinea	None	None	Moisture,light	Significant	Malcolm,1966
Comandra umbellata	None	Required but not specified	None	Significant	Piehl,1963a, 1965c; Hedgecock, 1915
	None	None	Removal of mesocarp	Significant	Piehl,1965c
Cordylanthus, several spp.	None	Required;higher altitude species require more vernalization than lower altitude ones	None	Significant	Chuang and Heckard,1971
Euphrasia, several spp.	None	Required but not specified	None	Significant	Koch,1891; Wettstein, 1896; Heinricher, 1898a,b

Table 3. (Cont.)

Species	Pretreatment	Vernalization	Other Treatment	Germ.Rate	Reference
Euphrasia americana	None	10 weeks in the cold	None	Significant	Nichols,1934
Lathraea spp.	None	None	Host root exudate	Significant	Heinricher, 1893
Lathraea clandestina	2 to 3 months moist storage at room temp.	None	None	Significant	Chemin,1925
	11 weeks moist storage at room temp.	None	None	Significant	Renaudin, 1968
Melampyrum cristatum	None	1°C for 8 weeks	None	85%	Horrill,1972
Melampyrum lineare	None	5 months	None	30%	Malcolm,1964
	28 days at room temp.	40-100 days	None	35%	Curtis and Cantlon,1965
	None	60-120 days	None	35%	
	None	None	0.1% KNO_3 for 5 weeks at 12.5°C	84%	Zalasky,1962
	None	None	0.01% gibberellic acid for 5 weeks	95%	
	None	None	Distilled H_2O for 5 weeks at 12.5°C	95%	
	Storage for 2 weeks	None	0.1% KNO_3 for 5 weeks at 12.5°C	91%	

Table 3. (Cont.)

Species	Pretreatment	Vernalization	Other Treatment	Germ.Rate	Reference
Melampyrum lineare (cont.)	Storage for 2 weeks	None	0.01% gibberellic acid for 5 weeks at 12.5°C	90%	
	Storage for 2 weeks	None	Distilled H_2O for 5 weeks at 12.5°C	87%	
	Storage for 6 months	None	0.1% KNO_3 for 5 weeks at 10°C	62%	
	Storage for 6 months	None	0.01% gibberellic acid for 5 weeks at 10°C	64%	
	Storage for 6 months	None	Distilled H_2O for 5 weeks at 10°C	25%	
	Storage for 6 months	None	0.1% KNO_3, 0.01% gibberellic acid or distilled H_2O for 5 wks. at 15°C	0%	
Orthocarpus faucibarbatus	None	None	Moisture and light	Significant	Thurman, 1966
Rhinanthus sp.	None	Required but not specified	None	Significant	Heinricher, 1909
Rhinanthus cristi-galli	None	17 weeks at 2°C	None	95%	Vallance, 1952
	5 months wet storage	16 weeks at 2°C	None	95%	
	Dry storage	4 weeks at 2°C	2 weeks at 15°C	10%	
	Dry storage	12 weeks at 2°C	None	25%	
	Dry storage	7 weeks at 2°C	2 weeks at 15°C	20%	

Table 3. (cont.)

Species	Pretreatment	Vernalization	Other Treatment	Germ.Rate	Reference
Rhinanthus cristi-galli (cont.)	Dry storage	9 weeks at 2°C	2 weeks at 15°C	25%	
Rhinanthus serotinus	None	8 weeks at 4°C	None	Significant	Bourget,1965
Rhinanthus major	None	8 weeks at 2-5°C	None	Significant	Bourget,1965
Rhinanthus minor	None	8 weeks at 2-5°C	None	Significant	Bourget,1965
Santalum album	None	None	Moisture	Significant	Rama Rao, 1910a
	None	None	White's medium + coconut milk	11%	Rao and Ranga Swamy, 1971
	None	None	White's medium + casein hydrolysate + coconut milk	44%	

pretreatment in order to become susceptible to vernalization (Curtis and Cantlon, 1965) but this requirement can be satisfied by 24 hours' treatment in gibberellic acid or by eight weeks' exposure to low CO_2 air (Curtis, Cantlon and Malcolm, 1963). Removal of the mesocarp of *Comandra umbellata* seeds will remove their need for vernalization (Piehl, 1965c).

It is possible, as Kuijt (1969) points out, that parasites which do not require a host root factor for germination may still have their germination rates raised by the presence of a host root factor. Kuijt states that "indications of this sort have been presented for *Melampyrum* (Sperlich, 1908; Heinricher, 1908a)." Chemin (1925) has also demonstrated this for *Lathraea clandestina* and Becker, Guyot and Montegut (1951) have found that aqueous extracts of soil on which *Brachypodium pinnatum* had been growing stimulated the germination of *Melampyrum lineare* seeds.

2. *Parasites Requiring a Host Root Exudate*

More advanced root parasites have developed a mechanism to ensure the proximity of a host root upon germination of their seeds. These parasites consist of perhaps the entire Orobanchaceae as well as the genera *Alectra* (Botha, 1948, 1950a, b, 1951a, b), *Striga* (Stephens, 1912b; Saunders, 1933) and *Tozzia* (Heinricher, 1901) of the Scrophulariaceae. This mechanism relies on the release by the roots of host plants of a substance or substances stimulatory to the germination of the parasite seeds (Brown, 1946).

a. After-ripening

A dry period of maturation following seed release from the capsule but prior to pretreatment may be required in order to make the seed maximally responsive to the germination stimulant. This period of maturation is termed after-ripening. It is important in the germination of the seeds of *Striga asiatica* (Saunders, 1933), *Striga hermonthica* (Vallance, 1950, 1951b) and *Orobanche* sp. (Edwards, 1972). If after-ripening is continued past a certain length of time the ability of the seed of *S. hermonthica* to germinate diminishes.

b. Pretreatment

Frequently the seeds of these parasites also require a period of warm, moist incubation, called pretreatment, in order to germinate at a maximal rate. Pretreatment requirements for a number of species of parasites are shown in Table 4. If pretreatment is continued for too long the capacity of the parasite seeds to germinate may decline. This has been reported for seeds of *Striga asiatica* (Brown and Edwards, 1945) and *S. hermonthica* (Vallance, 1950). The seeds of *Alectra vogelii* (Botha, 1950b, 1951b) and *Orobanche minor* (Brown, Greenwood, Johnson, Long and Tyler, 1951; Sunderland, 1960b) seem capable of sustaining germination-readiness indefinately under pretreatment. *Orobanche crenata* seed show a periodicity in their germination potential while in the pretreatment stage (Hiron, 1973). Brown and Edwards (unpublished, quoted in Brown, 1946) have determined that the length of time necessary to achieve maximal pretreatment in *Striga asiatica* decreases as the temperature of pretreatment increases. Sunderland

Table 4.

~~Pretreatment~~ Requirements of Parasites Needing a Host Root Exudate for Germination

Species	Pretreatment	Reference
Striga asiatica	A week or more at an elevated temperatura for enhanced germination	Brown and Edwards,1944
	21 to 28 days for maximal germination	Brown and Edwards,1946
	15 to 20 days at 23 to 24°C for maximal germination	Worsham,Moreland and Klingman,1959
Striga gesnerioides (=*S.orobanchoides*)	42 days at 22°C	Wild,1948
Striga hermonthica	12 to 18 days at 22°C for a maximal rate	Vallance,1950
Alectra vogelii	Germination increases as moist storage at 35°C continuas	Botha,1950b
Orobanche aegyptiaca	9 to 59 days at 23°C	Kasasian,1973
Orobanche crenata	11 to 44 days at 18°C	Kasasian,1973
Orobanche minor	21 days at 25°C for maximal germination	Sunderland,1960b
Orobanche speciosa	14 days at a high temperature	Chabrolin,1938

(1960b) notes that parasite seeds undergoing pretreatment may be dried and will respond normally to pretreatment when rewetted.

C. Germination Stimulants

1. Characterization and Actions

Characterization of the germination stimulants (see Tables 5. and 6.) indicates that a number of different compounds may be released by the roots of various plants effective in stimulating the germination of these parasites. Furthermore, it seems likely that different parasite species require different compounds for stimulation (Brown, 1949). These conclusions are supported by several reports in the literature. Sunderland (1960a) found more than one stimulatory substance to be released by the roots of corn. Two of them were active on *Orobanche minor* seeds and another, different one was active on *Striga hermonthica* seed. Two of these three substances had properties resembling those of the stimulatory substances from linseed and sorghum. Sunderland further reports that linseed, sorghum and corn all produce a similar complex of stimulants, differing only in the proportions of the different constituents. Cezard (1965) obtained two (possibly three) substances from the root exudates of *Centaurea scabiosa* which broke dormancy in *Orobanche minor* seeds. One of these compounds was also active in causing the germination of *O. picridis* seeds.

Vallance (1949, 1951a) has found the specific action of the germination-stimulatory substance to be enhancement of the rate of respiration

Table 5. <u>Physical Characterization of the Germination Stimulant</u>

Species	Characterization	Reference
Striga asiatica	Heat-labile	Saunders, 1933; Worsham, Moreland and Klingman, 1964
	Acid-stable	Worsham, Moreland and Klingman, 1964
Striga hermonthica (=*S. orobanchoides*)	Heat- and acid-labile	Brown, Johnson, Robinson and Tyler, 1952
Alectra vogelii	Heat-labile	Botha, 1948, 1951b
	Less heat-labile than the stimulant for *Striga asiatica* seed	Saunders, 1933
Orobanche cernua	Heat-stable	Rao, 1955
Orobanche cumana	Heat-stable, alkali-labile	Barcinsky, 1934
Orobanche speciosa	Heat-stable	Chabrolin, 1938
Orobanche minor	Acid-stable	Brown, Greenwood, Johnson, Long and Tyler, 1951

Table 6. Active Concentration of the Germination Stimulant

Species	Concentration	Reference
Striga asiatica	0.001ppm	Worsham, Moreland and Klingman, 1964
	0.02ppm	Brown and Edwards, 1946
Orobanche minor	10^{-8} or 10^{-9}M	Sunderland, 1960b
Orobanche speciosa	1ppm	Chabrolin, 1938

of both pretreated and non-pretreated *Striga hermonthica* seeds. The stimulant is known to be effective at very low concentrations (see Table 6.) and following very short treatment periods (see Table 7.). The stimulant active on the seeds of a number of these parasites has been shown to be of fairly complex structure and probably a hormone (see Table 8.). The stimulant of *Striga hermonthica* has been shown to cause extension growth of pea root segments (Brown, Robinson and Johnson, 1949b).

Plant root exudates may also affect the growth of the radicle of *Striga* and *Orobanche.* The radicles of *Striga asiatica* (Pearson, 1913; Saunders, 1933; Martin, 1949; Williams, 1960b, 1961a, b, 1962; Rogers and Nelson, 1962) and of *Orobanche* spp. (Kuijt, 1969) are reported to be attracted towards the host root during growth. Doughty (1942), however, feels, that the radicle of *Striga hermonthica* is not attracted towards the host roots and Sunderland (1960b) states flatly that "the seedling of the parasite is not attracted towards its host". Both Pearson (1913) and Williams (1961b) find that the closer the germinating parasite seed is to the host root the more pronounced is its attractive effect on the radicle. However, Williams notes that even very close to the host root chemotropism is not evidenced by every parasite. He finds the host root exudates to have three major effects on parasite radicles. They may induce the formation of root hairs on the parasite radicle, may cause greater extension growth of the radicle in seeds further away from the root

Table 7.

Speed of Activity of the Germination Stimulant

Species	Speed of Activity	Reference
Striga asiatica	30 min. exposure greatly enhanced the germination rate	Brown and Edwards, 1944; Brown, 1965
	2 hr. exposure for maximal germination	Brown and Edwards, 1946
Orobanche minor	As little as 10 min. exposure for a high germination rate	Cezard, 1965
Orobanche speciosa	60% germination after 30 sec. exposure	Chabrolin, 1938
Striga hermonthica and *Orobanche minor*	30 sec. exposure increases germination rate	Sunderland, 1960b

Table 8. *Chemical Characterization of the Germination Stimulant*

Species	Characterization	Reference
Striga asiatica	Probably a coumarin derivative or a related substance. Contains an ester or lactone or potential ester or lactone bond	Worsham, Moreland and Klingman, 1964
	General formula is $C_{19}H_{22}O_6$. Named strigol	Cook *et al.*, 1966
	Structure of strigol published. It is a complex unsaturated lactone	Cook *et al.*, 1972
Striga hermonthica	Probably D-xyloketose	Brown, Robinson and Johnson, 1949a
	Probably a hormone	Brown, Johnson, Robinson and Todd, 1949
	Contains a lactone, ester or other potential acid group, a hydroxyl group, a methyl group and a double bond	Brown and Tyler, 1952
Orobanche sp.	Probably a complex unsaturated lactone	Lansdown, 1956
Orobanche crenata	Probably a complex unsaturated lactone	Mallett, 1973
Orobanche minor	Contains a hydroxyl group, two ester (or δ-lactone) groups, a methyl group and a double bond	Brown, Greenwood, Johnson, Long and Tyler, 1951; Brown, Johnson, Robinson and Tyler, 1952
Striga sp. and *Orobanche* sp.	Contains a lactone, ester or other potential acid group, a hydroxyl group, a methyl group and a double bond	Brown, Greenwood, Johnson, Lansdown, Long and Sunderland, 1952

than in those that are close to it and may induce proliferation of the cortical cells of the radicle.

The structure of the *Striga asiatica* germination stimulant has recently been published by Cook *et al.* (1972). Strigol, the stimulant is a complex, unsaturated lactone. It will promote 50% germination of *Striga asiatica* seed at a concentration of 10^{-11} molar.

The germination stimulants active on these parasites appear in all cases to be released from the vicinity of the root tips although the exact area of release is in dispute. The area of release of the *Striga asiatica* germination stimulant is reported to be the root tip (Brown and Edwards, 1944), the piliferous region (Saunders, 1933) and the "absorptive" region (Uttaman, 1950), the *Orobanche speciosa* stimulant is considered to be released from the piliferous region (Chabrolin, 1938), and Sunderland (1960b) reports the germination stimulants of *Striga* and *Orobanche* species generally to be released from the region of the root in which cells are nearing completion of their growth in length.

2. Presence in the Plant

The stimulants are apparently synthesized within the plant prior to their release as they have been found present in various plants in low concentrations. Edwards (1972) found the roots of host plants of *Orobanche* sp. to contain the germination stimulant at a concentration of 0.1ppm. Mallett (1973) reported *Vicia faba* roots to contain the *Orobanche crenata* germination factor at a concentration of one part per thousand. Host root extracts have also proven able to germinate the seeds of *Orobanche speciosa* (Chabrolin, 1938) and *Striga senegalensis* (Okonkwo, 1966b). Worsham, Moreland and Klingman (1964) found the *Striga asiatica* germination factor to be present in the shoots of corn plants grown in the dark but not of those grown in the light. Dale and Egley (1971) developed a bioassay for the germination stimulant of *Striga asiatica* seeds which demonstrated this compound's presence in the stems of 118 species in 57 families. A total of 163 plant species were tested. As the active substances are found in both shoots and roots the area of synthesis within the plant remains to be determined.

3. Presence in the environment

The naturally-released chemical (or chemicals) capable of stimulating germination appears to be rather stable in the environment and is probably released in appreciably large quantitites as Egley and Dale (1970) have found it present in active concentrations in small bodies of water surrounded by vegetation. It is detectable from seven to eight weeks after the last winter frost until ten to twelve weeks after the first frost.

4. Synergistic activity

Compounds in the root exudates of different plants may act synergistically in their promotion of the germination of seeds of the parasites under consideration. Greenwood (unpublished, quoted in Sunderland, 1960b) reports that linseed root exudate alone has no effect on the germination of *Orobanche hederae* seeds but when added to the exudate of the usual host, *Hedera helix,* enhances its ability to promote the germination of the seeds of *O. hederae.* Sunderland (1960b) reports that solutions of sorghum or linseed root exudates too dilute to induce germination of *Orobanche minor* or *Striga hermonthica* seeds when used alone may induce over 50% germination of the seeds of these parasites when added together. Sunderland (1960a) also notes that sorghum root exudate will interact synergistically with corn exudate to increase the germination rates of *O. minor* and *S. hermonthica*.

5. Production by non-hosts

In general, plants considered natural hosts of a given parasite are probably capable of stimulating the germination of the seeds of that parasite. However, plants not capable of being hosts of these parasites (for reasons to be discussed later) may also be able to cause germination of the seeds of those parasites. Plants not parasitized in nature which may stimulate the germination of *Striga asiatica* are several solanaceous plants (Brown, 1946), *Crotolaria juncea, Dolichos lablab* and *Gossypium* sp. (Rose and Lochrie, 1941) and *Arachis hypogaea, Glycine max, Helianthus annuus* and *Phaseolus vulgaris* (U.S. Dept. Agr., 1957). *Orobanche aegyptiaca* may be stimulated to germinate by *Sorghum vulgare; Orobanche crenata* by *Cicer arietinum* and *Trigonella faenum-graecum* and *Orobanche cumana* by *Helianthus tuberosus* (Barcinsky, 1934). None of these are known to be parasitized in nature. This is an indication of the wide distribution of the compound among plants.

The stage of development of the host plant may be important in the stimulation of germination of the seeds of these parasites. Kadry and Tewfic (1956a) report that host plants of Orobanche crenata release larger amounts of the substance (or substances) stimulatory to the germination of the seeds of Orobanche crenata beginning about one week after flowering.

d. Stimulation of germination by synthetic chemicals

A wide range of synthetic compounds have proven able to stimulate the germination of the seeds of parasites in the genera Striga and Orobanche (see Table 9.). The mode of action of most of these chemicals is unclear though most of them are only active at higher concentrations than are necessary for the natural germination stimulant to be effective. Of particular note is the general activity of gibberellic acid in stimulating the germination of seeds of parasites in the genus Orobanche.

e. Effect of pH and light on germination

Both pH and light may be important to the germination of the seeds of these parasites (see Table 10.). The importance of pH may be somewhat indirect and related to its ability to destroy the activity of the germination stimulation substance. The role of temperature (outside of vernalization considerations) probably lies in its control of the rate of the reactions involved in the chain of events leading to the germination of the seeds.

f. Endogenous germination inhibitors

Seeds may also contain germination inhibitors. This has been reported for Striga asiatica (Kust, 1966) and Orobanche sp. (Edwards,

Table 9. Chemicals That Increase the Germination Rate of Parasites Requiring a Host Root Exudate for Germination

Species	Chemicals	Reference
Striga angustifolia	Kinetin	Ranga Swamy and Rangan,1969
Striga asiatica	1-allyl-2-thiourea,1-methionine,two carbamate derivatives,twelve 6-(substituted) purines,two coumarin derivatives including acopoletin	Worsham,1961;Worsham, Moreland and Klingman, 1959,1962
	Ethylene,2-chloroethyl-phosphic acid	Egley and Dale,1970
	Gibberellic acid (if soed is scarified)	Egley,1972
	Sarveroside	Cook et al.,1966
	Thiourea,allylthiourea	Brown and Edwards,1945
Striga hermonthica	d-xyloketose	Brown,Johnson,Robinson and Todd,1949;Long,1955
	A large numbar of compounds including carbamates, diazine derivatives,halogenated aliphalic acids and a few phenoxy,triazine and urea derivatives	Kasasian and Parker,1971
Cistanche tubulosa	Casein hydrolysate plus coconut milk	Rangan and Ranga Swamy,1968
Orobanche several spp.	Vitamin K-1,proline,tyrosine,methyl-histidine, thiol-histidine,thiamine phosphate	Cezard,1973
Orobanche aegyptiaca	Gibberellic acid	Kasasian,1973
	GA_3,Kinetin,casein,hydrolysate,yeast extract, coconut milk	Usha,1968
	A large number of compounds including carbamatea, diazine derivatives,halogenated aliphatic acids and a few phenoxy,triazine and urea derivatives	Kasasian and Parker,1971

Table 9. (Cont.)

