

Root Parasites of Southern Forests

LYTTON J. MUSSELMAN
and WILLIAM F. MANN, JR.

Southern
Forest
Experiment
Station

Summary

The five families of root parasites of the South are discussed relative to selection of hosts, ecology, and potential for damage to commercial species. An identification key to all genera of root parasites is included. Plants and flowers of 29 species are illustrated and their distribution in the South mapped.

Care should be taken not to disturb or damage plant species that have been classified as threatened or endangered by Federal or State Agencies.

Acknowledgments

We wish to thank Dr. W. H. Duncan, Dr. R. Teulings, and Mr. C. S. Harris for contributing pictures. Much credit for the successful growth of parasites in pot culture goes to Mr. C. M. Stangle. Dr. R. E. Eplee, and Dr. P. R. Atsatt reviewed drafts and made helpful suggestions. Finally, Harold Grelen contributed in many ways including substantial improvements in the identification key.

Disclaimer

If herbicides are handled, applied, or disposed of improperly, they may be injurious to humans, domestic animals, desirable plants, and pollinating insects, fish, or other wildlife, and may contaminate water supplies. Use herbicides only when needed and handle them with care. Follow the directions and heed all precautions on the container label.

Root Parasites of Southern Forests

Lytton J. Musselman

Assistant Professor, Department of Biological Sciences,
Old Dominion University, Norfolk, Va.

William F. Mann, Jr.

Chief Silviculturist, U.S. Department of Agriculture Forest Service
Southern Forest Experiment Station, Alexandria, La.

Published by the

**Southern Forest Experiment Station
Southeastern Area, State and Private Forestry
Forest Service, U.S. Department of Agriculture**

1978

Contents

Foreword	4
Identification Key to Root Parasites of the Southern United States	7
Parasite Descriptions	12
Range Maps	12
Species Identification	13
<hr/>	
• Olacaceae (Olax family)	13
<i>Schoepfia schreberi</i>	15
<i>Ximenia americana</i>	16
<hr/>	
• Santalaceae (Sandalwood family)	17
<i>Buckleya distichophylla</i>	19
<i>Comandra umbellata</i>	20
<i>Pyralaria pubera</i>	21
<hr/>	
• Scrophulariaceae (Figwort family)	23
Agalinis	26
<i>A. aphylla</i>	27
<i>A. divaricata</i>	28
<i>A. fasciculata</i>	29
<i>A. filicaulis</i>	31
<i>A. linifolia</i>	32
<i>A. purpurea</i>	33
<i>A. tenella</i>	34
<i>A. tenuifolia</i>	36

Aureolaria	37
<i>A. flava</i>	38
<i>A. grandiflora</i>	40
<i>A. laevigata</i>	42
<i>A. pedicularia</i>	43
<i>A. virginica</i>	46
<i>Buchnera americana</i>	48
<i>Dasistoma macrophylla</i>	49
<i>Macranthera flammea</i>	50
<i>Pedicularis canadensis</i>	52
<i>Schwalbea americana</i>	53
Seymeria	54
<i>Seymeria cassioides</i>	54
<i>S. pectinata</i>	56
<hr/>	
• Orobanchaceae (Broomrape family)	58
<i>Epifagus virginiana</i>	60
<i>Conopholis americana</i>	61
<i>Orobanche minor</i>	63
<hr/>	
• Krameriaceae (Rattany family)	65
<i>Krameria lanceolata</i>	67
<hr/>	
Literature Cited	68
Appendix I. Root parasites of the Southeast	70
Appendix II. Commercial tree species used in pot studies	72
Appendix III. Haustorial attachments by 19 root parasites on commercial tree species	73
Appendix IV. Glossary	74

Foreword

Root parasitic plants were virtually unknown to southern foresters until 1969 when it was reported that senna seymeria (*Seymeria cassioides*) was killing 3- and 4-year old slash pines (*Pinus elliottii*) in a large plantation in northwest Florida (Mann and others (1969)). Since then several publications have appeared on senna seymeria, but other root parasites that occur widely in the South have been ignored.

Perhaps the most familiar parasitic plants are the mistletoes that penetrate stems and branches of trees and shrubs. Root parasites act similarly below ground, forming specialized knob-like organs termed haustoria that attach to and penetrate the roots of neighboring plants to provide a pathway for the transfer of water and food from the host to the parasite. These parasites, part of a heterogenous group of flowering plants, depend on host plants for their subsistence in varying degrees. Several species, in fact, are capable of maturing and producing seed without attachment to a host. Some parasites attach to a wide variety of hosts, while others are much more specific.

Root parasites can be divided into two categories based on the presence or absence of chlorophyll. Holoparasites lack chlorophyll, cannot produce their own food, and are entirely dependent on host plants for food and water. Semiparasites (sometimes referred to as hemiparasites) contain chlorophyll and are able to produce all or part of their own food. The green appearance of these plants belies their parasitic nature, so they can easily be overlooked as pathogens of other plants. Root parasites are diverse in growth form and habitat and may be annuals, biennials, perennials, shrubs, vines, or trees. A list of all native root parasites of the South is given in Appendix I. An excellent volume by Kuijt (1969) deals with all parasitic angiosperms.