Species	Chemicals	Reference
Orobanche crenata	Gibberellic acid	Hiron,1973
	Calcium hypochlorite	Cezard,1973
Orobanche hederae	Gibberellic acid	Privat,1960
	Calcium hypochlorite	Cezard,1973
Orobanche ludoviciana	Casein hydrolysate plus coconut milk	Nash and Wilhelm,1960
Orobanche minor	Trimethyl glycocoll,lipoic acid,a mixture of ADP and maleic acid,calcium hypochlorite	Cezard,1973
Orobanche picridis	Trimethyl glycocoll,lipoic acid,a mixture of ADP and maleic acid,calcium hypochlorite	Cezard,1973
Orobanche ramosa	Gibberellic acid as a pretreatment	Abu-Shakra,Miah and Saghir,1970
	Giberellic acid	Izard and Hitier,1958; Nash and Wilhelm,1960
	Pyridoxine and nicotinamide	Izard,1957
	$MgCO_3$ and $MgSO_4$	Izard and Hitier,1954
	Calcium hypochlorite	Cezard,1973

Table 10. Environmental Germination Considerations

Species	Consideration	Reference
Striga asiatica	Germinated more readily in an acid than in a neutral medium	Pearson,1913
	pH unimportant	Saunders,1933
	Germination better in the dark	Kumar and Solomon,1940
Striga euphrasioides	Germinates better in the light	Kumar and Solomon,1940
Orobanche sp.	Will not germinate in soil with a pH of over 6.5	Naumov,1952
Orobanche aegyptiaca	Germinates only in the dark	Ranga Swamy,1963
Orobanche crenata	Germinates only in the dark	Hiron,1973
Orobanche cumana	Will germinate readily in soil with a pH of 4.6 to 8.0 but not at a pH of 9.0	Barcinsky,1934
Orobanche hederae	Germinates equally well in light or dark	Privat,1960

1972). Ranga Swamy and Rangan (1969) note that the seeds of *Striga angustifolia* must be washed in running water for 48 hours to allow germination to occur. Kust (1966) isolated the inhibitor in *S. asiatica* seeds and found it to be heat-stable and water-soluble. He postulated that when water sufficient to support the growth of *Striga* seedlings was present in the soil the inhibitor would be leached out of the seed and would allow germination of the seeds. Edwards (1972) found the inhibitors in *Orobanche* sp. seeds to be phenolic compounds. No evidence was found for the presence of endogenous inhibitors in the seeds of *Alectra vogelii* (Botha, 1950a).

g. "Spontaneous" germination

The seeds of a number of root parasites which normally require a host factor for germination show some "spontaneous" germination (see Table 11.). Brown and Edwards (1944) found that "spontaneous" germination in *Striga asiatica* reaches a maximum in the stage of pretreatment when the seeds are most susceptible to the host root germination stimulant. Brown (1965) suggests that the stimulatory substance is endogenous to seeds of the parasite, though not at a high enough concentration to induce germination. He further suggests that during pretreatment the concentration of this substance increases in the seeds and in a few individuals may become high enough to induce germination.

3. Discussion

Kuijt (1969) concludes that the host root exudate requirement of the advanced parasites is an evolutionary addition to the germination

Table 11. Spontaneous Germination

Species	Germination Rate	Reference
Striga asiatica	0.1 to 1.0%	Brown and Edwards,1944
Striga euphrasioides	44.4% in the light	Kumar and Solomon,1940
Striga hermonthica	Up to 42%, the rate increasing as the length of prior dry storage increases	Vallance,1950
Orobanche arenaria	Occurs but the rate is not specified	Privat,1959
Orobanche crenata	0.01 to 0.1%	Nash and Wilhelm,1960
	Never occurs	Miron,1973
Orobanche ludoviciana	20.5%	Nash and Wilhelm,1960
Orobanche ramosa	Occurs but the rate is not specified	Izard,1957

requirements of the more primitive Scrophulariaceae rather than replacement of a pre-existing mechanism. It is significant, however, that no parasite requiring a host root exudate for germination also needs vernalization. This is true even of plants from temperate regions. The host root exudate requirement seems to replace the need for vernalization. Since proximity of a host root is the most important requirement of the young parasite seeds and since roots probably show little growth during the winter in temperate areas vernalization may not be a necessary germination mechanism in advanced parasites. The root exudate requirement to ensure proximity of a host root upon germination, however, would be crucial to these highly specialized parasites. An investigation into the germination requirements of _Conopholis americana_ and _Epifagus virginiana_, two species whose ranges extend into the north temperate zone, might clarify this situation.

A method by which a vernalization requirement for germination could evolve into a host root exudate requirement for germination is provided by gibberellic acid. Gibberellic acid treatment is known to replace the vernalization requirement in a number of autotrophic plants (Torrey, 1967) and has been shown in this laboratory to induce germination of the seeds of parasites previously determined to have a vernalization requirement for germination (see the research report). If gibberellic acid or a compound with similar action were found to be present in root exudates then a mechanism by which a vernalization requirement could be converted to a host root exudate requirement appears.

C. Parasite roots and root systems

1. Root Systems

The root systems of the more primitive parasites show little modification as a result of their hemiparasitic mode of life. The advanced parasites, however, frequently show reduction in the length and branching of the root system.

a. Scrophulariaceae

The root systems of the Scrophulariaceae appear very much like the root systems of autotrophic plants. In the genus *Striga,* however, the root systems are similar to the root systems of the Orobanchaceae so these taxa will be considered together. Some modification of the root systems of the Scrophulariaceae may be present, however, as Musselman (1973a) states, "Root dimorphism is well developed in the parasitic Scrophulariaceae. There appears to be a reduction in the number of lateral haustoria from members of the presumed primitive tribe Buchneriae to the advanced Euphrasiae." He notes in a later work (Musselman, 1974) that roots bearing haustoria are frequently coiled around the host roots but that roots not bearing haustoria do not coil; indicating a response to proximity of a host root. All roots of the Scrophulariaceae (less *Striga*) may apparently bear haustoria.

In the genus *Agalinis* the species *A. aphylla* is reported to have a short, condensed primary root from which the secondary roots spread (Boeshore, 1920). *A. maritima* has relatively short roots three to five centimeters long. Ramification is generally confined to a few lateral branches bearing several capillaries of the second order (Holm, 1929).

The genus *Aureolaria* is considered to have a spreading, fibrous, massive root system (Musselman, 1974). *A. flava* has firm, strong, fibrous roots. The primary root system is spreading, loose, and expanded. From this the secondary rootlets pass outward and down (Boeshore, 1920). *A. grandiflora* has a branching root system (Musselman, 1969). *A. pedicularia* has a root system that is more compressed than that of *A. flava* (Boeshore, 1920) and has few branch roots (Musselman, 1969). *A. purpurea*, *A. parvifolia* and *A. setacea* have root systems like that of *A. maritima*. *A. tenuifolia* also has a similar root system but the roots may reach 10 cm. long (Holm, 1929).

Buchnera americana possesses a persistant primary root which bears several laterals of about the same thickness near the base (Holm, 1929).

The root system of *Centranthera humifusa* consists of several rather stout main branches up to a decimeter long from which numerous "thread-like" secondary roots spread (Barnes, 1941).

Cordylanthus produces well-developed root systems with abundant laterals (Chuang and Heckard, 1972).

Dasistoma has a spreading, fibrous and massive root system (Musselman, 1974). The crown and large roots are concentrated near large host roots (Piehl, 1962a).

Neidhardt (1947) reports that *Euphrasia rostkoviana* develops a deep root system if grown alone but if grown with hosts the root system consists of a short tap root with abundant laterals.

Boeshore (1920) found the root system of *Lathraea* to be limited. The seedling initially produces a primary root with laterals but later on in growth roots are produced adventitiously from the stem. This pattern has been correlated for *L. clandestina* by Chemin (1925) and Renaudin (1968) and for *L. squamaria* by Massee (1886) and Heinricher (1893).

The root system of *Melampyrum cristatum* usually consists of a primary root with several laterals (Horill, 1972). *M. lineare*, however, has a shallow root system consisting of a poorly defined primary root which is surpassed in length by a few of the laterals (Piehl, 1962b).

Odontites verna develops a limited root system consisting of a few large roots supporting a sparse network of finer roots (Govier, Brown and Pate, 1968).

The seedling of *Orthocarpus faucibarbatus* establishes a shallow, much-branched root system. However, when a functional haustorium is attached to a host the root system immediately around the point of penetration expands enormously, often dwarfing the rest of the root system (Thurman, 1966). *O. purpurascens* has a strong tap root, which may be branched, and a few laterals. The form of the root system, however, depends on the host being attacked (Cannon, 1909).

Piehl (1963b) considers the root system of *Pedicularis canadensis* to be of the diffuse type.

b. Orobanchaceae and *Striga*

The root systems of the advanced parasites are typified by reduction. Upon germination an elongate structure generally considered to be the radicle emerges from the seed. The only possible exception to this is Aeginetia indica, which Kusano describes in 1903 as following the above pattern while in 1908 he describes a different course of development: The first event is the appearance of about fifteen cells outside the testa at the micropylar end of the seed. Each cell produces what appears to be a branched root hair. When a host root is contacted the hair attaches to it.

The filament or radicle produced by the other members of this group of parasites need not grow in a straight line. That of Orobanche hederae is reported to follow a spiral course (Tate, 1925) and Williams (1960) described the radicle of Striga asiatica as undergoing a "fixed growth movement" ranging from a spiral path to apparently anomalous curvatures in any direction. Racovitza (1973), however, found the radicle of Orobanche ramosa to generally be straight or rippled and rarely branched at the tip.

If the radicle does not contact a host root within a certain period of time growth ceases and the parasite dies. The maximum length a parasite radicle can attain varies from plant to plant. The recorded maximum lengths are: Striga asiatica - 2 to 4 mm. (Williams, 1958) or 2 to 3 mm. (Kadry and Tewfic, 1956b); Orobanche hederae - 3 to 4 mm. (Privat, 1960); Orobanche ludoviciana - 2 to 3 mm. (Nash and Wilhelm, 1960); Orobanche minor - 1 to 2 mm. (Sunderland, 1960b); Orobanche *ramosa* - 1.5 mm. (Nash and Wilhelm, 1960) and 2.24 mm. (Durbin, 1953).

If the radicle contacts and successfully attaches to a host root (produces a primary haustorium) a swelling known as a tubercle is formed. This tubercle has been reported for *Striga asiatica* (Saunders, 1933; Williams, 1958), *S. gesnerioides* (Williams, 1958), *S. senegalensis* (Okonkwo, 1966a), *Aeginetia indica* (Kusano, 1903, 1908), *Conopholis americana* (Boeshore, 1920), *Epifagus virginiana* (Cooke and Schively, 1904), *Orobanche crenata* (Kadry and Tewfic, 1956b), *O. hederae* (Privat, 1960) and *O. ramosa* (Durbin, 1953). The tubercle produces the flowering stalks and roots.

Striga euphrasioides has a root system similar to those of more primitive genera. The roots are long with many branches and they may bear secondary haustoria (Van Buuren, 1914-1915). Van Buuren further reports that *S. asiatica* and *S. densiflora* have root systems that are somewhat reduced as compared to that of *S. euphrasioides.* They are also reported to bear fewer haustoria. Stephens (1912b), however, finds *S. asiatica* to produce many adventitious roots from the underground part of the stem and Saunders (1933) notes that the *S. asiatica* roots may branch several times and produce secondary haustoria. *S. senegalensis* also produces adventitious roots and these are also capable of forming secondary haustoria (Okonkwo, 1966a). The greatest reduction of the root system in the genus *Striga* occurs in *S. gesnerioides,* which has very short roots or none at all (Van Buuren, 1914-1915; Kuijt, 1969) and forms no secondary haustoria (Van Buuren, 1914-1915).

The genus Orobanche also shows a pattern of reduction in the root system. Orobanche minor has a mass of secondary roots produced from a swollen, shortened primary root. The secondary roots may form secondary haustoria (Boeshore, 1920). O. ramosa has a well-developed root system (Ungurean and Serbanescu-Vitarui, 1973) produced from the tubercle (Durbin, 1953). They may form secondary haustoria (Ungurean and Serbanescu-Vitarui, 1973). O. uniflora produces a mass of secondary roots from the tubercle (Smith, 1901; Boeshore, 1920; Kuijt, 1969). The roots produce many lateral haustoria (Kuijt, 1969). O. epithymum develops roots up to 8 cm. long (Privat, 1960). O. crenata produces numerous roots up to 5 cm. long. They may bear haustoria (Kadry and Tewfic, 1956b). O. hederae has short roots up to 1 to 2 cm. long that do not form secondary haustoria (Tate, 1925). O. grayana forms a mass of short secondary roots around the point of attachment. These roots do not form secondary haustoria (Kuijt, 1969). O. fasciculata seems to show the greatest reduction of any member of the genus. It produces no or vitually no roots at all (Kuijt, 1969).

A similar trend towards root system reduction occurs in the other genera of the Orobanchaceae. Aeginetia indica forms many long, branching roots which may form secondary haustoria (Kusano, 1903; Juliano, 1935). The roots of Melasma develop profusely around the point of attachment (Saunders, 1934). Epifagus virginiana produces numerous, short, much-branched roots (termed grapplers) over the surface of the tuber. These roots do not form secondary haustoria (Cooke and Schively, 1904; Brooks, 1960 (1961)). *Conopholis* (Boeshore, 1920; Kuijt, 1969) and *Boschniakia* (Gavriliuk (1965), quoted in Kuijt, 1969) form no roots at all.

C. Santalaceae

The root systems of the Santalaceae, like those of the Scrophulariaceae, show little modification as a result of the parasitic habit though a small degree of specialization is noted by Fineran (1962) in the *Exocarpus bidwillii* root system (see next paragraph).

Choretrum lateriflorum has a well-developed lateral root system (Herbert, 1924-1925). *Comandra* has a root system with both the primary and lateral roots well-developed and with an adventitious root system which develops from the base of the stem and from the rhizomes (Piehl, 1965c). *Exocarpus bidwillii* has a widely spreading root system consisting of several main roots which produce laterals at intervals. Some of these laterals may continue to grow and become new main roots while most will remain short. Most of the short laterals are shed but those that form haustoria may be persistent. Adventitious roots may also be produced (Fineran, 1962). *E. spartea* has a branched taproot with a large number of shallow, ramifying lateral roots (Herbert, 1924-1925). *Fusanus acuminatus* has a deep taproot with long laterals while *F. spicatus* has a branching taproot with a shallow, ramifying root system (Herbert, 1924-25). *Leptomeria preissiana* and *L. spinosa* have well-developed, branched taproots and root systems that are profusely branched in loose soil while in heavier loam it is less branched and more deeply rooted.

Santalum album has a poorly developed but ramifying root system (Barber, 1907; Rama Rao, 1910b).

2. Presence of Root Hairs

Root hair frequency is compiled in Tables 12., 13., and 14. Heinricher (1898a, b, 1917) attempted a correlation between the frequency of root hairs and the degree of dependence on parasitism. Heckard (1962), however, found great variation in the frequency of root hairs within various species of *Castilleja*. Furthermore, several *Castilleja* species which seemed to have no root hairs could complete their life cycle without a host.

A number of genera of Scrophulariaceae have a collar of root hairs at the radical/hypocotyl junction as seedlings. This has been reported for *Agalinis* and *Aureolaria* (Musselman, 1974), *Castilleja* (Heckard, 1962), *Euphrasia* (Wettstein, 1898; Yeo, 1961) and *Orthocarpus* (Thurman, 1966). Hair-like structures are also associated with haustorial development in many species of parasites but this phenomenon will be covered later.

3. Root Structure

The structure of parasite roots appears similar to that of angiosperms generally, though the roots of the Orobanchaceae may show a reduction in complexity.

a. Scrophulariaceae

The primary root structure of the Scrophulariaceae is similar to that of nonparasitic dicots. The outermost tissue of the root is a two-layered epidermis (Musselman, 1974). Holm (1929), working with

Table 12. *Frequency of Root Hairs of Parasitic Scrophulariaceae*

Species	Frequency of Root Hairs	Reference
Agalinis aphylla	Present on seedling radicles	Musselman,1974
Agalinis maritima	Absent	Holm,1929
Agalinis obtusifolia	Absent	Holm,1929
Agalinis setacea	Absent	Holm,1929
Agalinis tenuifolia	Absent	Holm,1929
Alectra vogelii	Absent	Botha,1948
Aureolaria flava	Present on seedling radicles	Musselman,1974
	Present but frequency not specified	Boeshore,1920
Aureolaria virginica	Present on seedling radicles	Musselman,1974
Buchnera americana	Absent	Holm,1929
Castilleja affinis	Few to absent	Heckard,1962
Castilleja coccinea	Present on seedling radicles	Musselman,1974
	Few	Malcolm,1966
Castilleja franciscana	Common to rare on different individuals	Heckard,1962
Castilleja inflata	Few to absent	Heckard,1962
Centranthera humifusa	Absent	Barnes,1941
Cordylanthus spp.	Present in scattered groups	Chuang and Heckard,1971

Table 12. (Cont.)

Species	Frequency of Root Hairs	Reference
Euphrasia spp.	Few	Wettstein,1898;Yeo,1961
Euphrasia minima	Abundant	Heinricher,1898a,b
Lathraea clandestina	Generally abundant	Chemin,1925
Melampyrum lineare	Few	Piehl,1962b
Odontites verna (=*O. odontites*)	Present on seedling roots	Govier,Brown and Pate, 1968
	Abundant	Heinricher,1898a,b
Orthocarpus faucibarbatus	Few to absent	Thurman,1966
Orthocarpus purpurascens	Present on seedling radicles	Musselman,1974
Pedicularis canadensis	Present on seedling roots	Piehl,1963b
Schwalbea americana	Present on seedling radicles	Musselman,1974
Sopubia ramosa	Present but frequency not specified	Williams,1960
Striga asiatica	Absent	Stephens,1912a,b; Saunders,1926,1933; Hattingh,1954; Musselman,1973b,1974
Striga densiflora	Very few	Luthra,1921
Striga euphrasioides	Very few	Luthra,1921
Striga senegalensis	Sparsely scattered *in vitro*	Okonkwo,1964,1966a

Table 13. Frequency of Root Hairs on the Roots of Orobanchaceae

Species	Frequency of Root Hairs	Reference
Aeginetia indica	Absent	Kusano,1903; Juliano,1935
Orobanche hederae	Absent	Koch,1887
Orobanche minor	Absent	Koch,1887
Orobanche ramosa	Absent	Koch,1887
Orobanche speciosa	Absent	Koch,1887
Orobanche uniflora	Absent	Boeshore,1920;Kuijt,1969

Table 14. Frequency of Root Hairs on the Roots of Santalaceae

Species	Frequency of Root Hairs	Reference
Comandra umbellata	Abundant	Piehl,1965c
Exocarpus bidwillii	Abundant	Fineran,1962
Exocarpus spartea	Absent	Herbert,1924-1925
Fusanus spicatus	Absent	Herbert,1924-1925
Leptomeria preissiana	Few	Herbert,1924-1925
Leptomeria spinosa	Few	Herbert,1924-1925
Santalum album	Few	Barber,1906
Thesium sp.	Few	Barber,1907b

several species of *Agalinis, Aureolaria* and *Buchnera,* considers this to be an outer epidermis and an inner exodermis. Holm further reports that the epidermis in *Agalinis* and *Aureolaria* is soon lost and the root is then covered by the suberized exodermis. The cortex is generally composed of thin-walled parenchyma containing numerous starch grains (Musselman, 1974). The cortex of *Lathraea clandestina* (Chemin, 1925) and *Striga senegalensis* (Okonkwo, 1966a) contains large air spaces and the cortex of the semi-aquatic species *Agalinis linifolia* and *A. maritima* consists of aerenchyma (Musselman, 1974). The very young cortex of *Agalinis* and *Aureolaria* was found by Boeshore (1920) to consist of rows of parenchyma cells connecting the stele with the epidermis. The rows of cells were separated by large air spaces. The spaces fill in with parenchyma cells as the root ages. The endodermis of the Scrophulariaceae is single-layered and has Casparian strips (Boeshore, 1920; Chemin, 1925; Holm, 1929; Musselman, 1974). *Sopubia ramosa* has a pericycle of one to several rows of thin-walled cells (Williams, 1960a) but a pericycle is not mentioned in other members of this group. Musselman (1974) considers the primary xylem to be triarch or tetrarch and to alternate with regions of phloem in the parasitic Scrophulariaceae generally but Williams (1960a) reports a pentarch xylem configuration for *Sopubia* and Holm (1929) reports the xylem arrangement of *Agalinis, Aureolaria* and *Buchnera* to be diarch. Boeshore (1920) found the xylem of *Agalinis* and *Aureolaria* to consist of pitted vessels and spiral tracheids. *Odontites verna* (Govier, Brown and Pate, 1968) has poorly developed phloem. *Pedicularis vulgaris* (Maybrook, 1917), *Striga asiatica* (Stephens, 1912a; Uttaman, 1950) and *S. senegalensis* (Okonkwo, 1966a) have all been reported to lack phloem. Okonkwo considered the phloem region of *S. senegalensis* to be made up largely of parenchyma. Rogers and Nelson (1962), however, found phloem in the roots of *Striga asiatica* and Musselman (1974) reported phloem in the roots of all of the species of parasitic Scrophulariaceae with which he worked.