The efforts that led to this paper were begun because experience with senna seymeria indicated that intensive site preparation practices can lead to damage to commercial tree species by root parasites. The research, a cooperative effort of the U.S. Forest Service's Southern Forest Experiment Station and Old Dominion

University, was initiated to determine if southern root parasites are pathogens of commercial forest species. Research has consisted of surveys and of field and greenhouse studies. This booklet, based largely on the investigations, gives geographic range, host selection, habitats, and keys for identification of the most prevalent southern root parasites. We believe it will be a valuable tool for botanists and practicing foresters.

One of the objectives of the 2-year cooperative agreement was to determine if native root parasites would attach to trees of commercial importance in greenhouse cultures. Susceptible hosts could thereby be identified and necessary precautions taken in planting and maintaining the hosts in areas where the parasite was known to occur. Such studies are only indicative of the potential for a species to be a suitable host, and many other field conditions, such as the influence of microorganisms and exudates from non-host species, may influence these phenomena. We tried to collect seeds of every native parasite in the southern states. This proved difficult because of low or sporadic fruit set in some (*Pyrularia*, *Schoepfia*) and the difficulty of locating fertile plants of others (for example, *Nestronia* and *Agalinis heterophylla*). We were unable to grow some parasites because they have germination requirements we do not understand (*Conopholis* and *Epifagus*).

For pot studies, seeds were collected from various sites throughout the South. Where possible, more than one seed source per species was used to record any variation in vigor among populations of the same parasite. Immediately after collection, seeds were mailed to the Alexandria Forestry Center where they were stored in airtight jars at 3°C until used. They were then sown in pots with a mixture of peat moss and vermiculite containing a 1-year-old host plant. Species chosen for hosts (listed in Appendix II) are the most important species in the South for timber and fiber production.

Most seeds germinated readily, and within 6 months many plants had begun to flower or initiate flowering. Pots were broken down at this time or when the parasites bolted (initiated height growth). When the plants were ready for examination, soil was gently washed from the roots of host and parasite, which were then carefully examined for haustoria. All haustoria, regardless of size, were counted. Each haustorium represents an invasion of the vascular tissue of the host and thus the number of haustoria was considered an indication of parasite vigor and host damage. Numerous self-haustoria were produced in some parasites (*Aureolaria grandiflora*, *A. virginica*, *A. laevigata*, *A. flava*, *Macranthera flammea*, *Dasistoma macrophylla*, *Agalinis purpurea*, and *Ximena americana*). These are haustoria that attach to the roots of the

parasite itself. Self-haustoria are included in the totals, but we estimate that they amounted to less than 1 percent of the total number of haustoria.

We found little basis for assuming any sort of host specificity in most native parasites (Appendix III). In other words, most native root parasites, given the opportunity, attack almost any species of woody plant. This is particularly significant in light of the widespread distribution of many parasites. While it remains to be seen if infestations of these plants in commercial stands will cause damage of the magnitude of that caused by *Senna Seymeria* (Mann and others 1969), foresters should be aware of the pathogenic potential of these plants and which hosts they will attack.

Little is known about the control of southern root parasites. Succulent annuals and perennials can undoubtedly be controlled with 0.5 lb. ai of 2,4,5-T per acre in a water carrier and applied in a total volume of 5 pounds per acre. Woody species like *Ximenia* will probably require 2 pounds ai of 2,4,5-T per acre, also applied in 5 gallons of water. However, their resistance to the various herbicides has not been determined, so some small-scale trials would be needed to guide operational programs.

Fire does not seem like a good alternative for control, even in pine plantations, because work should be started before the pines are fire hardy. Then, too, annual species are often dead before weather is suitable for prescribed burning, and the seeds for a new crop have already been shed.

In the past 10 years several compounds that stimulate germination in the root parasites *Striga* and *Orobanche* have been discovered and synthesized. One of these is strigol, isolated from the roots of corn and other plants. Strigol has been found to be a potent germination stimulant for witchweed (Cook and others 1972). Recently Johnson and others (1976) described synthetic germination stimulants which caused a high rate of germination in both *Striga* and *Orobanche* even at very low concentrations. We ran some preliminary tests using both compounds on seeds of most species of root parasites in the South. Most seeds of these species do not respond to these stimulants; therefore control of native root parasites with these compounds does not seem feasible. We did not, however, test the effect of ethylene (a germination stimulant used widely to control witchweed) on parasites discussed in this paper.



Identification Key to Root Parasites of the Southern United States

The purpose of this key is to provide a simple means of identifying any root parasite growing in the South. Technical terms have been kept to a minimum to allow anyone without botanical training to use the key, but a short glossary is provided. Most genera included in the key are illustrated. While every effort has been made to provide for the identification of plants in vegetative condition, to determine many species accurately, flowers are needed.

The key employs dichotomies or branches to lead to the correct identification of a plant. Of two choices in each couplet, only one will apply to the plant being identified. For example, if the plant contains chlorophyll, the second line of couplet 1 is true. The user is then directed to couplet 6. If the plant is woody, the first line of couplet 6 will then lead to couplet 7 and so on until the plant is identified. If identification proves exceptionally difficult or if determination is needed immediately but all parts of the parasite are not yet developed, it may be possible to get assistance by contacting the curator of the herbarium at a state university.

1. Plants without chlorophyll; brown or yellow; leaves reduced to scales 2.
1. Plants with chlorophyll; leaves normal 6.

2. Main stem uniformly thick; fruit fleshy; seeds very hard, shiny; plant perennial *Conopholis americana* (p. 61).
2. Main stem thickest at base, tapering to top; fruit dry; seeds dust-like, dull; plants annual 3.

3. Flowers in late fall; found only with beech; underground portion of plants swollen, with hook-like outgrowths *Epifagus virginiana* (p. 60).
3. Flowers in spring; found with various hosts; lacks hook-like outgrowths on underground portions 4, *Orobanche* spp.

4. Stem whitish; flowers solitary on long stalk . . . *Orobanche uniflora*.
4. Stem yellow-brown; flowers numerous, crowded on main stem 5.

5. Calyx with five distinct lobes; mainly western *Orobanche ludoviciana*.
5. Calyx with four lobes; rare species of east coast *Orobanche minor* (p. 63).

6. Trees or shrubs 7.
6. Herbs, not woody (except at base) 11.

7. Thorns present (widespread shrub of Florida) *Ximenia americana* (p. 16).
7. Thorns absent 8.

8. Leaves alternate 9.
8. Leaves opposite 10.

9. Leaves shiny on upper surface; evergreen, small tree of southern Florida; flowers small, red *Schoepfia schreberi* (p. 15).
9. Leaves dull on upper surface, deciduous shrub of the Appalachians; flowers small, greenish, inconspicuous *Pyrularia pubera* (p. 21).
-
10. Bark of young twigs green; rare shrub of the southern Appalachians *Buckleya distichophylla* (p. 19).
10. Bark of young twigs reddish brown; uncommon shrub of the Piedmont *Nestronia umbellula*.
-
11. Leaves alternate 12.
11. Leaves opposite (though upper leaves associated with flowers may be alternate) 16.
-
12. Leaves lobed 15.
12. Leaves not lobed 13.
-
13. Broadest leaves less than 2 cm wide 14.
13. Broadest (basal) leaves more than 2 cm wide *Schwalbea americana* (p. 53).
-
14. Leaves hairy; main stems prostrate on ground; fruit spiny *Krameria lanceolata* (p. 67).
14. Leaves not hairy; main stems erect; fruit not spiny *Comandra umbellata* (p. 20).
-
15. Stem leaves with 5 or more lobes; corolla yellow to purplish; seeds egg-shaped; widespread but most common in mountains *Pedicularis canadensis* (p. 52).
15. Stem leaves with 5 lobes or less; bracts scarlet (rarely yellow); corolla yellow; seeds angular; northern *Castilleja coccinea*.
-

- 16.** Some leaves (at least the lowermost) lobed or dissected 20.
- 16.** Leaves not lobed (a few teeth may be present) 17.
-
- 17.** Broadest (basal) leaves scale-like, absent, or never wider than 2 cm 19.
- 17.** Broadest (basal) leaves always wider than 2 cm 18.
-
- 18.** Leaves and stem hairy, rough to the touch; flowers blue to red-purple; seeds numerous, shiny, black *Buchnera americana* (p. 48).
- 18.** Leaves and stem not hairy, smooth to the touch; flowers bright yellow; seeds numerous, dull, brown *Aureolaria laevigata* (p. 42).
-
- 19.** Flowers white with a spot of yellow on the upper lip; fruit with one to four smooth seeds; plants 0.5 m tall or less *Melampyrum lineare*.
- 19.** Flowers pink or purple (one or two plants in a large population may have white flowers), fruit with numerous honey-combed seeds; plants 0.5 m tall or more . . . *Agalinis* spp. (p. 26).
-
- 20.** Plants perennial (buds present on rootstock, last season's fruiting stalks attached to living roots) 21.
- 20.** Plants annual or biennial (although often very large) 23.
-
- 21.** Plants with dense short, soft hairs . . . *Aureolaria virginica* (p. 46).
- 21.** Plants without dense hairs 22.
-
- 22.** Plants to 2.0 m tall, sparsely branched, upper leaves not lobed; widespread *Aureolaria flava* (p. 38).
- 22.** Plants to 1.5 m tall, much branched; upper leaves lobed; common in Ozarks *Aureolaria grandiflora* (p. 40).
-

- 23.** Flowers pink; upper stem leaves with two prominent lobes at base (very rare plant in the South) *Tomanthera auriculata*.
- 23.** Flowers not pink; upper stem leaves usually lacking two prominent lobes at base 24.
-
- 24.** Plants densely covered with sticky hairs 25.
- 24.** Plants without sticky hairs 26.
-
- 25.** Ultimate sections of leaves thread-like, less than 1 mm wide; flowers less than 2 cm long *Seymeria cassioides* (p. 54).
- 25.** Ultimate sections of leaves not thread-like, more than 1 mm wide; flowers more than 2 cm long *Aureolaria pedicularia* (p. 43).
-
- 26.** Basal leaves with more than 8 main lobes (rare) *Pedicularis lanceolata*.
- 26.** Basal leaves with less than 8 main lobes 27.
-
- 27.** Basal leaves 10 cm wide or more *Dasistoma macrophylla* (p. 49).
- 27.** Basal leaves 5 cm wide or less 28.
-
- 28.** Plants more than 1.5 m tall; basal stem leaves more than 6.0 cm long; flowers orange; Gulf Coastal Plain *Macranthera flammea* (p. 50).
- 28.** Plants less than 1.5 m tall; stem leaves less than 4.0 cm long; flowers yellow; more widespread *Seymeria pectinata* (p. 56).
-

Parasite Descriptions

An attempt was made to photograph each species in its natural habitat, but in some cases we had to use plants from our pot studies to obtain an adequate picture of a typical parasite. Descriptions of plants are based almost entirely on our field observations. Where it was not possible to examine a plant for a particular feature such as a flower or fruit, we have based descriptions on herbarium material and botany manuals. The descriptions are purposely brief. Characters distinctive for that species are emphasized. Short discussions of families and larger genera are also provided.