A storied cambium begins activity 7 to 10 mm. behind the apex in all parasitic Scrophulariaceae (Musselman, 1974). Holm (1929) also reported cambial activity in several species of *Agalinis* and *Aureolaria.* Xylem and phloem consists of vessel elements with simple, terminal perforation plates and libriform fibers. Secondary phloem is produced but not abundantly and consists of parenchyma cells. In older roots the outer layers of the periderm become suberized and filled with tannins and other substances (Musselman, 1974). Though sclerenchyma is not common in the parasitic Scrophulariaceae Musselman (1974) found the cortical parenchyma and secondary phloem of *Schwalbea americana* to become sclerified. Holm (1929) reports sclereids in the mature cortex of several *Aureolaria* species and Boeshore (1920) notes the same for *Aureolaria flava.*

The root apices of a number of parasitic Scrophulariaceae have been studied by Musselman (1974). He found them all to possess an initial giving rise to both the root cap and the epidermis. All parasitic Scrophulariaceae except *Striga asiatica* have a root cap (Musselman, 1973b, 1974). The organization of the root apex is also distinctive in that a clear differentiation of initials is lacking and the region of elongation is particularly prominent. The apex of *Macranthera* contains a mucilaginous layer (Musselman, 1974).

b. Orobanchaceae

An epidermis seems generally present in the Orobanchaceae. It is single-layered in *Aeginetia indica* (Juliano, 1935) and in *Epifagus* (Cooke and Schively, 1901). Tate (1925) reports the epidermis of *Orobanche hederae* to be corky and several cell layers thick and Privat (1960) finds it to become suberized and sloughed off as the root matures. The cortex of *Aeginetia indica* (Juliano, 1935), *Epifagus* (Cooke and Schively, 1901), *Orobanche ramosa* (Ungurean and Serbanescu-Jitarui, 1973) and *O. uniflora* (Smith, 1901) consist of parenchyma cells containing starch granules. Cooke and Schively (1901) report the cortex of *Epifagus* to also contain cells which have no starch granules, are spindle-shaped and occur in groups of two or three. Smith (1901) notes that the cortex of *Orobanche uniflora* is 10 to 12 cells thick. The endodermis is reported as being well-differentiated only in *Christisonia bicolor* (Worsdell, 1895). It is indistinct in *Aeginetia indica* (Juliano, 1935), *Christisonia subacaulis* (Worsdell, 1895) and *Orobanche hederae* (Privat, 1960). Smith (1901) notes the bundle sheath as being absent or present only in patches in *Orobanche uniflora.* An endodermis is lacking entirely in *Epifagus* (Cooke and Schively, 1901). No mention of a pericycle is available in the literature. Primary phloem has been reported to be well-developed in *Aeginetia indica* (Juliano, 1935), *Epifagus* (Cooke and Schively, 1901), *Orobanche hederae* (Tate, 1925; Privat, 1960), *O. ramosa* (Ungurean and Serbanescu-Jitarui, 1973) and *O. uniflora* (Boeshore, 1920). The primary xylem of *Orobanche ramosa* consists of one or two tracheids (Ungurean and Serbanescu-Jitarui, 1973). That of *Aeginetia indica* is of reticulate tracheids in a triarch arrangement (Juliano, 1935). In *Orobanche uniflora* the xylem is usually diarch but may be triarch or of indefinite arrangement. It is composed of short, pitted-reticulate tracheids (Smith, 1901). *O. hederae* has xylem of reticulate tracheids (Tate, 1925) in a diarch or tetrarch arrangement (Privat, 1960). The primary xylem of *Epifagus* consists of a few spiral or reticulate tracheids (Cooke and Schively, 1901). No sieve tubes were found in the root of *Orobanche uniflora* (Smith, 1901).

Cambial activity has been reported in *Aeginetia indica* (Juliano, 1935), *Orobanche hederae* (Privat, 1960) and *O. ramosa* (Ungurean and Serbanescu-Jitarui, 1973). In *O. ramosa* the cambial activity produces four vascular bundles (Ungurean and Serbanescu-Jitarui, 1973). Juliano (1935) found the cambial layer of *Aeginetia indica* to be incomplete so that only a small amount of secondary thickening occurs even though some secondary phloem of sieve-tubes and companion cells and xylem of reticulate tracheids separated by parenchyma cells is formed. The inner cortical parenchyma cells become liquified and a sclerenchymatous ring is formed around the central cylinder. In *Orobanche hederae* much secondary thickening occurs at the base of the short roots. The wood produced is of reticulate tracheids.

In the Orobanchaceae a root cap may or may not be present. *Aeginetia indica* (Kusano, 1903; Juliano, 1935), *Christisonia neilgherrica*, *C. subacaulis* (Worsdell, 1895), *Cassytha filiformis* (Boewig, 1904), *Epifagus virginiana* (Cooke and Schively, 1901), *Orobanche hederae* (Privat, 1960) and *O. uniflora* (Smith, 1901) have all been reported to lack one.

c. Santalaceae

Very little work has been done on the root structure of the Santalaceae. Only *Comandra umbellata* (Piehl, 1965c) and *Exocarpus bidwillii* (Fineran, 1962) have been thoroughly studied. As Fineran notes, their structure is similar to that of nonparasitic dicots. Both *Exocarpus* (Fineran, 1962) and *Comandra* (Piehl, 1965c) have an epidermis and a cortex. Fineran terms the outer cortical layer the exodermis as a result of the inclusion of substances such as tannins within its cells. *Exocarpus* also has intercellular spaces within the cortex (Fineran, 1962). An endodermis with Casparian strips is present in both parasites and Fineran (1962) notes an indistinct pericycle immediately inside the endodermis of *Exocarpus*. The primary phloem of *Exocarpus* is present in small groups within nonvascular parenchyma and alternates with the diarch, triarch or tetrarch protoxylem rays. Fineran (1962) reports finding sieve tubes and companion cells in the phloem of *Exocarpus* even though he could find no sieve plates. The xylem of *Comandra* is either diarch (Piehl, 1965a) or tetrarch (Holm, 1924). Kusano (1902) notes sieve tubes as being present in the roots of *Buckleya quadriala*. The development of xylem in Exocarpus follows an exarch pattern (Fineran, 1962).

Secondary thickening occurs in Exocarpus. The xylem produced by the cambium consists of small vessels with simple, oblique perforation plates, imperforate tracheary elements, fibers and multiseriate, homogenous parenchyma rays. The fibers make up the bulk of the wood. A reduced amount of phloem including phloem rays is also produced. In addition a phellogen produces radial rows of cork cells to the outside and a few cortical cells internally. The secondary cortex consists of several layers of parenchyma cells which may have starch grains. In Comandra Holm (1924) reports the pericycle to become a cork cambium, resulting in the loss of the cortex, but Piehl (1965c) finds the cortex to be maintained at maturity.

4. Discussion

The forms of the root systems of the more primitive parasites (which are those that produce only secondary haustoria) are not well documented. Reported differences between taxa may be as easily attributable to variations in the substrates of these plants as to varying dependence on a parasitic mode of life. Even individual variation within a species might conceivably exceed reported variations between species or genera.

It seems likely that the occurence of a primary haustorium and the reduction of root systems, root structure and the frequency of secondary haustoria are somehow related. In Striga the form of the root system extends from that of S. euphrasioides, which has long roots that branch frequently and bear many haustoria, to that of S. gesnerioides, which has roots that are very short or nonexistent. In Orobanche the range in root system form is from O. minor, O. ramosa and O. uniflora, which have large numbers of roots that bear many haustoria (branching is not mentioned) to O. fasciculata, which has virtually no roots. In the Orobanchaceae as a whole the range in root system form is from Aeginetia indica, which forms long, branching roots bearing many haustoria, to Conopholis and Boschniakia, which have no roots at all. Some reduction in root structure occurs in all these taxa but not enough data is available to make a general statement. The most significant aspect of this situation, however, does not seem to be the trend in reduction present in each of these taxa (presumed to be natural taxa). Though reduction frequently occurs in root system length and branching, root structure and frequency of secondary haustoria in advanced species the permanent subterranean feature is the primary haustorium. It is possible that the appearance of the primary haustorium is the evolutionary advance that allowed reduction of the root system to take place. Taxa not having a primary haustorium do not show significant reduction trends.

D. Hosts

Most root parasites appear to have wide host ranges. Some, however, may show varying degrees of host range restriction and others can complete their life cycle without a host. The relationship between a parasite and its host is a complex one and not fully understood.

1. Host range

The reported host ranges of a number of parasites are compiled in the Appendix. Report of few hosts for a parasite probably indicates lack of data. Data on host ranges taken exclusively from field studies has certain disadvantages. Parasites may occasionally establish haustorial contact with a plant whose unsuitability as a host is masked by the simultaneous parasitism of other plants.

A number of species have host ranges without any apparent restriction. This is documented for *Agalinis holmiana*, *A. purpurea*, *A. virgata*, *Castilleja coccinea*, *Euphrasia salisburgensis*, *Melampyrum arvense*, *M. lineare*, *Odontites verna*, *Orthocarpus orianthus*, *O. faucibarbatus*, *O. purpurescens*, *Pedicularis canadensis*, *P. lanceolata*, *Striga densiflora*, *Comandra umbellata* and *Santalum album*. Other parasites show a rather narrow host range, but their researchers have felt them to have a wide host range anyway. For instance, section Chyta of *Agalinis* (Pennell, 1935), species in *Euphrasia* (Heinricher, 1898a, b, 1910) and *Fusanus acuminatus* and *F. spicatus* (Herbert, 1924-1925). Still other parasites have a wide host range within a major plant taxon but appear virtually restricted to that taxon: *Alectra vogelii* on Leguminosae (Rattray, 1932; Botha, 1948), *Striga asiatica* (Saunders, 1933; Nelson, 1958; Shaw *et al.*, 1962), *S. euphrasioides* (Kumar and Solomon, 1941) and *S. hermonthica* (Andrews, 1945, 1947) on the Poaceae, *Striga gesnerioides* on dicots (Van Buuren, 1914-1915), *Aeginetia indica* on monocots (McWhorter, 1922; Teodoro, 1925; Roxas, 1927) and *Orobanche aegyptiaca*, *O. cernua*, *O. minor* and *O. ramosa* (Beck von Mannagetta, 1890, 1930; Hayek and

Hegi, 1918) on dicots. However, *Striga asiatica*, *S. euphrasioides* and *S. hermonthica* have been reported on a few dicots and *Aeginetia indica* has been reported on members of the families Ericaceae and Gleicheniaceae (Beck von Mannagetta, 1890, 1930). Thus, a parasite may show a strong preference for a plant taxon and yet not be totally restricted to it.

A few parasites seem to have a truly restricted host range. *Conopholis alpina* and *C. americana* have never been found to have a host outside of the genus *Quercus* and have generally been felt to be restricted to subgenus *Erythrobalanus* of *Quercus*. Thieret (1971), however, notes that collection data in herbaria indicates that *C. americana* also attaches to members of subgenus *Lepidobalanus* of Quercus. This needs clarification. *Epifagus virginiana* appears restricted to *Fagus grandifolia*. No other hosts have been reported. Finally, *Pedicularis densiflorus* and *P. semibarbatus* are felt by Sprague (1962) to be virtually specific to *Pinus ponderosa* but this has not been corroborated.

Further study has broadened the host range of many parasites once believed to show a high degree of host specificity. *Buckleya distichophylla* has been presumed to be parasitic only on *Tsuga* spp. (Fernald, 1958). Piehl (1965b), however, found *B. distichophylla* to have attachments to 25 species of plants, including angiosperms and ferns. Similarly, Pennell (1928, 1935) felt subgenus *Panctenis* of *Aureolaria* to be parasitic only on subgenus *Erythrobalanus* of *Quercus* and subgenus *Euaureolaria* of *Aureolaria* only on subgenus *Lepidobalanus* of *Quercus*.

Musselman (unpublished) has found members of each subgenus of *Aureolaria* attached to oaks of both subgenera of *Quercus* as well as to many other species of plants. However, he notes that the hosts felt to be specific by Pennell are always present in areas where each *Aureolaria* species is found. Pennell (1928, 1935) also considered *Dasistoma macrophylla* to be parasitic only on *Aesculus glabra* but Piehl (1962a) was able to demonstrate two other trees in two families as hosts.

Host specificity is perhaps more likely in root parasites which form only a single primary haustorium, such as *Conopholis* and *Epifagus,* than in parasites which form multiple haustoria and have an unspecialized germination mechanism, such as *Aureolaria* and *Dasistoma.* A plant which forms multiple haustoria would have repeated chances to contact other hosts unless a very specialized haustorial initiation mechanism were operating - a situation which does not appear to occur. However, these latter plants could still have an absolute necessity for substances provided by the apparently specific host. That is, *Buckleya distichophylla* might have an absolute requirement for a nourishing substance from *Tsuga* but could obtain beneficial nourishment from other hosts. If it were not attached to *Tsuga,* though, it would not survive. This could explain the association of the above-described plants. On the other hand, a plant forming only one host attachment and requiring that host would die if it should attach to any other plant.

Not all hosts are of the same benefit to a parasite or are parasitized as frequently. Piehl (1963b) notes that *Pedicularis canadensis* frequently parasitizes Asclepias exaltata and Aster laevis while Equisetum arvense and Prenanthes alba are rarely attached to and Pteridium aquilinum and Viola pubescens bear many old haustorial scars but few attached haustoria. Castilleja coccinea (Malcolm, 1962a, b), Comandra umbellata (Harrington, 1945) and Santalum album (Rama Rao, 1910b) are also reported to have preferred hosts. A plant might be preferred by a parasite capable of utilizing any plant as host because this particular plant is the dominant member of an ecological community (Sprague, 1962; Kuijt, 1969; Chuang and Heckard, 1971). This might be the case in Sprague's (1962) report of the possibility of the host-specificity of Pedicularis densiflorus and P. semibarbatus. However, in each of the examples mentioned earlier in this paragraph at least a few of the little-used host plants appear in some way to be unsuitable as hosts. Methods of host resistance to parasitic attack are discussed in the next section.

It is likely that any parasite capable of forming multiple haustorial attachments will at one time be attached to more than one host. This has been reported as being the case in Pedicularis canadensis (Piehl, 1963b). The vigor of the parasite, then, might depend on the various plants to which it attaches.

Some confusion as to the most common host extent still exists. Kuijt (1969) states "In root parasites generally we find little specialization with regard to hosts" and Piehl (1962a) notes that "all chlorophyllous parasites of the Scrophulariaceae and Santalaceae that have been studied in some detail are known to parasitize a number of hosts". The compilation in the Appendix would appear to indicate that the above position is not entirely correct. It seems that *Alectra, Striga* and the Orobanchaceae, all of which are considered to be relatively advanced parasites, tend to have greater or lesser host range restriction while most of the less specialized parasites seem to have unrestricted host ranges.

Host specificity may be related to a plant's growth form as well as to its taxonomic relations. For instance, *Exocarpus bidwillii* is reported to prefer woody hosts (Fineran, 1962) and the only known hosts of *Dasistoma macrophylla* are trees (Piehl, 1962a). Such a preference also seems likely in *Lathraea.* It would seem logical that a perennial parasite might require attachment to a perennial host. Annual hosts would die each year - leaving the parasite periodically without a host and certainly requiring the continued establishment of haustoria for the purpose of maintaining a supply of nourishment. It might be that a parasite which utilizes woody hosts might itself need to be woody to maintain its haustorial connections during secondary growth of the host roots.

Atsatt (1970) and Atsatt and Strong (1970) contribute some interesting ideas on the above questions. They note, in regard to another phenomenon, that each host may represent a "distinct environmental element to the parasite with different physical and chemical properties in addition to the usual environmental factors of soil, water, temperature, etc." Furthermore, they point out that promiscuous root grafting may be a liability because some hosts reduce the reproductive potential of their attached parasites. At the same time, however, use of a wide range of host plants acts as a buffer which may even allow genotypes which would be autotrophically lethal to survive.

2. Resistance of Potential Hosts to Attack

There are a number of factors involved in host resistance. The mechanisms of resistance may be ecological, physiological or mechanical. Resistance of a plant to one species of parasite does not necessarily indicate that it is resistant to other spcies of parasites, even when the parasites are closely related. For example, it has been noticed in plant breeding programs in Africa that a variety of sorghum resistant to one species of *Striga* is not necessarily resistant to another *Striga* species (Doughty, 1941; Doggett, 1953).

Reported resistance mechanisms are:

1. Growth in an unfavorable environment (Kuijt, 1969).

2. Shading by a potential host of a shade-intolerant parasite. Such a mechanism has been reported to provide protection against *Orthocarpus faucibarbatus* (Thurman, 1966) and *Striga hirsuta* (Bouriquet, 1946).

3. Differing root system configurations (Malcolm, 1962b; Piehl, 1963). For instance, a deeply rooted potential host species might only rarely be attacked by a parasite with a shallow root system.

4. Mechanical obstruction of haustorial penetration. Saunders (1933) reports that some strains of *Andropogon sorghum* are resistant

to Striga asiatica as a result of their resistance to dissolution of the cell walls by the intrusive organ or as a result of an especially thick wall layer in the cells of the endodermis. Rama Rao (1910b) noticed that potential host species of Santalum album with tough, dry periderm on the roots are not so heavily attacked as hosts with a thick, sappy periderm. Mechanical obstruction of parasitic attack has also been discussed for hosts of Dasistoma (Piehl, 1962a), Euphrasia (Yeo, 1964), Orobanche (Cubero, 1973), Santalum (Barber, 1906; Rao, 1942) and Striga asiatica (Saunders, 1942; Williams, 1959).

5. Formation of a layer of cork around the intrusive organ following penetration. This has been reported with Rhus typhina attacked by Comandra richardsiana (Moss, 1926).

6. Dislodging of the haustorium by callusing of the parenchyma cells of the inner cortex. Reported in hosts of Leptomeria preissiana (Herbert, 1924-1925).

7. Hypertrophy of the root tissue in the vicinity of the haustorial intrusion. Reported for Hedera helix attacked by Orobanche hederae (Privat, 1960).

8. Physiological obstruction of parasitic attack. This would be due to toxicity of the host tissues to the invading parasite tissues (Saunders, 1942; Kuijt, 1969).

9. Inability of the host to provide proper or sufficient nourishment to the parasite (Saunders, 1933; 1942; Yeo, 1964; Kuijt, 1969).

10. Toxic root exudates. These might either damage the roots of

the parasite, inhibit haustorial initiation or in some other way prevent the initiation of parasitic attack (Chuang and Heckard, 1971).

11. Failure to provide the seed germination stimulant to parasite seeds that require such stimulants in order to germinate (Doggett, 1964; Cubero, 1973). This can apply to species in *Alectra*, *Striga*, and Orobanchaceae. Varieties of *Sorghum vulgare* that do not release the *Striga asiatica* germination factor have been reported (Kumar, 1940; Williams, 1959) and Robinson (1962) found that Smooth Cayenne pineapple is not attacked by *Striga asiatica* for the same reason.

3. Necessity of a Host

Although in nature a parasite will probably always form haustorial connections with other plants it has been discovered, primarily through pot or greenhouse culture, that some parasites are capable of completing their life cycles without a host. It is an indication that some autotrophic capabilities remain within certain (probably less specialized) parasitic taxa.

Parasites capable of an autotrophic existence have been reported only in the Scrophulariaceae. Heckard (1962) grew several species of *Castilleja* to flowering and seed production without a host. Only *C. latifolia* seemed as vigorous when growing alone. Chuang and Heckard (1971) determined that most of the species of *Cordylanthus* they studied, including all six members of section Cordylanthus, were able to complete their life cycles without a host in greenhouse culture. Heinricher (1917) found considerable variation among species of *Euphrasia* in regard to their ability to grow without a host. *Euphrasia minima* would flower readily without a host, *E. salisburgensis* would usually flower without a host but was less vigorous than when growing with a host and *E. rostkoviana* rarely flowered when growing alone. *Odontites verna* can grow to flowering without a host (Govier and Harper, 1965). Atsatt (1970) and Atsatt and Strong (1970) found populations of *Orthocarpus purpurescens* and other *Orthocarpus* species to contain individuals with a full range of autotrophic capabilities - from those which can complete their life cycles without a host to those which show little development. However, plants are usually more vigorous and produce more seeds when they are grown with a host. *Rhinanthus minor* (Hambler, 1958; Bourget, 1965), *R. alectorolophus*, *R. burnati* and *R. major* (Bourget, 1965) are all capable of setting seed without a host. However, growth is somewhat slower when grown alone than with a host.

Plants of *Castilleja coccinea* (Malcolm, 1962b), *Comandra umbellata* (Piehl, 1965c), *Lathraea clandestina* (Chemin, 1925), *Melampyrum cristatum* (Horrill, 1972) and *Santalum album* (Rama Rao, 1910a) are capable of living for months without a host but remain severely stunted and eventually die.

4. Discussion

Reliance on fewer and fewer plants as hosts involves either an improved ability to recognize hosts, an inability to survive on other than the normal host species or both. Improved ability to recognize hosts probably takes the form of reception of the proper chemical for seed germination. Inability to survive without a certain host probably involves provision by the host of a chemical otherwise unavailable to the parasite and for which it has an absolute requirement.