Range Maps

Maps included indicate the approximate range of the parasites; that is, a broad area in which the plant may or may not be found. In some cases such as *Buckleya distichophylla* and *Orobanche minor*, where species are extremely rare or local, the counties have been indicated by dots.

These ranges have been taken from literature (Radford and others 1968, Pennell 1935, DeFillips 1968), herbarium data and field work conducted over the past 10 years.



Olacaceae
(Olax Family)

Olacaceae

(Olap family)

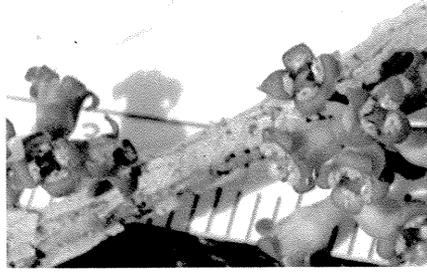
This family of woody plants is mostly tropical and is represented in North America by two species which occur only in Florida. Both have simple alternate leaves and may flower at any time of the year.

Flowers

Schoepfia schreberi/Whitewood

Whitewood is a small tree that occurs in hardwood hammocks in southern Florida and in the West Indies. Older portions of the trunk may be white, hence the common name.

The host selection of whitewood is poorly known but appears to be broad including poison ivy, live oak, and Virginia creeper.



Schoepfia schreberi



TREE: up to 4 m tall. **STEMS:** older portions often whitish. **LEAVES:** alternate, 5.5 cm long, 2.7 cm wide, tapering to tip. **FLOWERS:** very small, 2 mm wide bright red, borne in small clusters near the tips of younger branches. **FRUIT:** about the size of a small olive with one seed.

***Ximenia americana*/Hog plum,
Tallowwood**

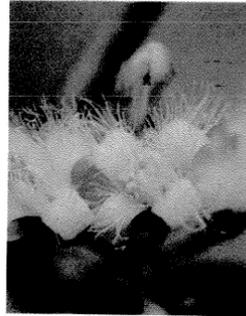
Unlike *Schoepfia*, *Ximenia* is a shrub and is widespread throughout central and southern Florida. It is particularly abundant in the sand pine scrub area, where it forms a conspicuous part of the vegetation.

Ximenia is seldom over 3 m tall. The entire plant is covered with short, sharp thorns. The leaves have a definite yellowish cast, are somewhat succulent and rather brittle. The small white flowers have a pleasant fragrance and the fruit, about the size of a small plum, has a sweet, juicy pulp.

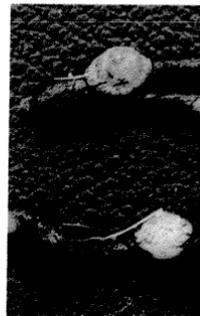
The haustoria of *Ximenia*, often more than 3 cm wide, are the largest of any root parasite in North America. They apparently live for many seasons, which accounts for their size. Large slit-like openings, which are scars caused by *Ximenia* haustoria, are frequently found on the roots of neighboring plants. A single parasite may inflict serious damage by forming hundreds of haustoria on host roots in a single season.



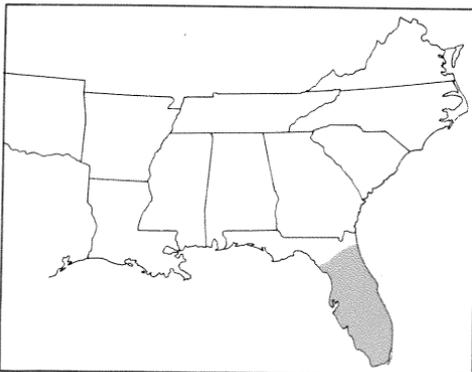
Ximenia americana with fruit



Flowers



Haustroria



SHRUB: many branches. **STEMS:** up to 3 m; armed with short, sharp thorns. **LEAVES:** up to 4 cm long, 2.2 cm wide, broadest at the middle. **FLOWER:** small, 4 mm wide; petals white, hairy; fragrant. **FRUIT:** 4 cm long, 2 cm wide, one seed.



Santalaceae
(Sandalwood Family)

Santalaceae **(Sandalwood family)**

This is a large tropical family which includes the sandalwood tree (*Santalum*) of commerce. In North America it is represented by four genera: *Buckleya*, *Nestronia*, *Pyrularia*, and *Comandra*. *Comandra* is a perennial rhizomatous herb. The other genera are shrubs or small trees. Each genus has only one species.

The habitats of the three woody species are somewhat different. *Nestronia* grows in dry pine woods in the Piedmont where we have seen it form abundant, large haustoria on shortleaf and loblolly pine. *Buckleya* is known from only eight locations in the southern Appalachians. Both *Buckleya* and *Nestronia* have small, opposite leaves. *Pyrularia*, also found in the southern Appalachians, is common and often abundant. It has alternate leaves. *Comandra* also has alternate leaves and is one of the more widely distributed vascular plants in North America.

The flowers of the three shrubs are small, greenish, and inconspicuous. *Buckleya*, *Nestronia*, and *Pyrularia* are dioecious. *Comandra*, on the other hand, has attractive, small, perfect, white flowers. The fruits of all species are fleshy and contain a single seed. Haustoria in this family resemble those of *Ximenia*.



***Buckleya distichophylla*/
Buckleya, piratebush**

Buckleya is familiar to most botanists. Despite its well documented rarity, there is no published information on the culture of this shrub. It has been prepared for the threatened species list.

Buckleya grows on steep rocky slopes always in association with hemlock (*Tsuga*). This has led to speculation that it is restricted in its host preference to this genus of gymnosperms. However, *Buckleya* will form haustoria on a variety of hosts both in nature and culture. At the University Botanic Garden in Copenhagen, it thrives on the roots of a yew (*Taxus*). In our studies, it parasitized the roots of pines, cypress, and several hardwoods. We were able to achieve about 60 percent germination of the seeds after cold treatment.

Buckleya distichophylla with fruit



SHRUB: many stems arising from large white rhizomes. **STEMS:** up to 3.5 m tall, lower portions of stem white. **LEAVES:** up to 6 cm long, 1.5 cm wide, tapering to a narrow point. The leaves are so arranged as to give the impression that the plant has large, compound leaves. **FLOWERS:** unisexual, green, inconspicuous, borne at the tips of lateral twigs in early spring. The female flowers have prominent bracts which persist on the fruit. **FRUIT:** up to 4 cm long, 1.5 cm wide, greenish yellow with white protuberances.

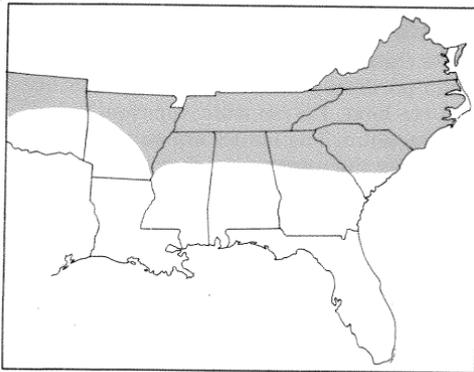
***Comandra umbellata*/Comandra,
bastard toadflax**

Although this is the only herbaceous member of this family in North America, it has a wide distribution. It prefers open, sunny, often dry areas such as prairies, roadsides, and openings in dry woods. *Comandra* has a remarkably broad host range of over 200 species,

including ferns, gymnosperms, and flowering plants. The host range and life history are discussed by Piehl (1965). The colorful common name, bastard toadflax, comes from the resemblance of this species to the toadflax (*Linaria*). The considerable variation among plants within the species has led some botanists to recognize several species.



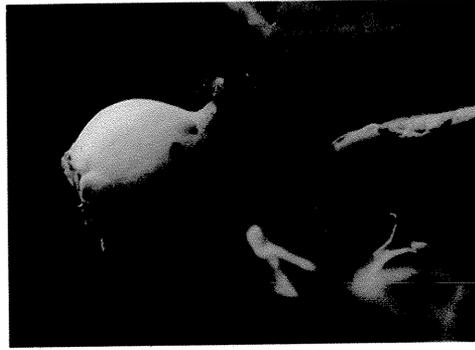
*Comandra
umbellata*



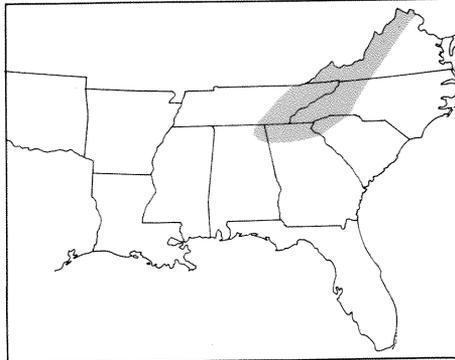
PERENNIAL: from deep rhizomes.
STEMS: up to 0.5 m tall, sparsely branched. **LEAVES:** up to 4.5 cm long, 1 cm wide, alternate, often densely crowded on the stems. **FLOWERS:** with five white sepals, borne in spring, 1 cm across. **FRUIT:** somewhat fleshy, one seed.

***Pyrularia pubera*/Buffalo nut,
oilnut**

Pyrularia is a very common shrub that may be found in almost any drier site in the southern Appalachians. It is often vigorous in forests disturbed by logging, fire, or wind and ice damage. The fruits are not usually abundant and are reported to be very poisonous.



SHRUB: from thick rhizomes. **STEMS:** up to 2 m tall, sparsely branched with gray-brown bark. **LEAVES:** clustered on short shoots, up to 10 cm long, 3.5 cm wide, margins entire to wavy, somewhat fleshy and easily broken when fresh. **FLOWERS:** small, unisexual, green, borne in drooping clusters. **FRUITS:** 1.5 cm in diameter, round, with a crown-like ridge on the bottom, one seed.





Scrophulariaceae
(Figwort Family)

Scrophulariaceae

(Figwort family)

This is the largest and most widespread family of root parasites in the southeastern United States, with 11 genera and about 30 species. More than half of these species are in the genus *Agalinis*, a group that is taxonomically difficult. Some parasites such as *Agalinis purpurea* and *Aureolaria pedicularia* are found throughout the South and often in very large populations. Other species such as *Macranthera flamma* and *Agalinis divaricata* are restricted in their range but often numerous where found. Still others are rare, as is *Schwalbea americana*, which is known from only three small populations.