Keeping the above discussion in mind it is of interest that parasites demonstrating only a limited restriction of host range (such as *Aeginetia indica* and most species of *Striga*) will occasionally be found attached to species not normally parasitized. Parasites showing a high degree of host specificity (such as *Conopholis* and *Epifagus*), however, are never found attached to plants outside the host taxon to which they are restricted. No conclusions may be drawn, though. For example, *Epifagus* might require beech root exudate in order to germinate but could develop successfully on any tree or else the exudates of any plant might stimulate the germination of *Epifagus* but it could only develop successfully on beech. The germination requirements of these parasites are not known but almost certainly involve root exudates.

Though more data is necessary there does appear to be some correlation between the degree of reliance on parasitism and restriction of host range. Parasites which rely only on secondary haustoria (most Scrophulariaceae and Santalaceae) tend to have unrestricted host ranges. Parasites which form both primary and secondary haustoria (*Alectra*, most *Striga* species and many Orobanchaceae) tend to show some restriction of host range. Parasites which rely only on primary haustoria (*Conopholis* and *Epifagus*) have great restriction of host range.

There are striking comparisons between *Conopholis* and *Epifagus*, the only two parasites which are clearly restricted to one or a few hosts. Both are found in forest types which cover large geographical areas and have clearly dominant tree species and both form only primary haustoria and have highly reduced root systems. *Conopholis* is restricted to oaks (perhaps red oaks). In the oak-chestnut-hickory forest in which it occurs oaks are the dominant species. However, oak forests are not normally dominated by one species of oak but by several. *Epifagus* is restricted to beech. In a beech forest this is the only dominant species. In each case the holoparasite has become restricted to the dominant species in its forest. Moreover, the restriction is not so great for the parasite that occurs in a forest dominated by several closely related species as it is for the parasite that occurs in a forest dominated by just one species. In each case restriction is to the plant taxon which, by its dominance, is most likely to ensure the survival of the parasite species. This restriction of host range is coupled in both cases with the loss of the ability to form secondary haustoria and a great reduction of the root system. Association with a host which is capable of supplying all the nutritional requirements of a parasite would make contact with other plants and, therefore, the production of multiple haustoria unnecessary. Loss of the ability to produce secondary haustoria and reduction or loss of the root system would not be selected against. By this sequence of events an advanced parasite of the Conopholis or Epifagus type could be derived from a less specialized orobanchaceous parasite such as Aeginetia indica or Orobanche ramosa. Perhpas this is the general route most likely to be followed by specializing parasites in the Orobanchaceae. Correlation of these ideas with other evolutionary trends would be interesting.

E. The Haustorium

The primary haustorium forms directly following seed germination in advanced parasites (see Kuijt, 1969) and Germination in this paper). Secondary haustoria seem to be formed over much of the growth period of the plant and are apparently the only means of heterotrophic nutrition in the Santalaceae and in most genera of the parasitic Scrophulariaceae. In the Orobanchaceae and the genera Alectra and Striga of the Scrophulariaceae the secondary haustoria, where present, supplement the primary haustorium.

The initiatory stimulus for the development of the haustorium is unknown at present. It could be a chemotropic response to exudates from a host root (see the research report) or a thigmotropic response to contact with a host root. The haustorium probably initiates in immature cortical tissues near the root tip. Much work on haustorial initiation and early development is necessary before a general understanding of these processes can be reached.

1. Initiation

a. Earliest initiation

Haustoria may be initiated very early in the life of the parasite.

Haustorial formation has been reported in five-day-old seedlings of Castilleja (Heckard, 1962), two-week-old seedlings of Comandra umbellata (Piehl, 1965c), the first-formed roots of Exocarpus bidwillii (Fineran, 1963), shortly after radicle germination and before epicotyl dormancy is broken in Melampyrum lineare (Curtis, Cantlon and Malcolm, 1963), in seven-day-old seedlings of Orthocarpus faucibarbatus (Thurman, 1966) and shortly after the first leaves are formed in Santalum album (Rama Rao, 1910a).

b. Location on the root

Haustoria are probably initiated only in relatively young root tissues. Musselman (1974), working with a number of species of parasitic Scrophulariaceae, found that haustoria could be produced on the primary, secondary and adventitious roots of these plants but that the specific location of initiation was the area of tissue maturation near the root apex. Thurman (1966) reported that haustoria in Orthocarpus faucibarbatus were initiated 0.1 to 0.3 mm. behind the root tip, an area roughly corresponding to the zone of vascular element maturation. In the Santalaceae, Herbert (1924-1925) notes that haustorial initiation in Leptomeria spinosa occurs very close to the root tip and Fineran (1963, 1965a) determined that the haustoria of Exocarpus bidwillii were initiated in a region of primary tissues which extended from just basipetal to the zone of elongation to approximately where the lateral roots began to appear. The initiation sequence in Exocarpus is generally acropetal but some haustoria are formed between existing haustoria within this region. However, the older the tissues are the less frequent is this interstitial haustorial initiation. Kuijt, (1969), commenting on root parasites generally, states that secondary haustoria are usually initiated only within a zone corresponding to the root-hair zone of normal plants.

c. Radius on which initiation occurs

Musselman (1974) finds that haustorial initiation, unlike lateral root initiation, takes place regardless of protoxylem pole position. Haustorial initiation has been reported to occur only on the side of the parasite root nearest the host root in *Exocarpus bidwillii* (Fineran, 1965a), *Melampyrum pratense* (Leclerc du Sablon, 1887) and in the secondary haustoria of *Orobanche crenata* (Kadry and Tewfic, 1956b). Only in *Leptomeria spinosa* does haustorial initiation take place on any radius regardless of the direction to the host root (Herbert, 1924-1925).

d. Nature of the initiatory stimulus

The nature of the haustorial initiation stimulus has been largely a matter of speculation. Sprague (1962) felt that contact with a host root was necessary for haustorial initiation in *Pedicularis* and Stephens (1912b) thought contact with the root hairs of a host was necessary in *Striga asiatica*. However, Malcolm (1962a), working with *Castilleja coccinea*, and Chuang and Heckard (1971), with *Cordylanthus*, concluded that the stimulus must be more than physical contact alone. Kuijt (1969) believed the pressure exerted by unyielding objects to be the more important haustorial initiation stimulus. Thurman (1966), working with *Orthocarpus faucibarbatus*, came to the same conclusion. He reported that haustoria occasionally formed on *O. faucibarbatus* roots growing in agar without contact between the parasite root and any other object while a study of haustorial initiation showed that only 47% of contacts between host and parasite roots caused the formation of haustoria. Rao (1942) also reports that both chemical and tactile stimuli are capable of initiating haustoria while Heinricher (1926) and Uttaman (1950) conclude that the initiatory stimulus consists only of a chemical or chemicals found in host root exudates.

Only two experiments elucidating the nature of the stimulus have been reported. Rao and Ranga Swamy (1971) were unable to get haustorial formation on *Santalum album* roots *in vitro* by wounding them. Atsatt (1973), however, found that a chemical which leaches from a cotton string will cause haustoria to form on the roots of *Orthocarpus* plants grown in agar.

Finally, Fineran (1965b), commenting on the attachment of *Exocarpus bidwillii* haustoria to various decaying plant materials and a small stone, notes that living tissue is not necessarily a prerequisite for haustorial initiation but that the stimulus is largely restricted to organic materials. He concludes that the wide variety of both living and dead objects attacked indicates that the stimulatory substances are diverse and of a general nature. In all cases, however, the compounds are probably formed by living plants.

2. Development

a. Place of origin in the parasite root tissues.

It is generally agreed that the secondary haustoria of all of these parasites arise in the middle or outer layers of the cortex of the root (see Table 15.). Two authors have reported the epidermis to also be involved in haustorial initiation. The only modern proponent of pericyclic initiation is Sprague (1962) in relation to *Pedicularis.* She feels that haustoria are modified lateral roots and, thus, endogenously initiated. Her picture of a young haustorium, however, appears to be a lateral root initial and is rather unlike the pictures of young haustoria published by other workers.

b. Development prior to host contact

Among members of the Scrophulariaceae the initial event in haustorial development seems to be the expansion of cells in the cortex. A preferred direction of expansion is frequently not noted, as in *Sopubia* (Williams, 1960a), *Castilleja* spp. (Dobbins and Kuijt, 1972a, b) and a number of other genera (Musselman, 1974) but Leclerc du Sablon (1887) and Maybrook (1917) with *Melampyrum* described this expansion as elongation and in *Orthocarpus* (Thurman, 1966) and *Striga* (Stephens, 1912b) this elongation is considered to occur in a radial direction. These expanded or elongate cells then divide. In *Sopubia* only the inner expanded cortical cells divide at this time, forming a group of meristematic cells which interact with the outer expanded cortical cells to for a collapsed layer between them (Williams, 1960a). The first

Table 15. Origin of Secondary Haustoria

Genus	Place of Origin	Reference
Agalinis	Cortex	Musselman,1974
Aureolaria	Cortex	Musselman,1974
Castilleja	Cortex	Dobbins and Kuijt,1973a,b
Christisonia	Exogenous but tissue not specified	Boeshore,1920
Cordylanthus	Mid and outer cortex	Chuang and Heckard,1971
Dasistoma	Cortex	Musselman,1974
Euphrasia	Cortex	Philipson,1959
Exocarpus	Mid and outer cortex	Fineran,1965a
Macranthera	Cortex	Musselman,1974
Melampyrum	Cortex	Leclerc du Sablon,1887; Musselman,1974
Mida	Cortex	Simpson and Fineran,1970
Orobanche	Epidermis and outer cortex	Kadry and Tewfic,1956b
Orthocarpus	Cortex	Thurman,1966
Pedicularis	Cortex	Musselman,1974
	Mid and outer cortex	Maybrook,1917
	Pericycle	Sprague,1962

Table 15. (Cont.)

Genus	Place of Origin	Reference
Santalum	Epidermis and outer cortex	Rao,1942
Seymeria	Cortex	Musselman,1974
Sopubia	Cortex	Williams,1960a
Striga	Inner cortox	Uttaman,1950
	Mid and outer cortex	Stephens,1912b
Thesium	Cortex	Leclerc du Sablon,1887

divisions in *Pedicularis* form radial walls in both epidermis and hypodermis but shortly thereafter tangential walls also begin to be formed in hypodermal cells while the epidermal cells continue to form radial walls (Maybrook, 1917). Thurman (1966) reports the first divisions in the haustorial initial of *Orthocarpus* as forming tangential walls. Musselman (1974), however, reports that prior to division a population of cells in the center of the expanded cells which form the haustorial rudiment develop enlarged nuclei and dense cytoplasm to form the nucleus of the haustorium. This event is followed by periclinial divisions in the multiple epidermis to form four to six layers of cells termed the tiered layers. In *Castilleja* the cells formed by these first divisions enlarge as their parent cells did and cells of the pericycle then undergo division to contribute to the developing haustorial bulge (Dobbins and Kuijt, 1973a, b). In *Melampyrum,* following the initial divisions, both pericyclic and endodermal cells elongate. This is followed by several divisions of the elongated epidermal cells. The daughter cells of these divisions may themselves elongate and the elongated pericyclic cells later divide (Leclerc du Sablon, 1887). Chuang and Heckard (1971) report the initial event in haustorial formation in *Cordylanthus* as being dedifferentiation of cortical cells (a process they do not describe). Following dedifferentiation the cells divide repeatedly to form the bulging haustorial rudiment.

Uttaman (1950) reports the developmental sequence of the secondary haustoria of *Striga* as being much different from the process just described. The initial event is considered to be repeated division of cortical cells just peripheral to the pericycle. This pushes up the overlying collenchyma of the mid and outer cortex as well as the epidermal cells. The outer of the dividing cells begin to divide by tangential walls alone to produce radial files of cells. The fate of the overlying cells is not discussed.

The early development of secondary haustoria in the Orobanchaceae has been described only for *Orobanche crenata*. The initial event is enlargement of the nuclei and an increase in density of the cytoplasm in cells of the epidermis and cortex. These cells then undergo division to form the protruding haustorial rudiment (Kadry and Tewfic, 1956b).

In the Santalaceae early haustorial development is reported only for *Mida* and *Exocarpus*. In *Mida* early development is localized proliferation of cortical cells to form a small, conical swelling. This swelling continues to grow by the meristematic activity of cells at its tip. Localized division in a single file of cells in the center of the rudiment leads to the formation of a procambial strand. This activity begins near the parent xylem and proceeds towards the tip of the rudiment (Simpson and Fineran, 1970). In *Exocarpus* the initial event is transverse divisions in mid and outer cortical cells. These divisions then become longitudinal and finally variously oriented. This produces a small lateral swelling on the parasite root. Initially just a few cells are involved but the activity extends to adjacent cells as the haustorium increases in size. As divisions continue in the mid and outer cortex the cells of the inner cortex and pericycle begin dividing. These divisions are predominantly transverse. Enlargement of the daughter cells of these divisions contributes to the increase in size of the haustorial rudiment. While all of these internal divisions have been occurring the epidermal and outermost cortical layers have been undergoing mostly anticlinical divisions to maintain the continuity of the surface layers over the enlarging rudiment. Division of the cells within the mass now begins to cease and by the time the rudiment attains a conical shape meristematic activity is restricted to cells near the tip and along the flanks of the rudiment. As the rudiment has grown through the soil the outer layers of cells have gradually eroded away and been replaced at the haustorium surface by the next-innermost cell layers. After attainment of the conical stage a few of the cells near the parent xylem in the central mass of tissue differentiate into procambial tissue distinguished by its narrow cells and dense cytoplasm. Differentiation of procambial tissue continues acropetally. If host contact is long delayed a few of the procambial cells near the parent xylem may differentiate into xylem elements but this is the maximum amount of development shown by an unattached haustorium.

The only parasite for which any description of primary haustorium development exists is <u>Striga asiatica.</u> Initially a change in the organization of the root apex occurs, including enlargement of the apical cells and their nuclei and vacuolization of the cells peripheral to the apex. The apical cells then divide to form chains of cells up to three cells long which effect the penetration of the host root (Musselman, 1973a, 1974). Much more research is needed to establish the general pattern of development here.

A secondary haustorium that does not contact a host ceases development when it is about as long as broad in *Exocarpus bidwillii* (Fineran, 1965a) and *Mida salicifolia* (Simpson and Fineran, 1970) and about twice as long as broad in *Exocarpus spartea* (Herbert, 1924-1925) and *Striga asiatica* (Stephens, 1912b). Piehl (1963b) notes that the surface of haustoria of *Pedicularis canadensis* that remain without a host contact for a long period of time frequently become suberized.

c. Association with root hairs

Most of the parasites presently under consideration have root-hair-like structures associated with their haustoria. This has been established for *Castilleja* (Kuijt, 1969; Dobbins and Kuijt 1973a, b), *Cordylanthus* (Chuang and Heckard, 1971), *Euphrasia* (Koch, 1891; Philipson, 1959), *Lathraea* (Heinricher, 1931), *Macranthera* (Musselman, 1973b, 1974), *Melampyrum* Knorz, 1848; Koch, 1887; Piehl, 1962a, 1963b; Musselman, 1973b), *Odontites* (Govier, Brown and Pate, 1968), *Orthocarpus* (Thurman, 1966), *Pedicularis* (Piehl, 1963b; Musselman, 1973b, 1974), *Rhinanthus* (Kuijt, 1969), *Santalum* (Barber, 1907b), *Seymeria* (Musselman, 1973b) and *Striga* (Saunders, 1933; Musselman, 1973a, 1974). The only parasite which does not show this correlation is *Dasistoma* (Piehl, 1962a). Not all individuals of a species may have haustorial hairs. Thurman (1966) notes that although most *Orthocarpus* haustoria are associated with root hairs approximately one fifth have none.

In most genera of parasitic Scrophulariaceae the root hairs are reported to form early in haustorial development from epidermal cells around the flanks of the haustorium (Chuang and Heckard, 1971; Musselman, 1974). In Castilleja (Dobbins and Kuijt, 1973a) and Rhinanthus (Kuijt, 1969), however, the development of the hairs may precede the obvious external formation of the haustorium.

The function of the haustorial hairs is not clear. They have been considered to be important in the absorption of water and mineral nutrients in Orthocarpus (Thurman, 1966) or in the superficial attachment of the haustorium to its host root (Piehl, 1962a, 1963b). Musselman (1974) reports that these hairs attach to cells of the host root by what appears to be a cementing substance.

Musselman further mentions that these haustorial hairs are longer than normal root hairs, are not sloughed and produce a papilla-like growth in the region of contact with host cells.

3. Attachment

a. Characteristics of host roots attacked.

It seems likely that haustoria may initiate attacks on any region of a host root. Both large and small roots have been reported to be attacked by the haustoria of Exocarpus bidwillii (Philipson, 1959; Fineran, 1963), Melampyrum lineare (Piehl, 1962b), Orthocarpus faucibarbatus (Thurman, 1966) and Santalum album (Barber, 1907a). Musselman (1974) reports that the haustoria of the Scrophulariaceae will attack roots of any age. Yeo (1961) has found Euphrasia to attack Plantago lanceolata roots up to six or seven times as thick as its own root and Piehl (1962a) noted that Dasistoma macrophylla will attack host roots up to seven millimeters in diameter. Specific areas of haustorial attack have been noted, however. Ungurean and Serbanescu-Jitarui (1973) report Orobanche ramosa as forming hasutoria only on young host roots and Uttaman (1950) felt the secondary haustoria of Striga asiatica to attack only root tips of rice. Musselman (1974) noted that Alectra vogelii seems to form haustoria more frequently near the root nodules of Vigna unguiculata while several other species of Scrophulariaceae attack their hosts in the vicinity of mycorrhizal roots.

b. Self-attachment

Probably most parasitic plants that form secondary haustoria are capable of self-attachment. Self-attachment is two roots of the same species joined by a haustorium. A list of species reported to self-attach is presented in Table 16. Small differences in the morphology and anatomy of the self-attached haustorium as compared to an inter-specific haustorium seem to exist. Reports of these differences are available for Dasistoma macrophylla (Piehl, 1962a) and Exocarpus bidwillii (Fineran, 1962, 1965b).

Some attempt has been made to demonstrate an adaptive advantage to self-parasitism. Fineran (1965a) has hypothesized that self-parasitism could be beneficial to a weak Exocarpus plant by allowing it to obtain nutrients from a well-established individual. He further suggests that self-parasitism might allow an older plant to act as a

Table 16. Species That Self-attach

Species	Source
Scrophulariaceae	
Aureolaria flava	Piehl, 1967; Musselman, 1974
Aureolaria grandiflora	Musselman, 1969
Aureolaria laevigata	Piehl, 1967
Aureolaria virginica	Musselman, 1974
Castilleja cusickii	Dobbins and Kuijt, 1973a, b
Castilleja lutescens	Dobbins and Kuijt, 1973a, b
Cordylanthus spp.	Chuang and Heckard, 1971
Dasistoma macrophylla	Piehl, 1962a; Musselman, 1974
Euphrasia spp.	Yeo, 1961, 1964
Melampyrum lineare	Piehl, 1962b; Musselman, 1974
Odontites verna	Heinricher, 1898a; Govier, Nelson and Pate, 1967
Orthocarpus faucibarbatus	Thurman, 1966
Orthocarpus spp.	Atsatt and Strong, 1970
Pedicularis canadensis	Piehl, 1963b
Pedicularis vulgaris	Maybrook, 1917
Rhinanthus alectorolophus	Bourget, 1965
Rhinanthus burnati	Bourget, 1965
Rhinanthus major	Bourget, 1965
Rhinanthus minor	Bourget, 1965

Species	Source
Santalaceae	
Choretrum lateriflorum	Herbert, 1924-1925
Comandra livida	Moss, 1926
Comandra umbellata	Piehl, 1963a, 1965c
Exocarpus aphylla	Herbert, 1924-1925
Exocarpus bidwillii	Fineran, 1962, 1965b
Fusanus acuminatus	Herbert, 1924-1925
Fusanus spicatus	Herbert, 1924-1925
Leptomeria preissiana	Herbert, 1924-1925
Mida salicifolia	Simpson and Fineran, 1970
Santalum album	Barber, 1906; Rao, 1942
Thesium sp.	Benson, 1910

"nurse" for a seedling. These benefits are possible but it is more likely that self-parasitism is a result of the indiscriminacy of the haustorial initiation mechanism. As Herbert (1924-1925) points out in reference to the frequency of self-parasitism in *Leptomeria,* "Owing to the profuseness of the branching of the root system of *Leptomeria preissiana* and the sparseness of the surrounding vegetation . . . it is natural that in their searching after a host the haustoriogenic roots should come into contact with others of their kind more frequently than with roots of other species. This is actually the case. Far more self-haustoria were found than haustoria on other species."

c. Attachment to miscellaneous objects

The haustoria of parasitic plants have frequently been reported attached to a wide variety of objects other than living plant roots (see Table 17.). A number of workers have considered the attachments to dead plant remains as evidence that the plants are saprophytes. Among these are Leclerc du Sablon (1887), Koch (1891), Sperlich (1962), Hartley and Ellis (1931), Piehl (1962a, 1963b) and Sprague (1962). However, Piehl (1963b), Thurman (1966) and Musselman (unpublished) have noted that attachments to dead roots may have been initiated before the death of the roots. Furthermore, Heinricher (1909, reported in Thurman, 1966), working with *Melampyrum lineare,* and Sprague (1962) with *Pedicularis* spp. were unable to get haustorial formation when these parasites were grown in pots of humus. Thurman (1966) also points out that there

Table 17. Haustorial Attachment to Miscellaneous Objects

Species	Objects Attached To	Reference
Agalinis obtusifolia	Decayed matter	Holm, 1929
Agalinis purpurea	Decayed matter	Holm, 1929
Agalinis tenuifolia	Decayed matter	Holm, 1929
Aureolaria grandiflora	Decaying plant parts	Musselman, 1969
Aureolaria parvifolia	Decayed matter	Holm, 1929
Aureolaria pedicularia	Decaying plant parts	Musselman, 1969
Castilleja coccinea	Pebbles, grains of sand, leached pith, other organic matter	Malcolm, 1966
Euphrasia spp.	Dead plant material	Koch, 1891; Yeo, 1961
Euphrasia pseudokerneri	Dead roots	Yeo, 1961
Exocarpus bidwillii	Seeds, various dead plant parts, a stone	Fineran, 1965
Lathraea squamaria	Dead roots	Hartley and Ellis, 1931
Melampyrum lineare	Dead fragments of plant tissue	Piehl, 1962a
	Puff-balls, dead roots, dead plant parts, slivers of elder pith	Cantlon, Curtis and Malcolm, 1963
Melampyrum pratense	Dead plant fragments	Knorz, 1848; Koch, 1887
Mida salicifolia	Dead plant material	Simpson and Fineran, 1970
Orthocarpus faucibarbatus	Dead roots	Thurman, 1966

Table 17. (Cont.)