The Scrophulariaceae is a natural group. It is easy to distinguish plants of this family. All southern species are herbaceous. The leaves are always simple (although often dissected) and opposite, except in *Pedicularis canadensis*, *Castilleja coccinea*, and *Schwalbea americana*. The

flowers have five petals, five sepals, four stamens, and one ovary. For convenience, two parts of the corolla may be distinguished, the corolla tube, and the corolla lobes. The shape and size of the tube and the relative sizes of the lobes are useful in distinguishing species. Two general types of flowers are present in parasitic figworts. The first is found in *Aureolaria* where the corolla lobes are at right angles to the tube and the mouth of the tube is open, like a trumpet. In the second corolla type, the five lobes are not spreading and the tube does not appear open. Such corollas are found in *Schwalbea*, *Pedicularis*, *Melampyrum*, *Castilleja*, and *Macranthera*.

The fruit of all of the parasitic figworts is a capsule. Capsule structure is similar throughout the group.

Pedicularis, *Melampyrum*, *Castilleja*, *Dasistoma*, and *Schwalbea* all flower in the spring or early summer. All other species flower in the summer or fall. The seeds of all species are small but there is considerable variation in seed size among the various genera. *Melampyrum*

and *Pedicularis* have few seeds (10 or less) per capsule, while other genera have hundreds. Larger seeds are apparently distributed by ants, smaller seeds by wind or water.

Our tests have shown that most species lack specialized germination requirements. As expected, species of more northerly distribution or that grow at higher elevations in the mountains require a period of cold treatment to break dormancy.

The root systems of these plants are fibrous and often wiry. Roots are usually white or yellow and shallow in the soil. Haustoria may be borne at any point on the root system. Size of haustoria varies greatly between genera but tends to be uniform among species in the same genus. Largest haustoria, which may be as much as 10 mm in diameter, are those of *Aureolaria*, *Seymeria*, *Dasistoma*, and *Macranthera*. Haustoria of the remaining genera tend to be no larger than 1 mm. All haustoria have a yellowish substance at the host-parasite interface.

For many years, it was thought that certain genera were restricted to specific hosts. It has often been recorded that *Aureolaria pedicularia* restricted its host preference to members of the black oak group. Our tests over a 2-year period show clearly that this parasite will attach to almost any host. For example, *Aureolaria pedicularia* grew vigorously when parasitizing the roots of water tupelo. Other species will also grow on a variety of hosts. Thus most of these plants can be considered to be potential parasites of commercial species.

Agalinis/Gerardia

This is the largest group of root parasites in the South. As many as 30 species are recognized by some authors (Pennell 1935). The taxonomy of the group is confused and needs much work. Likewise, the nomenclature of the genus is tangled and has a complex history. The name *Gerardia* was formerly used not only for the plants now included in *Agalinis*, but also those now included in the genera *Aureolaria* and *Tomanthera*. *Gerardia* has been rejected under the rules of botanical nomenclature and should not be used at all. However, many manuals and keys still use it. Unfortunately, most species do not have widely accepted common names, even though *Gerardia* is often used as a common name for the genus as a whole.

The genus is characterized by showy, often large, pink to purple (rarely white) flowers that appear in fall and persist for only one day. Flowers open two at a time per flowering branch and are usually necessary for critical identification of species. For example, the throat (interior of the tube) of the flower may have two yellow lines that guide insects to the pollen-bearing stamens (commonly called guide-lines), the presence or absence of which distinguishes species. The size and shape of the sepals on the capsules may also be of taxonomic value. *Agalinis* seeds are brown to black and somewhat wedge shaped, with a honeycombed surface. Vegetatively, species of *Agalinis* vary in overall size and in leaf structure. Leaves are generally opposite and always linear in shape. In *A. filicaulis*

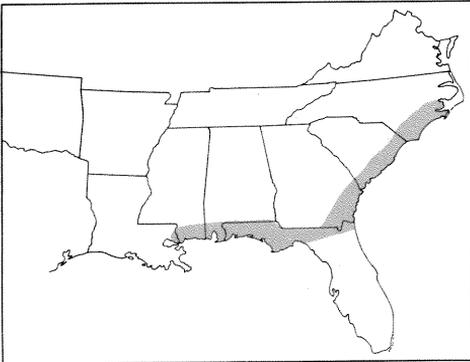
the leaves are reduced to very small structures, and in *A. aphylla* leaves are entirely lacking. Haustorial structure is fairly uniform throughout the genus. *Agalinis linifolia* is the only perennial; all other species are annuals.

All gerardias typically grow in open, sunny areas in a variety of habitats. For example, *A. aphylla* is almost entirely restricted to pine savannahs. *Agalinis purpurea* could be considered weedy, because it often grows along roads and on other disturbed sites. The genus reaches its greatest diversity on the Atlantic and Gulf Coastal Plains, although three species, *A. fasciculata*, *A. purpurea*, and *A. tenuifolia*, are found throughout the South.

The parasitic behavior of these plants has been known for a long time. Our pot culture work indicates that *Agalinis* has the broadest host range of any root parasite in the South. All species that we investigated attached to a variety of pines and hardwoods. All host species were parasitized by at least one of the eight species of *Agalinis*. At present it appears that there is no definite host preference by any species. In some cases over 2,000 haustoria were formed in 6 months by one parasitic plant on a single 1-year-old host. Damage could be severe in a young plantation where bare soil, full sun, and ready access to hosts could foster attacks by several parasites. The pathogenic potential of this genus, especially of *A. setacea*, *A. tenuifolia*, *A. purpurea*, and *A. fasciculata*, is great because of their tolerance for a variety of hosts and their widespread distribution.



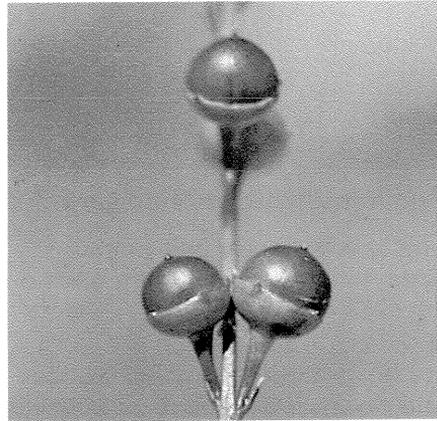
Agalinis aphylla showing flower and stalk.



Agalinis aphylla/Leafless gerardia

Leafless gerardia is one of the rare species of *Agalinis*. Its habitat is restricted to pine savannas of the Atlantic and Gulf Coastal Plains where large populations are noticeable in late fall with their large, showy corollas borne on wiry, leafless stems. It is abundant only in recently burned areas.

Little is known about the host selection of the leafless gerardia, as its parasitism was only recently documented.



Capsules showing calyx.

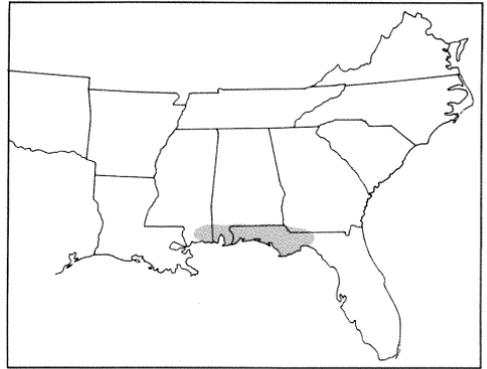
ANNUAL. STEMS: up to 1 m tall, seldom branched below the top half, ridges present. **LEAVES:** absent, represented by small, appressed scales. **FLOWERS:** up to 2 cm long; bottom lobes are not at right angles to tube; wooly within the throat.



***Agalinis divaricata*/Gulf gerardia**

Agalinis divaricata

This species grows only in low, open, longleaf pine communities on the Gulf Coastal Plain of Alabama and Florida. It is recognized by its conspicuously flattened corollas and downward pointed lower leaves. Like *A. filicaulis*, nothing is known concerning its host range.



ANNUAL. STEMS: up to 0.5 m tall, regularly branched. **LEAVES:** up to 1.7 cm long, 1 cm wide, larger leaves pointing down. **FLOWERS:** 1.5 cm long, the entire corolla strongly flattened in one plane and lacking guidelines, the upper lobes arched forward over the mouth of the corolla.

Flower showing flattened corolla.

***Agalinis fasciculata*/Fascicled gerardia, beach gerardia**

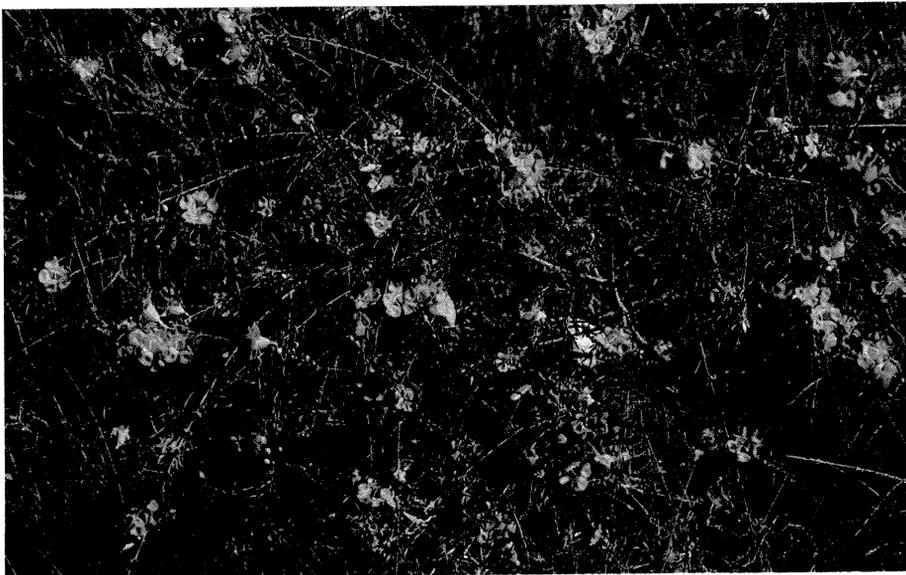
This is one of the tallest species in the genus. It has a wide geographic range, but is most common on the Coastal Plain. It is one of the more weedy species of *Agalinis* and often forms large populations of a hundred or more plants. The big, light-purple flowers are attractive. The common name is derived from the

bundles of leaves (actually short, leafy branches) found at the base of the larger leaves on the stems. The host selection of *A. fasciculata* appears to be broad and without preference for any particular species. The haustoria are among the largest in the genus.