Species	Objects Attached To	Reference
Pedicularis canadensis	Fungal mycelium, dead roots and other plant structures	Piehl, 1963b
Santalum album	Pebbles, bits of bark, the chrysalis of a lepidopteran	Barber, 1906
	Fruit of *Arachis hypogaea*	Rao, 1942

is presently no evidence that the haustoria of root parasites are able to break down organic materials.

The amount of penetration of an object attached to generally depends on its hardness and thickness (Thurman, 1966). Fineran (1965b) reports that a haustorium of *Exocarpus bidwillii* may penetrate completely through the leaf. Rao (1942) found that a haustorium of *Santalum album* could penetrate the outer layers of *Arachis hypogaea* fruits but was unable to force its way through the mechanical tissue layers of the pericarp. Penetrable objects attached to, however, may not be pentrated at all. Fineran (1965b) reports that haustoria of *Exocarpus bidwillii* may not penetrate dead leaves to which they are attached. Development of the intrusive organ is the maximum extent of development of a haustorium attached to a nonliving object. Connective tracheary elements never form (Sperlich, 1902; Fineran, 1965b).

4. Discussion

Haustoria apparently only form in young root tissues near the parasite root tip. Thus, the only type of contact between a host and a parasite root that will result in haustorial initiation is proximity of the parasite root tip to any part of the host root. Proximity of any part of a host root to a mature area of a parasite root will not result in haustorial initiation. This would explain why Thurman (1966) found less than half of the contacts between *Orthocarpus* and host roots to result in the formation of haustoria.

Considerable controversy exists as to whether haustoria have arisen evolutionarily as modified lateral roots (Sprague, 1962; Kuijt, 1969; Musselman, 1974), as modified root grafts (Piehl, 1967) or as nodules similar to the nodules of legumes formed symbiotically with and under the influence of bacteria (Atsatt, 1973). The arguments in each case are unconvincing. The epidermis and cortex form much of the body of the haustorium while they are ruptured by lateral root emergence. In addition, the division of cells in the pericycle and endodermis late in the development of the mature unattached haustorium results in vacuolate daughter cells with nuclei that are not noticeably enlarged whereas the division of the pericycle cells is the initial event in formation of the lateral root initial and results in densely cytoplasmic cells with enlarged nuclei. Root grafting is not known to occur in herbaceous plants and Woods and Brock (1964) report that though interspecific grafting is common in trees it does not normally occur before the plants are 25 to 40 years old. The only report of root grafting in parasitic plants that I have been able to find is that of Piehl (1967). The evidence presented by Atsatt (1973) for bacterial initiation, as he admits, is inconclusive and the presence of bacteria within haustoria has not been established.

The pattern of haustorial development seems fairly well established but the specific sequence of division, enlargement and differentiation is in doubt. This is understandable as work on this problem to date has apparently entirely utilized material dug randomly from the soil. The haustorial initiation event would be difficult to detect in material whose relationship to potential host roots is unknown. If, however, haustoria form similarly in agar to those that form in soil then in vitro work should allow a precise developmental sequence to be determined.

F. General Discussion

Holoparasites show two patterns of development prior to making host contact. One pattern is exemplified by Striga and the Orobanchaceae and the other by Lathraea. The first pattern involves the reception of a dormancy-breaking host root exudate by the seed of the parasite. This assures the proximity of a host root upon germination so the embryo and the food-storage capacity of the seed have been greatly reduced. The seed produces a germ tube or radicle that can reach a length of not over four millimeters. Contact with and attachment to a host root must occur within this distance or the parasite will die. The second pattern does not involve reception of a host root exudate or the proximity of a host root in order to induce germination. The seed is rather large and contains a large endosperm. Under the appropriate environmental conditions the seed germinates and the root may grow and ramify for an extended period of time before host contact must be made. A primary haustorium is not present.

While the Scrophulariaceae and Orobanchaceae are considered to be closely related the Santalaceae are isolated from these parasites taxonomically. If root parasitism has arisen several times, however, it seems to have arisen in the same way (that is, as modified lateral roots or as modified root grafts, etc.) each time. It is unlikely that disparate starting points could result in organs of the similarity which the haustoria of these respective families show prior to attachment. Development following attachment to a host root diverges from this common point somewhat, but does not obliterate the striking parallels in early development.

Since present studies already show that root exudates may regulate seed germination in advanced parasites it is logical to assume that such a system could also be capable of regulating haustorial initiation in the same plants and their relatives. Studies to determine whether germination stimulants and haustoriogenic chemicals are the same seem important. These compounds could provide a biochemical link between advanced and primitive parasites. In both cases the chemical initiates the parasitic attack of the plant.

Plants appear to release the greatest amount and widest variety of exudates from the vicinity of the root tip (Ayers and Thronton, 1968; McDougall and Rovira, 1956; Brown and Edwards, 1944; Slankis, Runeckles and Krotkov, 1964) and yet a general survey of what is known about haustorial attack indicates that any part of a host root may have an attack initiated upon it. This indicates that either the exudation areas of plants are not well known or that haustorial attack is not a result solely of root exudates. Since preliminary results (see the research report) indicate that root exudates alone can initiate haustoria and since a root's rhizosphere seems to occur all along it (Hiltner, 1904) the most logical assumption at this point is that roots must release exudates along their entire lengths in nature.

The haustoriogenic chemical or chemicals must have a threshold concentration at which they become active. In nature the distance from the root at which the threshold concentration is reached for a particular parasite determines the maximum distance from that host root at which haustorial initiation could occur. Chemicals released by a root are diluted by having to fill a larger and larger cylinder as they move outward from the root and are inactivated by chemical and microbial processes in the soil.

An interesting point to ponder is the possibility that the microorganisms of the rhizosphere of host roots may be influential in haustorial initiation. This influence could occur in a way similar to Atsatt's (1973) hypothesis that haustoria are the equivalent of legume nodules (that is, due to bacterial invasion) but in the light of the results presented in the research report their influence might more logically be concluded to be a result of their exudates. A large number of authors, some of whom are listed in the research report discussion, have reported on the wide range of chemicals (including plant hormones) released by soil fungi and bacteria. Many of these microorganisms are associated with higher plants as a result of the exudates and other influences of the plant roots and frequently species of plants seem to have characteristic species or forms of microorganisms associated with them. Thus the microorganisms could release the chemicals which initiate haustorial attack on their associated root. The vast array of fungi and bacteria occurring in the soil with their undoubted tremendous range of chemical releasants could account for the host specificity shown by some root parasites. Occurrence of the microorganisms all along the roots of their host plants could help to explain haustorial attack on all sections of a root. Though preliminary results in the research report indicate that plant root exudates are capable of initiating haustoria, this does not rule out the possibility of microbial production of the haustoriogenic chemical. It seems possible that haustorial attachment to dead plant materials and sand grains could be a result of microbial exudates.

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III. Research Report

A. Introduction. The nature of the initiatory stimulus for the development of secondary haustoria is unknown. Previous comment on this problem has taken the form of speculation as to whether the formation of the haustorium is a thigmotropic response to contact with a host root or a chemotropic response to exudates from host roots or both. Some experimental evidence indicating that the stimulus is chemotropic exists. Evidence for a thigmotropic response rests mainly on reports in the literature of haustorial attachment to pebbles and grains of sand.

Little *in vitro* work has been done on parasitic plants. Growth of intact plants in the Scrophulariaceae has been largely unsuccessful. *Melampyrum lineare* (Curtis and Cantlon, 1968) and *Striga senegalensis* (Okonkwo, 1966a,b), however, have been grown to flowering on nutrient media containing sugars and inorganic salts, and *Orthocarpus faucibarbatus* (Thurman, 1966) has been shown to parasitize every host with which it has been grown *in vitro.*

It should be stressed again that the research reported here is strictly preliminary and allows no firm conclusions to be drawn. It does, however, provide a useful basis for discussion of haustorial initiation, parasite nutritional requirements and seed germination in the light of information gathered in the literature review. It also allows discussion of the potentiality of *in vitro* techniques for clarifying various aspects of parasitic plants.

Structures termed haustoria in this report should be considered presumptively so as histological work sufficient to positively establish them as hasutoria was not undertaken. This is especially true of early developmental stages prior to attachment as external views of emerging lateral roots and haustoria appear very similar. It may be noted that older cultures showed haustorial penetration.

B. Methods and Materials. Seeds of both hosts and parasites were surface-sterilized in a 25% or 33% Clorox solution, the concentration determined by the sensitivity of the seeds to the surface-sterilization technique. The seeds were then plated out on filter paper in petri plates or on standard Knop's medium in 125 ml. Ehrlenmeyer flasks for germination.

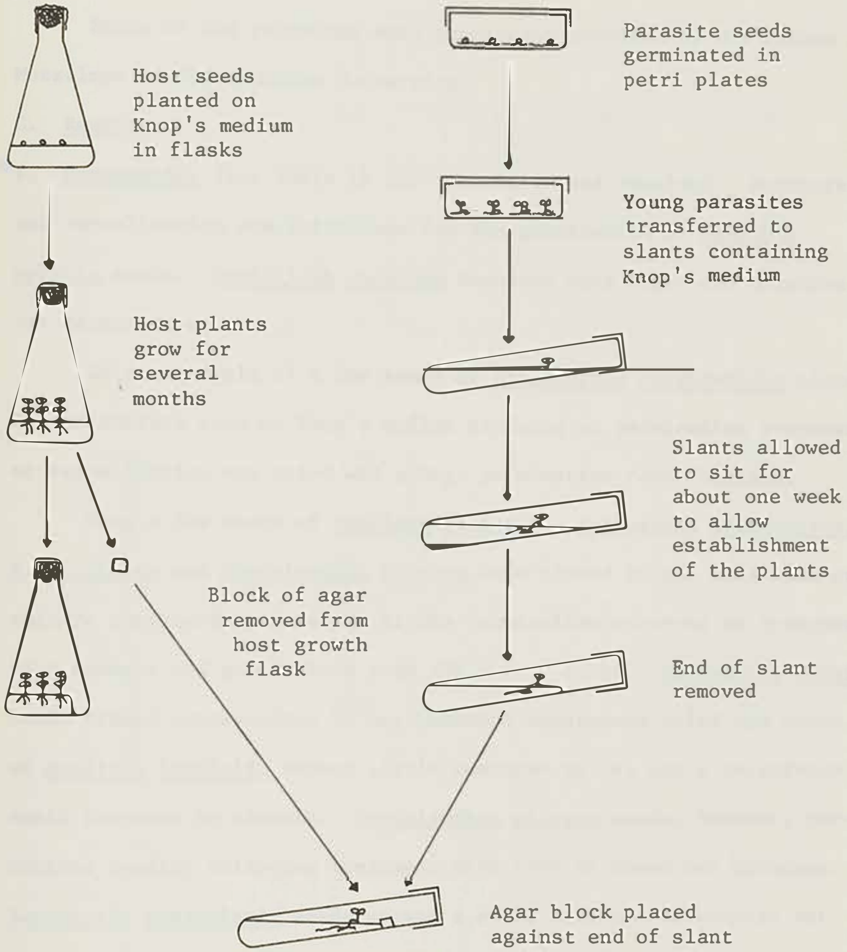
Both parasite and host plants were grown on standard Knop's medium with 2% sucrose. The pH was adjusted to 5.5 with potassium hydroxide. The medium was solidified with 0.8% agar.

The slant method by which root exudates or hormones were presented to the parasites is presented in Figure 1.

Culture room conditions were a continuous temperature of 21° ± 1°C, a photoperiod of 16 hours and illumination of 130 foot-candles provided by Westinghouse Plant-Gro and Cool White fluorescent bulbs. The cold room was maintained at 4° ± 1°C.

Parasite seeds treated with hormones were soaked in a solution of the hormone and distilled water for 24 hours and then transferred to

Figure 1. <u>Slant Technique</u>



petri plates containing distilled water for the duration of the experiment.

Seeds of the parasites were generously provided by Dr. Lytton J. Musselman of Old Dominion University.

C. Results

1. Germination (See Table 18 for techniques and results). Moisture without vernalization was sufficient for the germination of *Agalinis aphylla* seeds. *Castilleja coccinea* required only light and moisture for germination.

Initial trials of a few seeds of *Orthocarpus purpurescens* placed in the culture room on Knop's medium produced no germination response so vernalization was tried and a high germination rate obtained.

When a few seeds of *Agalinis linifolia, Aureolaria pedicularia, A. virginica* and *Cordylanthus pilosus* were placed in the cold room or culture room on Knop's medium little germination occurred so treatments with kinetin and gibberellic acid (GA_3) were tried. *Aureolaria virginica* seeds proved unresponsive to any hormonal treatments tried and seeds of *Agalinis linifolia* showed little response to GA_3 and a relatively small response to kinetin. *Cordylanthus pilosus* seeds, however, germinated readily following treatment with each of these two hormones. *Aureolaria pedicularia* seeds showed a small response to kinetin but dormancy in all seeds was broken by treatment with 100 ppm GA_3. In this last treatment germination began within five days and was probably complete even before the sixteen days indicated.

Table 18. Germination Procedures and Results

Species	Treatment	No.of Seeds	No.of Days	Germ.Rate (%)
Agalinis aphylla	Moisture,light	131	27	70
		141	25	82
Agalinis linifolia	20ppm Kinetin,light	13	26	31
	100ppm Kinetin,light	15	31	20
	100ppm GA3,light	15	34	7
Agalinis maritima	Vernalization for 115 days,light	492	23	3
	100ppm Kinetin,light	234	31	0
Aureolaria pedicularia	20ppm Kinetin,light	108	26	29
	100ppm Kinetin,light	167	31	23
	100ppm GA_3,light	102	16	100
Aureolaria virginica	20ppm Kinetin,light	38	26	0
	100ppm Kinetin,light	60	31	3
	100ppm GA3,light	77	34	3
Castilleja coccinea	Moisture,light	199	28	96
		156	31	83
	Moisture,dark	154	29	0
Cordylanthus pilosus	100ppm Kinetin,light	12	34	75
	100ppm GA_3,light	21	34	57
Orthocarpus purpurascens	Vernalization for 51 days,light	72	0	74
	Vernalization for 31 days,light	59	7	93
	Vernalization for 32 days,dark	82	10	77

None of the treatments tried was capable of breaking dormancy in *Agalinis maritima* seeds.

2. *Growth on Knop's Medium*. *Agalinis aphylla*, *Aureolaria pedicularia* and *Orthocarpus purpurescens* plants usually grow rather vigorously on Knop's. The roots show rapid elongation and the shoots show good expansion of the rosette (in *A. pedicularia*) or extension of the stem and production of leaves (in *A. aphylla* and *O. purpurescens*).

Aureolaria virginica and *Castilleja coccinea* plants are more erratic in their growth on Knop's. Some individuals show very little growth while others grow vigorously. The former usually die within two to three months.

Agalinis linifolia plants remain alive for up to four months but expansion of the roots and shoots is slow. No more than two small pairs of leaves are produced while the radicle reaches a length of not over one centimeter and produces only a few short laterals.

Cordylanthus pilosus plants exhibited an unusual response in that the root system always expanded very slowly and usually callused where it touched the agar. In approximately one-third of the plants, however, the shoot showed vigorous growth. One plant even flowered *in vitro*.

3. *Initiation of Haustoria*. Haustoria were initiated by the growth of the parasites with several potential hosts and a few haustoria were initiated by treatment with root exudates and with GA_3.

a. Growth with hosts

Five *Agalinis aphylla* plants produced hundreds of unattached haustoria when grown with four sunflower plants (cv. Burpee Teddybear) in a 125 ml. Ehrlenmeyer flask. *A. aphylla* plants being grown without hosts at the same time did not form haustoria. *Castilleja coccinea* produced haustoria, often profusely, when grown with sunflower (cv. Burpee Teddybear), carrot (cv. Burpee Imperator), leek (cv. Burpee Broad London) and snapdragon (cv. Burpee Sentinal Color Guard) (See Figure 3.). Attached haustoria were found with leek, carrot and sunflower. Controls without hosts never formed haustoria. *Orthocarpus pupurescens* plants produced haustoria when grown with *Nicotiana* (cv. Burpee Sensation) and the same carrot and snapdragon cultivars noted before (see Figure 4). Attached haustoria were seen only with carrot. Controls could self-initiate haustoria but usually did not do so in less than a month of growth. Growth with hosts usually resulted in haustorial initiation within two weeks.

b. Application of root exudates

Five of six test slants containing one *Castilleja* plant each produced four to thirteen haustoria each when supplied with agar blocks from flasks in which sunflowers had been growing for 95 days. Three controls produced no haustoria. The experiment was run for 32 days. In a similar experiment with *O. purpurescens* each of four slants containing one *Orthocarpus* seedling per slant produced ten to twelve haustoria per plant when each slant was provided with an agar block from flasks in which sunflowers had been growing for 132 days. This experiment was run for 32 days.

Blocks of autoclaved sunflower growth agar were then tried on slants containing *Castilleja coccinea* plants to see if the initiatory substance was heat-labile. Each of five test plants showed browning of the roots and surrounding agar as though the substances released into the agar had become toxic as a result of autoclaving. The parasite plants soon ceased growth. A check of the molten agar indicated that no pH change had taken place. Three untreated controls showed no toxicity reaction. Two of the five *C. coccinea* plants tested formed haustoria before dying.

c. Application of hormones

Agar blocks containing 200 ppm IAA or GA_3 were also supplied to slants containing either *Castilleja* or *Orthocarpus* plants. GA_3 caused the formation of dozens of haustoria on the one *Orthocarpus* plant to which it was supplied (see Figure 2) while three untreated controls formed just one haustorium. On the two *Castilleja* plants to which GA_3 was supplied swellings formed just behind the tips of both primary and lateral roots but these did not appear to be haustoria. The application of 200 ppm IAA agar blocks to one slant of *Orthocarpus* and two of *Castilleja* resulted in an apparent toxicity reaction at least superficially similar to that described for treatment with autoclaved agar blocks from sunflower growth flasks. Three controls in each case showed no such reaction.

Following the initial indication that GA_3 would initiate haustoria in *O. purpurescens* I wished corroborative evidence but was faced with a nearby time deadline. I thus placed a block of 200 ppm GA_3 agar into each of three 125 ml. Ehrlenmeyer flasks in which *Orthocarpus* plants had been growing for nearly two months on solidified Knop's medium. A fourth similar flask served as a control. The GA_3 agar had been autoclaved in order to resterilize it. Each of two of the test flasks contained three vigorous *Orthocarpus* plants with well-developed root systems growing within the agar. Hundreds of haustoria were formed on the roots of the plants in each of these flasks. The third test flask contained two *Orthocarpus* plants with poorly-developed root systems growing mostly on top of the agar. These plants produced a total of four haustoria. The three vigorous plants in the control flask produced no haustoria. No haustoria had been present in any of the flasks at the beginning of the experiment.

4. *Self-initiation of Haustoria.* Both *Aureolaria virginica* and *Orthocarpus purpurescens* plants self-initiated haustoria when grown alone *in vitro* (see Figure 1). This phenomenon proved particularly common in *Orthocarpus*. *Agalinis aphylla, Aureolaria pedicularia* and *Castilleja coccinea,* on the other hand, were never seen to self-initiate haustoria. *Agalinis linifolia* and *Cordylanthus pilosus* showed little root development so no determination of self-attachment could be made.

D. *Discussion.* The data presented here are obviously too preliminary to allow any firm conclusions to be drawn. They do perhaps provide a basis for discussion of the aspects of parasitic plants on which they touch.

Malcolm (1962, 1964) had previously reported that *Castilleja coccinea* required only light and moisture for germination and data presented here agree with this report.

GA_3 was tested as a germination stimulant for several parasites because it has previously been shown effective in stimulating the germination of the seeds of *Melampyrum lineare* (Curtis and Cantlon, 1968) and *Orobanche* spp. (Izard and Hitier, 1958; Nash and Wilhelm, 1960; Privat, 1960; Kasasian, 1973; Hiron, 1973). Kinetin was tried as it had been shown, along with other 6-substituted aminopurines, to stimulate the germination of *Striga asiatica* seed (Worsham, Moreland and Klingman, 1959). It is probable that the stimulatory effect of GA_3 on the seeds of *Aureolaria pedicularia* and *Cordylanthus pilosus* is a substitute for vernalization (see the literature review) even though vernalization did not break dormancy in these parasites when it was used in this set of experiments. GA_3 has been shown to substitute for vernalization in a number of autotrophic plants (Torrey, 1967). The significance of kinetin's apparent ability to break dormancy in *Agalinis linifolia*, *Aureolaria pedicularia* and *Cordylanthus pilosus* seeds is not clear. It is interesting, however, that each of these hormones seems able to break dormancy in the seeds of both advanced and primitive parasites. More research with larger samples, wider hormonal concentration ranges and more involved combinations of environmental variables is needed in order to gain an understanding of both the natural germination requirements of these plants and alternative methods of breaking dormancy.

The generally vigorous growth of Orthocarpus purpurescens on Knop's medium plus 2% sucrose may indicate that it has quite unspecialized nutritional requirements as well as some capacity for absorbing these nutrients without the aid of haustoria. As mentioned before, Melampyrum lineare (Curtis and Cantlon, 1968) and Striga senegalensis (Okonkwo, 1966a,b, 1970) have also shown vigorous growth on media containing only inorganic salts and sucrose (S. senegalensis must represent an autotrophic extreme in this advanced genus). In contrast to the apparently unspecialized growth requirements of the above parasites Malcolm (1964) reported that Castilleja coccinea never grew as well on a nutrient medium as with a host; even when the medium contained complex additives. I found, however, that a few individual Castilleja plants (out of hundreds observed) grew as well without a host in vitro as with a host in vitro. However, most Castilleja plants were not as vigorous unattached as those which were attached and a few showed very little growth. Perhaps there is a wide genetic variation in the autotrophic capabilities of this species. Further work on the growth of parasites alone in vitro should indicate whether or not they can absorb nutrients through their roots without the use of haustoria and if so (as seems likely in some cases), may allow a determination of their nutritional requirements. It would be interesting to know the taxonomic distribution of nutritional requirements.

Present results allow speculation that host root exudates will prove to play some role in haustorial initiation in the parasitic Scrophulariaceae, at least. This, of course, would not rule out the possibility that contact also has some importance. It is perhaps pertinent to note here, however, that contacts between parasite roots and the glass of the flasks in which they were grown was never seen to initiate haustoria, though *C. coccinea* did attach to dead leaves and the discarded testae of sunflowers *in vitro.* In one case a *C. coccinea* haustorium was also found to have penetrated a sunflower testa following attachment to it (see Figure 5). The greater potential specificity of the chemotropic mechanism would seem to make it the more useful to the parasite and therefore perhaps the more likely candidate. It should be stressed here that the reports of haustorial attachment to pebbles and grains of sand which appear in the literature (see the literature review) and which have been taken as evidence for a thigmotropic haustorial initiation mechanism may not indicate this at all. Attachment to an object does not necessarily mean initiation by that object. It is possible that these haustoria could have been initiated by exudates from a nearby host root. That is to say that the initiatory stimulus could be chemotropic while the attachment stimulus might need only to be contact with a resistant object (thigmotropic).

No previous evidence existed that the haustoriogenic substance might be a plant hormone but plant hormones seemed a logical place to begin such a search. Gibberellins and auxins are known to be released into the soil by bacteria and fungi (Katznelson and Cole, 1965; Holme and Zacharias, 1965; Lee, Breckenridge and Knowles, 1970; Shilina, 1971; Brown, 1972; Panosyan and Agadzhanyan, 1973) and it appears that in some cases these hormones do affect plant growth (Muroshtsev, 1971; Kazaryan and Agadzhanyan, 1971). Plants have proven able to absorb gibberellic acid through their roots (Khudakova and Zueva, 1963). However, though Vancura (1965) has found a gibberellin-like substance to be released by the roots of flowering red pepper plants, gibberellins are not generally known to be released by plant roots.

Preliminary results reported in this paper once again allow speculation that GA_3 plays some role in haustorial initiation in *Orthocarpus purpurescens*, at least. It is interesting that gibberellins are known to be primarily concerned (usually in conjunction with auxins) with cell enlargement in other plant systems and that the initial event in haustorial development in the parasitic Scrophulariaceae seems to involve cell enlargement (see the literature review). However, if further research positively establishes that GA_3 or other gibberellins are haustoriogenic then their place in haustorial initiation will still need to be worked out. It may be that they are not the active chemicals released by host roots but are produced in the cells of the parasite root in response to the haustoriogenic chemical. It would be of particular interest to see if the haustoriogenic chemical in these presumably more primitive parasites is the same as or similar to the chemical required for seed germination in more advanced parasites (see the literature review). This could provide a biochemical link between these potentially related phenomena.

The method by which Aureolaria virginica and Orthocarpus purpurescens self-initiate haustoria is unknown but it would appear to reduce their suitability as experimental subjects. The frequent appearance of haustoria on the roots of untreated controls might make unequivocal results difficult to obtain.

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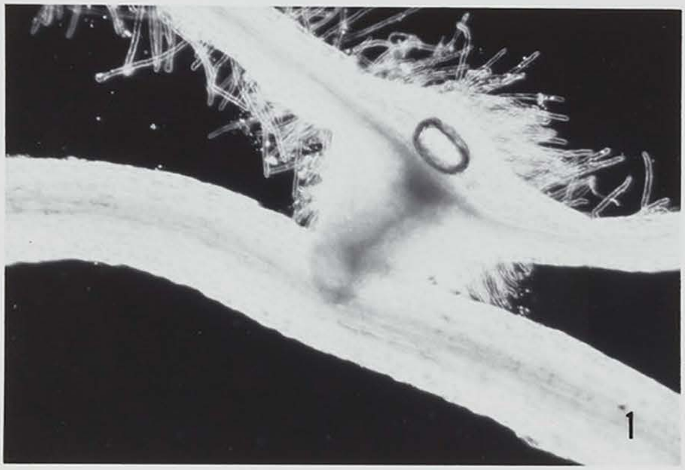
F. Figures:

1. Self-attached presumptive haustorium of *Orthocarpus purpurescens.* 25x.

2. Very young, unattached presumptive *Orthocarpus* haustorium formed as a result of treatment with GA_3, Hairs are beginning to develop on the flanks of the young haustorium. 50x.



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2

3. A fairly mature, unattached presumptive *Castilleja* haustorium formed by growth with *Helianthus in vitro.* 80x.

4. Very young presumptive *Orthocarpus* haustorium. 140x.

3

4

3. Elongating cells of a presumptive ([illegible]) bacteroides which is penetrating the testa of a [illegible] seed. 90x.

5. Elongating cells of a presumptive _Castilleja_ haustorium which is penetrating the testa of a _Helianthus_ seed. 80x.


5

IV. APPENDIX

Host Ranges

Scrophulariaceae

Agalinis spp.

The genus is parasitic on a wide range of hosts, including grasses and composites	Boeshore, 1920
Annual species have a wide host range	Pennell, 1928
Sections Purpureae and Tenuifoliae have wide host ranges. Section Linifoliae is parasitic on *Pinus*	Pennell, 1929
Section Chyta has a wide host range; Section Chloromone has only one member parasitic	Pennell, 1935

Agalinis filifolia

Chrysopsis graminifolia	Pennell, 1929
Quercus spp.	"

Agalinis holmiana

Andropogon scoparius	Pennell, 1929
Baptisia tinctoria	"
Cracca virginiana	"
Ionactis linariifolius	"
Panicum sp.	"
Pteridium aquilinum	"
Solidago erecta	"
" *odora*	"
" *nemoralis*	"
Vaccinium vacillans	"

Agalinis laxa

Aristida sp.	Pennell, 1929
Chrysopsis graminifolia	"
Quercus sp.	"

Agalinis maritima

Spartina and other salt marsh plants	Pennell, 1929
Borrichia frutescens	Musselman, 1975
Distichlis spicata	"
Iva frutescens	"
Salicornia virginica	"
Spartina alterniflora	"

Agalinis purpurea	
Andropogon scoparius	Pennell, 1929
" *virginicus*	"
Aster lateriflorus	"
Cerastium velutinum	"
Deschampsia caespitosa	"
Eleocharis tenuis	"
Eragrostis pectinacea	"
Euthamia graminifolia	"
Juncus acuminatus	"
" *effusus*	"
" *scirpoides*	"
" *tenuis*	"
Meibomia dillenii	"
" *paniculata*	"
Panicum depauperatum	"
" *philadelphicum*	"
Paspalum laeve australe	"
" *pubescens*	"
Solidago nemoralis	"
Sorghastrum nutans	"
Agalinis setacea	
Andropogon sp.	Pennell, 1929
Aristida purpurascens	"
Chrysopsis aspera	"
Lechea minor	"
Sorghastrum secundum	"
Sporobolus ejuncidus	"
Agalinis virgata	
Aletris farinosa	Pennell, 1929
Andropogon glomeratus	"
" *scoparium*	"
Aristida gracilis	"
Eleocharis sp.	"
Gaultheria procumbens	"
Juncus tenuis	"
Kalmia angustifolia	"
Neopieris mariana	"
Oxycoccus macrocarpus	"
Panicum meridionale	"
Paspalum setaceum	"
Alectra parasitica	
Vitex negundo	Bedi, 1967

Alectra vogelii		
	Arachis hypogaea	Rattray, 1932; Botha, 1948
	Phaseolus vulgaris	Rattray, 1932
	Cultivated leguminous crops	Botha, 1948
Aureolaria spp.		
	Each species is closely restricted to one or a few species of oaks	Pennell, 1928
	Subgenus Euaureolaria is parasitic only on subgenus Lepidobalanus of *Quercus;* subgenus Panctenis only on subgenus Erythrobalanus of *Quercus*	Pennell, 1935
	White oak or witch hazel	Gray, 1853
Aureolaria grandiflora		
	Eupatorium rugosum	Musselman, unpub.
	Hamamelis virginiana	"
	Heuchera richardsonii	"
	Juniperus virginiana	"
	Polygonatum pennsylvanicum	"
	Quercus alba	"
	" *velutina*	"
	Rosa blanda	"
	Rubus occidentalis	"
	Ulmus americana	"
Aureolaria pedicularia		
	Castanea pumila	Musselman, unpub.
	Gaylussacia baccata	"
	Helianthemum bicknellii	"
	Kalmia latifolia	"
	Menziesia pilosa	"
	Prunus serotina	"
	Pteridium aquilinum	"
	Quercus ilicifolia	"
	" *laevis*	Mathen, 1964
	" *marilandica*	Musselman, unpub.
	" *palustris*	Mathen, 1964
	" *prinus*	Musselman, unpub.
	" *velutina*	"
	Rhododendron nudiflorum	"
	Vaccinium vacillans	"
Aureolaria purpurea		
	Grasses and composites	Boeshore, 1920

Aureolaria virginica	
Quercus alba	Mathen, 1964
" *stellata*	"
Bartsia sp.	
Avena flavescens	Boeshore, 1920
Phleum pratense	"
Trifolium pratense	"
Buchnera hispida	
Andropogon contortus	Van Buurren, 1914-1915
" *monticola*	"
Buttonia natalensis	
Euphorbia grandidens	Boodle, 1913
Castilleja spp.	
Can parasitize any neighboring plant	Dobbins and Kuijt, 1973a
Castilleja affinis	
Diplaucus aurantiacus	Heckard, 1962
Helianthus annuus	"
Castilleja arachnoidea	
Polygonum shastense	Heckard, 1962
Castilleja coccinea	
Achillea millefolium	Malcolm, 1966
Alnus rugosa	"
Antennaria neglecta	"
Chrysanthemum leucanthemum	Malcolm 1962b, 1966
Danthonia spicata	Malcolm, 1966
Diplaucus aurantiacus	Heckard, 1962
Fragaria virginiana	Malcolm, 1962b, 1966
Helianthus annuus	Heckard, 1962
Hieracium aurantiacum	Malcolm, 1966
Krigia biflora	"
Lactuca canadensis	Malcolm, 1962b, 1966
Panicum sphaeroides	Malcolm, 1966
Populus deltoides	"
Rubus hispidus	"
Rudbeckia hirta	"
Solidago graminifolia	"
" *juncea*	"
" *rugosa*	"

Castilleja culbertsonii	
Carex exserta	Heckard, 1962
Castilleja cusickii	
Wide host range	Dobbins and Kuijt, 1973
Castilleja dixonii	
Artemisia sp.	Heckard, 1962
Castilleja foliolosa	
Diplaucus aurantiacus	Heckard, 1962
Eriogonum fasciculatum	"
Helianthus annuus	"
Castilleja franciscana	
Diplaucus aurantiacus	Heckard, 1962
Helianthus annuus	"
Castilleja inflata	
Diplaucus aurantiacus	Heckard, 1962
Helianthus annuus	"
Castilleja lanata	
Fallugia paradoxa	Heckard, 1962
Castilleja lutescens	
Wide host range	Dobbins and Kuijt, 1973b
Castilleja miniata x *linariaefolia*	
Achillea millefolium	Heckard, 1962
Castilleja parviflora	
Luetkea pectinata	Heckard, 1962
Castilleja peirsonii	
Phyllodoce breweri	Heckard, 1962
Vaccinium nivictum	"
Castilleja subinclusa	
Rhus diversiloba	Heckard, 1962
Castilleja thompsonii	
Artemisia sp.	Heckard, 1962

Castilleja wightii		
	Diplaucus aurantiacus	Heckard, 1962
	Helianthus annuus	"
Centranthera hispida		
	Native grasses	Van Buuren, 1914-1915
Centranthera humifusa		
	Desmodium triflorum	Barnes, 1941
	Fimbristylis dichotoma	"
	" *polytrichoides*	"
	Iseilema laxum	"
Cordylanthus spp.		
	Non-specific as to hosts	Piehl, 1966
	Wide host range	Chuang and Heckard, 1971
Cordylanthus maritimus		
	Helianthus annuus	Chuang and Heckard, 1971
Cordylanthus orcuttianus		
	Helianthus annuus	Chuang and Heckard, 1971
	Pinus sp.	"
	Plantago sp.	"
	Quercus sp.	"
Cordylanthus palmatus		
	Helianthus annuus	Chuang and Heckard, 1971
Cordylanthus pilosus		
	Quercus douglasii	Chuang and Heckard, 1971
Dasistoma macrophylla		
	Acer saccharum	Piehl, 1962a
	Aesculus glabra	Pennell, 1928, 1935
	Ulmus americana	Piehl, 1962a
Euphrasia spp.		
	Wide host range	Heinricher, 1910
	Monocots (Poaceae and Cyperaceae)	Wettstein, 1896
	Asteraceae, Caryphyllaceae, Fabaceae, Rubiaceae	Wettstein, 1897
	Capsella bursa-pastoris	Yeo, 1964
	Carex alba	"
	Dipsacus fullonum	"

Plantago coronopus	Wilkins, 1963
Poa annua	Yeo, 1964
Senecio vulgaris	"
Sonchus oleraceus	"
Trifolium pratense	"
" *repens*	Wilkins, 1963
Veronica peregrina	Yeo, 1964
" *persica*	"
Euphrasia angelica	
Medicago lupulina	Yeo, 1961
Euphrasia micrantha	
Lamium purpureum	Yeo, 1961
Medicago lupulina	"
Ranunculus sp.	"
Euphrasia nemorosa	
Hieracium pilosella	Yeo, 1961
Medicago lupulina	"
Plantago lanceolata	"
Trifolium repens	"
Euphrasia occidentalis	
Monocots	Fraysse, 1906
Plantago lanceolata	Yeo, 1961
Taraxacum sp.	Fraysse, 1906
Trifolium sp.	"
Euphrasia pseudokerneri	
Medicago lupulina	Yeo, 1961
Pelargonium x *hortorum*	"
Plantago lanceolata	"
Euphrasia rostkoviana	
Mohringia trinervia and a wide range of dicots	Heinricher, 1898b
Euphrasia salisburgensis	
Grasses and Carices	Koch, 1891; Wettstein, 1896
Avena distichophylla	Heinricher, 1898b
Capsella bursa-pastoris	"
Carex alba	Heinricher, 1898b; Yeo, 1964
" *brachystachys*	Yeo, 1964
" *firma*	Heinricher, 1898b Yeo, 1964

Carex sempervirens	Yeo, 1964
" *tenuis*	"
Dipsacus fullonum	Heinricher, 1898b
Drabus aizoides	Crosby-Browne, 1950
Dryas octopetala	"
Epilobium roseum	Heinricher, 1898b
Helianthus grandiflorum	Crosby-Browne, 1950
Luzula spadicea	Heinricher, 1898b
	Yeo, 1964
Medicago lupulina	Yeo, 1961
Poa annua	Heinricher, 1898b
Salix retusa	Crosby-Browne, 1950
Saxifraga aizoon	"
Senecio vulgaris	Heinricher, 1898b
Sesleria caerulea	Yeo, 1964
Silene acaulis	Crosby-Browne, 1950
Sonchus laevis	Heinricher, 1898b
Thymus subcitratus	Crosby-Browne, 1950
Trifolium pratense	Heinricher, 1898b
Trinia glauca	Crosby-Brown, 1950
Trisetum distichophyllum	Yeo, 1964
Veronica buxbaumii	Heinricher, 1898b
" *peregrina*	"
Euphrasia scottica	
Medicago lupulina	Yeo, 1961
Lathraea sp.	
Carpinus sp.	Boeshore, 1920
Corylus sp.	"
Fraxinus sp.	"
Populus sp.	"
Ulmus sp.	"
Lathraea clandestina	
Salix sp.	Kuijt, 1969
Lathraea squamaria	
Acer pseudo-platanus	Hartley and Ellis, 1931
Alnus sp.	Kuijt, 1969
" *rotundifolia*	Hartley and Ellis, 1931
Anemone nemorosa	
Corylus sp.	Bowman, 1833
" *avellana*	
Fagus sylvatica	Hartley and Ellis, 1931

Fraxinus sp.	Bowman, 1833
" *excelsior*	Hartley and Ellis, 1931
Ilex aquifolium	"
Larix decidua	"
Pteris aquilina	
Rubus idaeus	
Rumex obtusifolia	
Sambucus nigra	Hartley and Ellis, 1931
Spiraea ulmaria	
Stachys sylvatica	
Ulmus montana	Hartley and Ellis, 1931
Macranthera flammea	
Myrica cerifera	Musselman, 1972
Nyssa sylvatica	"
Rubus cuneifolius	"
Melampyrum sp.	
Grasses, shrubs and trees	Decaisne, 1847
Melampyrum arvense	
Cereals and annual and biennial dicots	Heinricher 1908
Achillea millefolium	Gislen, 1949
Artemisia campestris	"
Avena sativa	"
Euphorbia peplus	"
Geranium pusillum	"
Poa annua	"
Secale cereale	"
Triticum aestivum	"
Veronica peregrina	"
Melampyrum cristatum	
Deschampsia caespitosa	Horrill, 1972
Ligustrum vulgare	"
Lolium perenne	"
Poa annua	"
Rubus fruticosus	"
Trifolium pratense	"
" *repens*	"
Melampyrum lineare	
Acer saccharum	Cantlon *et al*., 1963
Amelanchier cf. *arborea*	Piehl, 1962b
Betula papyrifera	"
Carex pensylvanica	"
Diervilla lonicera	"
Gaultheria procumbens	

Pinus banksiana	Cantlon *et al*., 1963; Malcolm, 1964
" *resinosa*	Piehl, 1962b; Cantlon *et al*., 1963
" *rigida*	Malcolm, 1964
" *strobus*	Cantlon *et al*., 1963
" *sylvestris*	Cantlon *et al.*, 1963 Malcolm, 1964
Populus grandidentata	Piehl, 1962b; Cantlon *et al*., 1963
" *tremuloides*	Cantlon *et al.*, 1963
Pteridium aquilinum	Piehl, 1962b
Quercus rubra	Cantlon *et al*., 1963; Piehl, 1962b
Sphagnum capillaceum	Piehl, 1962b
Vaccinium angustifolium	Cantlon *et al*., 1963
Melasma sp.	
Legumes (cowpeas, peanuts, soybeans, sugarbeans)	Saunders, 1934
Odontites spp.	
Grasses, shrubs and trees	Decaisne, 1847
Leontodon autumnalis	Fraysse, 1906
Ranunculus repens	"
Trifolium repens	"
Odontites verna	
Agrostis stolonifera	Govier, 1966
Ballota nigra	"
Chamaenerion angustifolium	"
Cirsium arvense	"
Epilobium parviflorum	"
Hordeum vulgare	Govier and Harper, 1965b; Govier, Brown and Pate, 1968
Lolium perenne	Govier, 1966
Lotus uliginosus	"
Ranunculus acris	"
" *repens*	"
Scrophularia nodosa	"
Secale cereale	"
Stellaria media	Govier, Brown and Pate, 1968
Trifolium repens	Govier and Harper, 1965a; Govier, 1966

Orthocarpus faucibarbatus	
Ageratum grandiflora	Thurman, 1966
Aira caryophyllea	"
Anagallis arvensis	"
Brodiaea hyacinthina	"
Cerastium viscosum	"
Chrysanthemum segetum	"
Festuca dertonensis	"
Geranium dissectum	"
Hypochaeris radicata	"
Juncus bufonius	"
Lactuca serriola	"
Lepidium nitidum	"
Limnathes douglasii	"
Luzula subsessilis	"
Oxalis pes-caprae	"
Plantago hookeriana	"
Rumex crispus	"
Sidalcea malvaeflora	"
Soliva sessilis	"
Trifolium repens	"
Orthocarpus floribundus	
Trifolium repens	Thurman, 1966
Orthocarpus purpurascens	
Astragalus nuttallianus	Cannon, 1909
Bigelovia hartwegii	"
Bowlesia lobata	"
Daucus pusillus	"
Delphinium scaposum	"
Erithrichium pterocaryum	"
Erodium botrys	Atsatt and Strong, 1970
Eschscholtzia mexicana	Cannon, 1909
Festuca megalura	Atsatt and Strong, 1970
Gilia bigelovii	Cannon, 1909
Hypochoeris glabra	Atsatt, 1970; Atsatt and Strong, 1970
Lesquerella gordoni	Cannon, 1909
Lolium multiflorum	Atsatt and Strong, 1970
Lupinus sp.	Cannon, 1909
Mentzelia sp.	"
Pectocarya linearis	"
Phacelia tanaecetifolium	"
Plantago fastigiata	"
Silene antirhinum	"
Spergula arvensis	Atsatt and Strong, 1970

Streptanthus californicus	Cannon, 1909
Sysimbrium canescens	"
Trifolium repens	Atsatt and Strong, 1970
Orthocarpus pusillus	
Annual grasses	Davy, 1898
Erodium cicutarium	"
Pedicularis spp.	
Cyperaceae, Poaceae and *Salix*	Hayek and Hegi, 1918
Poaceae	Decaisne, 1847; Hoveler, 1892
Cyperaceae and Poaceae	Volkart, 1899
Pedicularis attollens	
Carex heteroneura	Sprague, 1962
Phleum alpinum (prob.)	"
Trifolium monanthum	"
Pedicularis canadensis	
Abies balsamia	Piehl, 1963
Acer rubrum	"
" *saccharum*	"
Achillea millefolium	"
Agrostis scabra	"
Allium cernuum	"
Amelanchier sp.	"
Anemone cylindrica	"
Antennaria sp.	"
Aquilegia canadensis	"
Aralia nudicaulis	"
Asclepias exaltata	"
Aster laevis	"
" *macrophyllus*	"
" *sagittifolius*	"
Betula papyrifera	"
Carex pensylvanica	"
Carya ovalis	"
Comandra umbellata	"
Convolvulus spithameus	"
Cornus racemosa	"
" *rugosa*	"
" *stolonifera*	"
Danthonia spicata	"
Diervilla lonicera	"
Erigeron strigosus	"
Equisetum arvense	

Fagus grandifolia	Piehl, 1963b
Fragaria virginiana	"
Galium boreale	"
Gaultheria procumbens	"
Gaylussacia baccata	"
Hamamelis virginiana	"
Hepatica americana	"
Hieracium aurantiacum	"
" *scabrum*	"
Hystrix patula	"
Lactuca sp.	"
Lonicera dioica	"
Maianthemum canadense	"
Melampyrum lineare	"
Melilotus albus	"
Oryzopsis asperifolia	"
" *pungens*	"
Ostrya virginiana	"
Panicum zanthophyllum	"
Phleum pratense	"
Pinus resinosa	"
" *strobus*	"
Polygala paucifolia	"
Populus tremuloides	"
Prenanthes alba	"
Prunus serotina	"
Pteridium aquilinum	"
Pycnanthemum virginianum	"
Quercus rubra	"
Rhamnus cathartica	"
Rhus typhina	"
Rosa acicularis	"
Rudbeckia hirta	"
Rumex acetosella	"
Salix humilis	"
Satureja vulgaris	"
Smilacena racemosa	"
Solidago hispida	"
" *juncea*	"
Thuja occidentalis	"
Trientalis borealis	"
Trillium grandiflorum	"
Tsuga canadensis	"

Vaccinium myrtilloides	Piehl, 1963b
Verbascum thapsus	"
Viburnum acerifolium	"
Viola pubescens	"
Zizia aureus	"
Pedicularis crenulata	
Deschampsia sp.	Sprague, 1962
Poa sp. (prob.)	"
Trifolium monanthum	"
Pedicularis densiflora	
Abies concolor (prob.)	Sprague, 1962
Adenostoma fasciculatum	"
Arbutus menziesii	"
Arctostaphylos glandulosa (prob.)	"
Ceanothus sp. (prob.)	"
Diplaucus aurantiacus	"
" *puniceus* (prob.)	"
Pinus coulteri (prob.)	"
'' *jeffreyi* (prob.)	"
" *ponderosa*	"
" *sabiana* (prob.)	"
Quercus dumosa (prob.)	"
" *kelloggii* (prob.)	"
Rhus diversiloba (prob.)	"
Pedicularis dudleyi	
Ceanothus thyrsiflorus	Sprague, 1962
Lithocarpus densiflora (prob.)	"
Vaccinium ovatum (prob.)	"
Pedicularis groenlandica	
Carex fissuricola (prob.)	Sprague, 1962
'' *helleri*	"
Deschampsia caespitosa	"
Poa sp.	"
Pedicularis lanceolata	
Apocynum cannabinum	Piehl, 1965a
Aster lateriflorus	"
'' *novae-angliae*	"
Carex sp.	"
Chelone glabra	"
Cornus racemosa	"

Cornus stolonifera	Piehl, 1965a
Daucus carota	"
Dryopteris thelypteris	"
Equisetum arvense	"
Eupatorium maculatum	"
Impatiens capensis	"
Iris virginica	"
Lysimachia quadriflora	"
Pellardia virginica	"
Polygonum coccineum	"
Pycnanthemum virginicum	"
Ranunculus septentrionalis	"
Rhamnus frangula	"
Solidago patula	"
" *riddellii*	"
Thalictrum dasycarpum	"
Typha latifolia	"
Verbena hastata	"
Pedicularis racemosa	
Abies concolor (prob.)	Sprague, 1962
Pinus monticola (prob.)	"
Pedicularis recutita	
Deschampsia caespitosa	Hayek and Hegi, 1918
Pedicularis semibarbata	
Abies concolor (prob.)	Sprague, 1962
Arctostaphylos patula	"
Pinus ponderosa	"
Poa scabrella (prob.)	"
Pedicularis verticillata	
Sesleria caerulea	Hayek and Hegi, 1918
Pedicularis vulgaris	
Calluna sp.	Maybrook, 1917
Rhamphicarpa sp.	
Rice, maize and cowpeas	Kuijt, 1969
Rhamphicarpa longiflora	
Poaceae	Van Buuren, 1914-1915
Rhamphicarpa veronicaefolia	
Sorghum sp.	Fuggles-Couchman, 1935
Rhinanthus sp.	
Cereal grains	Kuijt, 1969

Rhinanthus minor	
Poaceae	Kuijt, 1969
Sopubia delphinifolia	
Andropogon sorghum	Kumar and Solomon, 1941
Anthistria ciliata	"
Chrisopogon montanus	"
Peltophorus divergens	"
Sopubia rhamnosa	
Imperata cylindrica and other wild grasses	Williams, 1958, 1960
Striga asiatica	
Agropyron cristatum	Nelson, 1958; Shaw et al., 1962
" *repens*	"
" *trichophorum*	"
Agrostis alba	"
Andropogon annulatus	Sawyer, 1921
" *caricosus*	"
" *gerardi*	Nelson, 1958; Shaw, et al., 1962
" *monticola*	Kumar and Solomon, 1941
" *sorghum*	"
" *sudanense*	Chibber, 1911
" *virginicus*	Nelson, 1958
Arachis hypogaea	Williams, 1958
Aristida adscencionis	Kumar and Solomon, 1941
Avena sativa	Kumar and Solomon, 1941; Nelson, 1958; Shaw et al., 1962
Axonopus affinis	Nelson, 1958
Brachiaria distachya	Kumar and Solomon, 1941
Bromus catharticus	Nelson, 1958; Shaw, et al., 1962
" *inermis*	"
" *tectorum*	"
Celosia argentea	Kumar and Solomon, 1941
Cenchrus sp.	Nelson, 1958; Shaw et al., 1962
Chloris gayana	Kumar and Solomon, 1941; Shaw et al., 1962
" *virgata*	Kumar and Solomon, 1941; Shaw et al., 1962
Commelina hasskarli	Kumar and Solomon, 1941

Corchorus fascicularis	Kumar and Solomon, 1941
Cynodon dactylon	Nelson, 1958; Shaw et al., 1962
Cyperus rotundus	Kumar and Solomon, 1941
Dactylis glomerata	Kumar and Solomon, 1941; Nelson, 1958
Dactyloctenium aegypticum	Shaw et al., 1962
Digitaria sanguinalis	Kumar and Solomon, 1941; Nelson, 1958
Echinochloa crus-galli	Shaw et al., 1962
Eleusine aegyptiaca	Sawyer, 1921; Kumar and Solomon, 1941
Eleusine coracana	Kumar and Solomon, 1941
" *indica*	Nelson, 1958; Shaw et al., 1962
Eragrostis abyssinica	Pearson, 1913
" *spectabilis*	Nelson, 1958
" *tef*	"
Eremochloa ophiuroides	Nelson, 1958; Shaw et al., 1962
Eriochloa polystachya	Shaw, 1921
Euchlena mexicana	"
Eurochloa helopsis	Kumar and Solomon, 1941
" sp.	"
Helianthus sp.	Williams, 1958
Hordeum intermedium	Kumar and Solomon, 1941
" *vulgare*	Nelson, 1958; Shaw et al., 1962
Imperata arundinacea	Palm and Heusser, 1924
Indigofera glandulosus	Kumar and Solomon, 1941
Ipomoea reniformis	Sawyer, 1921
Lolium multiflorum	Nelson, 1958; Shaw et al., 1962
" *perenne*	"
Lycopersicon esculentum	Sharma et al., 1954
Oryza sativa	Nelson, 1958; Shaw et al., 1962
Panicum brizanthum	Kumar and Solomon, 1941
" *colonum*	Sawyer, 1921
" *coloratum*	Kumar and Solomon, 1941
" *distachyum*	Sawyer, 1921

Panicum flavidum	Sawyer, 1921
" *isachne*	Kumar and Solomon, 1941
" *maximum*	Kumar and Solomon, 1941 Shaw et al., 1962
" *miliaceum*	Kumar and Solomon, 1941; Nelson, 1958
" *prostratum*	Sawyer, 1921
" *repens*	Sawyer, 1921; Nelson, 1948; Shaw et al., 1962
" *virgatum*	Nelson, 1958; Shaw et al., 1962
Paspalum conjugatum	Nelson, 1958
" *dilatatum*	Pearson, 1913; Nelson, 1958, Shaw et al., 1962
" *notatum*	Nelson, 1958; Shaw et al., 1962
" *scrobiculatum*	Chibber, 1911
" *urvillei*	Nelson, 1958; Shaw et al., 1962
" *virgatum*	Kumar and Solomon, 1941
Pennisetum glaucum	Nelson, 1958; Shaw et al., 1962
" *typhoideum*	Sawyer, 1922; Kumar and Solomon, 1941
" *unisetum*	Kumar and Solomon, 1941
Phaseolus aconitifolius	Sharma et al., 1954
Poa annua	Nelson, 1958; Shaw et al., 1962
" *pratensis*	"
" *trivialis*	"
Saccharum officinarum	Kumar, 1940; Kumar and Solomon, 1941; Sharma et al., 1956; Nelson, 1958; Shaw et al., 1962
Secale cereale	Kumar and Solomon, 1941; Nelson, 1958; Shaw et al., 1962
Setaria gerradii	Kumar and Solomon, 1941
" *italica*	Sawyer, 1921; Kumar and Solomon, 1941; Nelson, 1958; Shaw et al., 1962
" *lindenbergiana*	Kumar and Solomon, 1941
" *nigrirostis*	"
Sorghum halapense	Nelson, 1958; Shaw et al., 1962

Sorghum sudanense	Chibber, 1911; Nelson, 1958
" vulgare	Chibber, 1911; Nelson, 1958; Shaw et al., 1962
Sporobolus coronandelianus	Sawyer, 1921
Striga sp.	Palm and Heusser, 1924
Tribulus terrestris	Kumar and Solomon, 1941
" vulgare	"
Zea mays	Fuller, 1900; Stephens, 1912; Kumar and Solomon, 1941; Sharma et al., 1954; Nelson, 1958; Shaw et al., 1962
Striga curviflora	
Themeda triandra	Van Buuren, 1914-1915
Striga densiflora	
Andropogon contortus	Van Buuren, 1914-1915
" pumilis	Kumar and Solomon, 1941
" sorghum	Van Buuren, 1914-1915
Commelina hasskarlii	Kumar and Solomon, 1941
Cyperus sp.	"
Desmodium diffusum	"
Digitaria royleana	"
Eleusine aegyptiaca	"
Eragrostis sp.	Van Buuren, 1914-1915
Euchlaena mexicana	Kumar and Solomon, 1941
Glossocardia linearifolia	"
Indigofera cordifolia	"
Iseilema laxum	"
" wightii	Barnes, 1941
Lophopogon tridentatus	Kumar and Solomon, 1941
Panicum isachne	"
Paspalum sanguinale	"
" scrobiculatum	"
Pennisetum typhoideum	Kumar, 1940
Saccharum officinarum	Luthra, 1920; Sharma et al., 1956
Setaria glauca	Kumar and Solomon, 1941
" italica	"
Tragus racemosa	"
Tripogon jacquemonti	"
Striga euphrasioides	
Andropogon contortus	Kumar and Solomon, 1941
" sorghum	Luthra, 1921
Aristida funiculata	"

Cyperus sp.	Kumar and Solomon, 1941
Digitaria royleana	"
Eragrostis cynosuroides	"
Oldenlandia aspera	"
Oryza sativa	Barnes, 1941
Panicum colonum	Kumar and Solomon, 1941
" *ramosum*	"
Polygala erioptera	"
Saccharum officinarum	Luthra, 1921; Sharma et al., 1956
Spermacoce stricta	Kumar and Solomon, 1941
Sporobolus diander	"
Zea mays	"
Striga hermonthica	
Poaceae	Doggett, 1965
Arachis hypogaea	Williams, 1958
Cynodon dactylon	Andrews, 1945
Dolichos lablab	Andrews, 1945; Williams, 1958
Eleusine sp.	Doggett, 1965
Oryza sp.	Andrews, 1945
Panicum miliaceum	"
" *miliare*	"
Paspalum commersonii	"
Pennisetum sp.	"
Setaria italica	"
Sorghum sp.	Andrews, 1945; Doggett, 1965
Vigna sp.	Williams, 1958
Zea mays	Andrews, 1945; Doggett, 1965
Striga orobanchoides	
Dicots; especially Acanthacea	Van Buuren, 1914-1915
Woody plants; especially *Indigofera* spp.	Heinricher, 1913
Indigofera spp. and other Fabaceae	Wild, 1948
Bergia decumbens	"
Dysophylla quadrifolia	Kumar and Solomon, 1941
Euphorbia abyssinica	Wild, 1948
" *antiquorum*	Kumar and Solomon, 1941
Hygrophila seryphyllum	"
Indigofera confusa	Wild, 1948
Ipomoea sp.	"
Lepidagathis cristata	Kumar and Solomon, 1941
Nicotiana tabacum	Williams, 1958
Sanseviera sp.	Wild, 1948

Setaria homonyma	Wild, 1948
Tephrosia sp.	"
" *pseudolongipes*	"

Tomanthera auriculata	
Attached but hosts not identifeid	Musselman, 1972

Tozzia sp.	
Alchemilla sp.	Boeshore, 1920
Petasites sp.	"
Ranunculus sp.	"
Rumex sp.	"

Orobanchaceae

Aeginetia spp.	
Monocots, as well as members of the families Ericaceae and Gleicheniaceae	Beck von Mannagetta, 1890, 1930

Aeginetia indica	
Calamagrostis arundinacea	Kusano, 1908
Canna indica	"
Carex japonica	"
" *lanceolata*	Kusano, 1903
" *morrowi*	Kusano, 1908
Luzula campestris	"
Miscanthus sinensis	Kusano, 1903, 1908
Oryza sativa	Kusano, 1903, 1908; McWhorter, 1922; Teodoro, 1925
Panicum miliaceum	Kusano, 1903, 1908
Pollia japonica	Kusano, 1908
Saccharum officinarum	McWhorter, 1922; Teodoro, 1925; Roxas, 1927
Setaria excurrens	Kusano, 1908
" *italica*	Kusano, 1903
Zea mays	Kusano, 1903; McWhorter, 1922; Teodoro, 1925
Zingiber mioga	Kusano, 1903, 1908; Teodoro, 1925

Aeginetia paniculata	
Saccharum officinarum	Hedayetullah and Saha, 1942

Aeginetia pedunculata	
Saccharum officinarum	Hedayetullah and Saha, 1942
Christisonia wightii	
Saccharum officinarum	Goseco, 1932; Quisumbing, 1940
Conopholis sp.	
Section Erythrobalanus of *Quercus*	Boeshore, 1920
Conopholis alpina	
Grey oak	Haynes, 1971
Quercus gambelli	"
" *grisea*	"
" *texana*	"
" *utahensis*	"
Conopholis americana	
Chestnut oak	Jennings, 1920; Haynes, 1971
Quercus alba	Haynes, 1971; Thieret, 1971
" *bicolor*	Haynes, 1971
" *falcata*	Haynes, 1971; Thieret, 1971
" *hemisphaerica*	"
" *marilandica*	"
" *nigra*	"
" *rubra*	Wilson, 1898; Jennings, 1920; Percival, 1931; Haynes, 1971; Thieret, 1971
" *shumardii*	Haynes, 1971; Thieret, 1971
" *velutina*	Jennings, 1920; Haynes, 1971; Thieret, 1971
Epifagus virginiana	
Fagus grandifolia	Cook and Schively, 1904; Boeshore, 1920; Fernald, 1958; Brooks, 1960 (1961)
Orobanche spp.	
Over 200 hosts known for all species of this genus combined. All confirmed hosts are Dicots.	Beck von Mannagetta, 1890
Orobanche aegyptiaca	
22 crops and weeds	Quaddus et al., 1969
Ammi majus	Ranga Swamy, 1963
Brassica campestris	Ranga Swamy, 1963; Battacharya, 1971

Brassica napus	Bhattacharya, 1971; Mijatovic and Stojanovic, 1973
" *rapa*	Garman, 1903
Citrullis vulgaris	Kabulov and Mukumov, 1969; Prokudina, 1972
Cucumis melo	Kabulov and Mukumov, 1969; Mukumov, 1970
" *sativa*	Garman, 1903
Cucurbita pepo	Kabulov and Mukumov, 1969
Gossypium sp.	Garman, 1903
Lycopersicon esculentum	Vestal, 1954; Bhattacharya, 1971
Raphanus sativus	Bhattacharya, 1971
Solanum melongena	Garman, 1903; Vestal, 1954; Bhattacharya, 1971; Mijatovic and Stojanovic, 1973
" *tuberosum*	Mijatovic and Stojanovic, 1973
Orobanche alba	
Thyme	Garman, 1903
Orobanche amythystea	
Daucus carota	Garman, 1903
Orobanche apiculata	
Pelargonium graveolens	Vaucher, 1823
Orobanche arenaria	
Artemisia sp.	Tsaturyan, 1970
Centuria arenaria	"
Orobanche cariophyllaca	
Thymus jankae	Lazarov and Andreev, 1969 (1970)
Orobanche cernua	
Acalypha indica	Marudarjan, 1950
Artemisia tunuisecta	Rakhimov, 1967
Cannabis sativa	Marudarjan, 1950
Cathamus tinctorius	"
Corchorus capsularis	"
Datura fastuosa	Shaw, 1918; Marudarjan, 1950
" *stramonium*	Shaw, 1918

Euphorbia helioscopa	Rao, 1953
" *prostrata*	Marudarjan, 1950
Helianthus sp.	"
" *annus*	Thomas, 1943
Leucas zeylanica	Rao, 1953
Lycopersicon esculentum	Shaw, 1918; Dalela and Mathur, 1971
Nicandra physaloides	Marudarjan, 1950
Nicotiana sp.	Garman, 1903; Dalela and Mathur, 1971
" *affinis*	Thomas, 1943
" *glutinosa*	"
" *rustica*	Marudarjan, 1950
" *sandarae*	Thomas, 1943
" *tabacum*	Shaw, 1918; Thomas, 1943
Petunia hybrida	Setty, 1971
Physalis minimum	Marudarjan, 1950
Pluchea lanceolata	Shaw, 1918; Gupta, Sharma and Dalela, 1969
Solanum melongena	Shaw, 1918; Dalela and Mathur, 1971; Misra and Saxena, 1971
" *nigrum*	Thomas, 1943
" *trilobatum*	Marudarjan, 1950
" *tuberosum*	Thomas, 1943
" *xanthocarpum*	"
Triticum aestivum	Sharma, 1953
Withania somnifera	Thomas, 1943
Orobanche coelestis	
Acanthophyllum subglabrum	Mishchenko, 1970
Orobanche crenata	
Peas	Piglionica and Spezzacatena, 1969
Vica faba	Kadry and Tewfic, 1956a,b; Abou-Raya et al., 1970
Orobanche cumana	
Cocklebur	Garman, 1903
Artemisia maritima	Petrov, 1970
Helianthus sp.	Garman, 1903; Barcinsky, 1934
Lycopersicon esculentum	Terpo, 1951; Mijatovic and Stojanovic, 1973

Nicotiana sp.	Garman, 1903; Terpo, 1951; Mijatovic and Stojanovic, 1973
Orobanche fasciculata	
Artemisia sp.	Fernald, 1958
Eriogonum sp.	"
Orobanche gracilis	
Esparsette	Garman, 1903
Melilotis officinalis	"
Thymus kotschyanus	Tsaturyan, 1970
Trifolium pratense	Garman, 1903
Orobanche hederae	
Conyza sp.	Kohler, (no date)
Fatsia japonica	Murphy, 1972
Hedera colchica	"
" *helix*	Tate, 1925; Privat, 1960; Murphy, 1972
Kalopanax pictus	Murphy, 1972
Pelargonium sp.	Tate, 1925
Orobanche lavandulacea	
Beans	Garman, 1903
Lactuca sp.	"
Orobanche ludoviciana	
Ambrosia and other Asteraceae	Fernald, 1958
Ambrosia trifida	Garman, 1903
Nicotiana sp.	"
Orobanche lutea	
Medicago lupulina	Garman, 1903
" *sativa*	Garman, 1903; Mijatovic and Stojanovic, 1973
Trifolium medium	Garman, 1903
Orobanche major	
Lycopersicon esculentum	Mijatovic and Stojanovic, 1973
Nicotiana sp.	"
Solanum melongena	"
Orobanche minor	
Serradella	Garman, 1903

Ammophila arenaria	Murphy, 1972
Aralia hispida	Koch, 1887
Campanula portenschlagina	Murphy, 1972
Chondrilla juncea	Agric. Gaz. New S. Wales, 1966
Chrysanthemum myconis	Koch, 1887
Coronilla emerus	"
" *minima*	"
Crepis virens	"
Crithmum maritimum	"
Daucus carota	"
Digitalis purpurea	"
Echium plantagineum	"
Eryngium amethystinum	"
" *campestre*	"
Galactites tomentosa	"
Gazania splendens	"
Helianthemum polifolium	"
Helichrysum italicum	"
Heliotropium peruvianum	"
Hypochaeris radicata	"
Lathyrus angulatus	"
Laurus nobilis	"
Linaria pedunculata	"
Lotus corniculatus	Koch, 1887; Mijatovic and Stojanovic, 1973
" *creticus*	Koch, 1887
Medicago arabica	"
" *lupulina*	"
" *sativa*	Koch, 1887; Mijatovic and Stojanovic, 1973
" *tribuloides*	Koch, 1887
Nerium olander	"
Ornithopus compressus	"
" *sativus*	Koch, 1887; Kropac, 1973
Pelargonium spp.	Koch, 1887; Elsley, 1971
" x *hortorum*	Murphy, 1972
Petunia sp.	Koch, 1887
Poterium sanguisorba	"
Salvia bertolonii	"
Scabiosa holosericea	"
Tolpis barbata	"
Trifolium arvense	Koch, 1887, Kropac, 1973
" *elegans*	Koch, 1887
" *filiforme*	"
" *hybridum*	Nuesch, 1958; Kropac, 1973
" *incarnatum*	Nuesch, 1958

Trifolium pratense	Koch, 1887, Holdsworth and Nutman, 1947; Nuesch, 1958; Vyas, 1966; Kropac, 1973; Mijatovic and Stojanovic, 1973
" *repens*	Koch, 1887; Nuesch, 1958; Kropac, 1973; Mijatovic and Stojanovic, 1973
" *striatum*	Koch, 1887
" *strictum*	"
" *subterraneum*	"
Yucca sp.	"
Orobanche mutelli	
Tobacco	Aleksiev, 1967; Lazarov and Andreev, 1969
Brassica rapa	Garman, 1903
Orobanche orientalis	
Amygdalus fenzliana	Tsaturyan, 1970
Haplophyllum villosum	"
Orobanche picridis	
Daucus carota	Garman, 1903
Orobanche platystigma	
Carduus acanthoides	Lazarov and Andreev, 1969
Orobanche ramosa	
More than 300 host species; none of them monocots	Racovita, 1959, 1960
Amaranthus retroflexus	Durbin, 1953
Ammi visnaga	Koch, 1887; Durbin, 1953
Archangelica officinalis	Durbin, 1953
Armoracia lapathaefolia	"
Begonia semperflorens	"
Brassica napus	Garman, 1903; Durbin, 1953
" *oleracea*	Durbin, 1953
" *rapa*	Garman, 1903; Durbin, 1953
Cannabis sativa	Koch, 1887; Kuijt, 1969; Mijatovic and Stojanovic, 1973
Capsella bursa-pastoris	Durbin, 1953
Cochlearia armorica	Koch, 1887
Coleus sp.	Koch, 1887; Durbin, 1953
" *blumei*	"

Conium maculatum	Koch, 1887; Durbin, 1953
Cuphea platycentra	Durbin, 1953
Daucus carota	Durbin, 1953; Wurgler, 1973
Dianthus caryophyllus (poss.)	Durbin, 1953
Eupatorium legustrinium	"
Fagopyrum sagittatum (poss.)	"
Galeopsis ladanum	Koch, 1887; Durbin, 1953
Galium tricome (poss.)	Durbin, 1953
Geranium pusillum	Koch, 1887; Durbin, 1953
Helianthus annuus	"
Heliotropium peruvianum	Durbin, 1953
Humulis lupulus (poss.)	"
Lactuca perennis	Koch, 1887; Durbin, 1953
Lamium album	Durbin, 1953
" maculatum	Koch, 1887; Durbin, 1953
" purpureum	Durbin, 1953; Wurgler, 1973
Lepidium virginicum	Garman, 1903; Durbin, 1953
Leucas martinicensis	Koch, 1887; Durbin, 1953
Lycopersicon esculentum	Koch, 1887; Durbin, 1953; Stout and Wagnon, 1953; Wilhelm, Benson and Sagen, 1958
Matricaria parthenoides	Koch, 1887; Durbin, 1953
Melilotus officinalis (poss.)	Durbin, 1953
Nerium oleander	Wurgler, 1973
Nicotiana glauca	Koch, 1887; Durbin, 1953
Nicotiana rustica	"
" tabaccum	Koch, 1887; Durbin, 1953; Aleksiev, 1967; Mijatovic and Stojanovic, 1973
Oenothera acaulis (poss.)	Durbin, 1953
Pastinaca sativa	Koch, 1887; Durbin, 1953
Pelargonium sp.	Durbin, 1953
" hybridum	Koch, 1887
" zonale	Durbin, 1953
Pentstemon gentianoides	"
Perilla nankingensis	"
Petunia hybrida	"
Polygonum hybridum (poss.)	"
" aviculare	Koch, 1887; Durbin, 1953
Primula sinensis	"
Pyrethrum sp. (poss.)	Durbin, 1953
" indicum	Koch, 1887; Durbin, 1953

Salvia coccinea	Durbin, 1953
" *splendens*	"
Solanum jasminoides	Koch, 1887; Durbin, 1953
" *nigrum*	"
" *pseudocapsicum*	Durbin, 1953
" *sarachoides*	"
" *tuberosum*	Koch, 1887; Durbin, 1953
Sonchus oleraceus	Wurgler, 1973
Taraxacum kok-saghyz	Durbin, 1953
Trifolium agrarium	Wilhelm, Benson and Sagen, 1958
" *pratense*	Mijatovic and Stojanovic, 1973
Tropaeolum majus	Durbin, 1953
Verbena chamaedryfolia (poss.)	"
Verbesina encelioides (poss.)	"
Veronica sp.	"
Vitis vinifera	"
Xanthium macrocarpum	"
" *spinosum*	Koch, 1887; Durbin, 1953
Orobanche schweinfurtii	
Trifolium alexandrinum	Garman, 1903
Orobanche speciosa	
Euonymus sp.	Garman, 1903
Lens culinarius	"
Pisum sp.	"
Vicia faba	Kuijt, 1969
Viola tricolor	Garman, 1903
Orobanche sulfurea	
Crambe kotschyana	Rakhimov, 1967
Orobanche terrae-novae	
Various plants	Fernald, 1958
Orobanche tinctoria	
Sugar beet	Garman, 1903
Orobanche uniflora	
Various plants	Fernald, 1958
Artemisia spp.	Beck von Mannagetta, 1890
Aster corymbosus	Smith, 1901; Boeshore, 1920
Sedum album	Kuijt, 1969
" *stenopetalum*	Beck von Mannagetta, 1890
Solidago spp.	Chatin, 1892; Beck von Mannagetta, 1890

Passiflora coerulea	
Euonymus japonicus	Pee-Laby, 1904

Santalaceae

Buckleya distichophylla	
25 host species including ferns, gymnosperms and angiosperms	Piehl, 1965b
Tsuga spp.	Fernald, 1958
Buckleya quadriala	
Abies firma	Kusano, 1902
Alnus firma	"
Carpinus japonica	"
" *yedoensis*	"
Cryptomeria japonica	"
Chamaecyparis obtusa	"
Fagus japonica	"
Fraxinus longicuspis	"
Ilex macropoda	"
Lespedeza buergeri	"
Quercus glandulifera	"
Rhododendron sinense	"
Choretrum lateriflorum	
Casuarina fraseriana	Herbert, 1924-1925
Pimelea sp.	"
Comandra lívida	
Ledum groenlandicum	Moss, 1926
Pinus banksiana	"
" *murrayana*	"
Comandra pallida	
Members of the families Asteraceae, Cornaceae, Fabaceae, Liliaceae, Poaceae, Rosaceae and Urticaceae	Brooks, 1937
Achillea millefolia	Fisher, 1922
Artemisia tridentata	"
Bouteloua curtipendula	Brooks, 1937
Cornus asperifolia	"
Leptoglottis nuttallii	"
Lupinus suksdorfii	Fisher, 1922
Prunus persica	"
Psoralia floribunda	Brooks, 1937
Pyrus malus	Woodcock and De Zeeuw, 1920; Fisher, 1920

Ulmus americana	Brooks, 1922
Yucca glauca	"
Comandra richardsiana	
Poaceae	Moss, 1926
Aster sp.	"
Fragaria sp.	"
Rhus typhina	"
Comandra umbellata	
200 host species in 61 families of 2 phyla	Piehl, 1963a, 1965c
50 host species	Hedgecock, 1915
Actinella fastigata	Harrington, 1945
Agropyron smithii	"
Ambrosia psilostachya	"
Andropogon hallii	"
" *scoparius*	"
Aragallus albiflorus	"
Argemone intermedia	"
Aristida fendleriana	"
Artemisia frigida	"
Astragalus drummondii	"
" *pectinatus*	"
" *tridactylicus*	"
Bouteloua curtipendula	"
" *gracilis*	"
Calamovilfa longifolia	"
Cercocarpus parviflorus	"
Cirsium undulatus	"
Eriogonum alatum	"
" *effusum*	"
" *campanulatum*	"
" *subalpinum*	"
Erysimum asperum	"
Eurotia lanata	"
Euphorbia greenii	"
Evolvulus pilosus	"
Gaura coccinea	"
Gaylussacia resinosa	Gray, 1853
Gilia spicata	Harrington, 1945
Gutierrezia sarothrae	"
Helianthus pumilis	"
Hymenopappus arenosus	"
Lavanxia brachycarpa	"
Malvastrum coccineum	"

Opuntia polycantha	Harrington, 1945
Paronychia purpureus	"
Pedicularis canadensis	Piehl, 1963b
Prunus melanocarpa	Harrington, 1945
Psoralia tenuifolia	"
Ratibida columnaris	"
Rhus trilobata	"
Sitanion hystrix	"
Stipa comata	"
Thelesperma gracile	"
Townsendia grandiflora	"
Tragopogon pratensis	"
Vaccinium vacillans	Gray, 1853
Exocarpus aphylla	
Acacia sp.	Herbert, 1924-1925
Exocarpus bidwillii	
Corokia cotoneaster	Fineran, 1962
Cyathodes colensoi	"
" *frazeri*	"
Dracophyllum uniflorum	"
Gaultheria depressa	"
" *rupestris*	"
Helichrysum selago	Philipson, 1959; Fineran, 1962
Leptospermum scoparium	Fineran, 1962
Nothofagus solandri	"
Pentachondra pumila	"
Podocarpus nivalis	"
Exocarpus spartea	
Acacia acuminata	Herbert, 1924-1925
Banksia ilicifolia	"
" *menziesii*	"
Casuarina humulis	"
Eucalyptus loxophleba	"
Gompholobium tomentosum	"
Fusanus acuminatus	
Acacia acuminata	Herbert, 1924-1925
Eucalyptus foecunda	"
Templetonia sulcata	"
Fusanus spicatus	
Acacia sp.	Herbert, 1924-1925
" *acuminata*	"
Dodonaea lobulata	"
Eremophila sp.	"

Eucalyptus foecunda	Herbert, 1924-1925
Templetonia sulcata	"
Geocaulon lividum	
Alnus sp.	Warrington, 1970
Arctostaphylos sp.	"
Aster sp.	"
Betula sp.	"
Carex sp.	"
Castilleja sp.	"
Cornus sp.	"
Dryas sp.	"
Equisetum sp.	"
Fragaria sp.	"
Galium sp.	"
Hedysarum sp.	"
Juniperus sp.	"
Ledum sp.	"
Linnaea sp.	"
Lonicera sp.	"
Lupinus sp.	"
Mitella sp.	"
Pedicularis sp.	"
Picea sp.	"
Pinus sp.	"
Populus sp.	"
Potentilla sp.	"
Ribes sp.	"
Salix sp.	"
Leptomeria preisiana	
Acacia signata	Herbert, 1924-1925
Duboisia hopwoodii	"
Leptomeria spinosa	
Eremaea pilosa	Herbert, 1924-1925
Mida salicifolia	
Wide host range	Simpson and Fineran, 1970
Agathis australis	Philipson, 1959
Nothofagus solandri	Simpson and Fineran, 1970
Nestronia umbellula	
Deciduous trees	Fernald, 1958
Osyris arborea	
Monocots	Rao, 1942
Botrychium virginianum	"

Pyrularia pubera	
Deciduous trees and shrubs	Fernald, 1958
Santalum album	
Acacia caesia	Barber, 1907a
" *concinna*	"
Acalypha sp.	"
" *indica*	"
" *fruticosa*	"
Achyranthes aspera	"
Adenanthera pavonina	"
Adhatoda vasica	"
Agave vera-cruz	"
Ailanthus excelsa	"
Alanguim lamarckii	"
Albizzia amara	"
Anona squamosa	Rama Rao, 1910b
Artabotrys odoratissimus	"
Bambusa auriculata	Barber, 1907a
Berrya ammomilla	"
Begonia sp.	"
Blepharis boerhaaviaefolia	"
Cansjera rheedii	"
Capparis zeylanica	Barber, 1907a; Rama Rao, 1910b
Caryota sobolifera	Barber, 1907a
" *urens*	"
Casearia tomentosa	"
Cassia auriculata	"
" *siamea*	"
Castanospermum australe	"
Casuarina equisetifolia	"
Celastrus paniculata	"
Cipadessa fruticosa	"
Citrus aurantium	"
Clausena indica	"
Clitoria ternatea	"
Cocos nucifera	"
Codiaeum sp.	"
Coffea arabica	Rao, 1942
Coleus sp.	Barber, 1907a
Combretum ovalifolium	"
Cordia myxa	"
Cynodon dactylon	"
Cyperus rotundus	"
Dalbergia scandens	"
" *sissoo*	"
Diospyros montana	"

Dondonaea viscosa	Barber, 1907a
Dolichos lablab	"
Dracaena sp.	"
Elaeodendron roxburgii	"
Eleusine aegyptica	"
Eucalyptus globulus	"
Ficus bengalensis	"
" *mysorensis*	"
" *religiosa*	"
Flueggea leucopyrus	"
Goniothalamus urynaadensis	Rama Rao, 1910b
Gossypium arboreum	"
Grewia hisuta	Barber, 1907a
" *tiliaefolia*	"
Guayzuma tomentosa	"
Gymnosporia montana	"
Gyrocarpus jacquini	"
Heptapleurum venulosum	"
" *verticillatum*	"
Holoptelea integrifolia	"
Jasminium sp.	Rao, 1942
" *malbaricum*	Barber, 1907a
" *rigidum*	"
Jatropha curcas	"
" *gossypifolia*	"
Kigelia pinnata	"
Lantana camara	"
Leucena glauca	"
Limonia acidissima	"
Litsaea zeylanica	"
Melia azadirachta	"
Meyena sp.	"
Mimusops indica	"
Morinda citrifolia	"
Ochlandra rheedii	"
Opuntia dillenii	"
Panax sp.	"
Parkia biglandulosa	"
Pavetta indica	"
Peltophorum ferrugineum	"
Phoenix sylvestris	"
Pithecolobium dulce	"
" *saman*	"
Plumbago zeylanica	"
Polyalthia longifolia	"
Polygala longifolia	Rama Rao, 1910b
Pongamia glabra	Barber, 1907a
Premna tomentosa	"
Protium caudatum	"

Psidium guyava	Barber, 1907a
Pterospermum heyneanum	"
" *suberifolium*	"
Pterolobium indicum	"
Pupalia atropurpurea	"
Ruellia prostrata	"
Saccharum spontaneum	"
Sansevieria zeylanica	"
Sarcostemma brevistigma	"
Sida carpinifolia	Barber, 1907a; Rama Rao, 1910b
" *rhombifolia*	"
Stachytarpheta indica	Barber, 1907a
Sterculia alata	"
Strebbus asper	"
Strobilanthes cuspidatus	"
Tamarindus indica	"
Tecoma stans	"
Terminalia arjuna	"
" *chebula*	"
Thespesia populnea	Barber, 1907a; Rama Rao, 1910b
Tinospora cordifolia	"
Toddalia aculeata	Barber, 1907a
Ventilago madraspatana	"
Webera asiatica	"
Wrightia tomentosa	"
Zizyphus oenoplia	"
" *rugosus*	"
" *xylopyrus*	"
Scleropyrum wallichianum	
Cinnamomum zeylanicum	Rao, 1942
Ficus spp.	"
Hopea parviflora	"
Memecylon indica	"
Nephelium sp.	"
Pavetta indica	"
Scleichera trijuga	"
Strobilanthes sp.	"
Terminalia paniculata	"
Thesium linophyllum	
Several Poaceae	Mitten, 1847
Anthyllis vulveraria	"
Carex glauca	"
Daucus carota	"
Lotus corniculatus	"
Scabiosa succisa	"
Thymus serphyllum	"