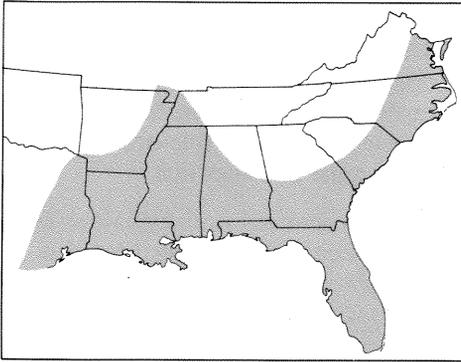
More herbarium and experimental work is needed to determine the taxonomic status of *A. fasciculata*. The taxonomic differences between it, *A. purpurea*, and *A. virgata* are not always clear. We treat *A. virgata* and *A. fasciculata* as a single species, *A. fasciculata*. These differences may be a matter of descriptive semantics. Several botanists recognize plants generally resembling *A. fasciculata* but with stiffly erect stems and fewer hairs on the stem and leaves than *A. virgata*. *Agalinis purpurea* may be distinct enough to warrant specific status, although it often intergrades morphologically with *A. fasciculata*.



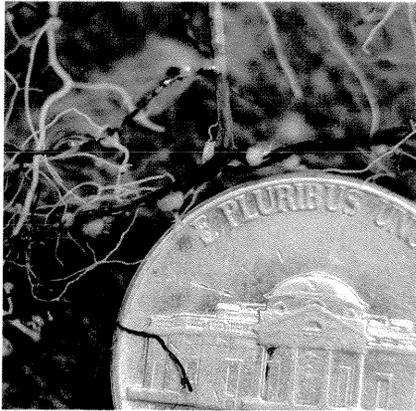
Flower



A large, much branched specimen of *Agalinis fasciculata*.



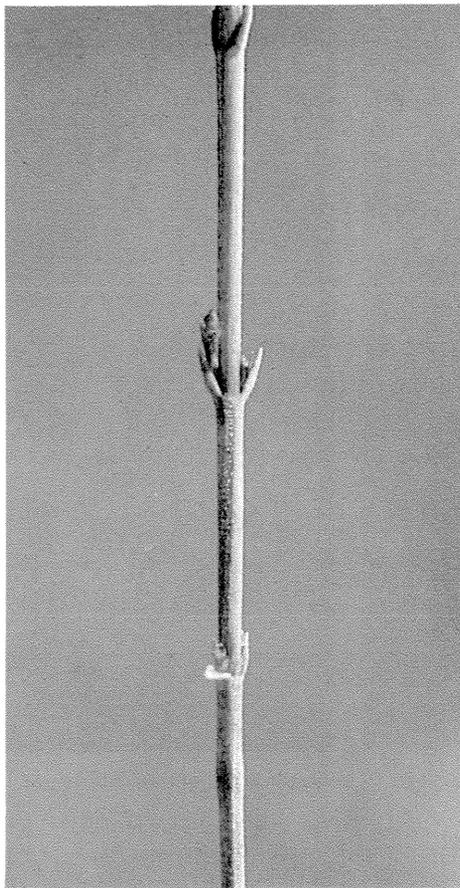
ANNUAL. STEM: up to 2 m tall, younger (green) portions of stem scabrous; seldom branched at base; most branches arise from upper portion of stems. **LEAVES:** up to 3 cm long, 2 mm wide; younger leaves somewhat hairy. **FLOWERS:** 2 cm wide, lobes approximately equal, at right angles to the corolla tube, throat with two yellow lines and conspicuous dark purple spots.



Haustoria.



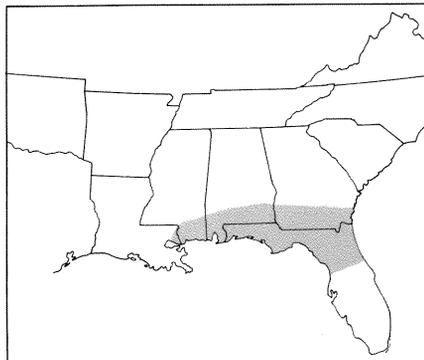
"Fascicles" of leaves



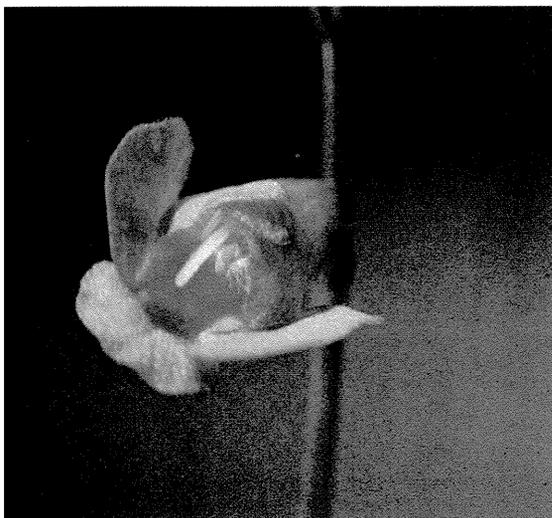
Agalinis filicaulis stem showing small, slightly divergent leaves.

Agalinis filicaulis/Slender-stemmed gerardia

Both the leafless gerardia and this species grow in savannas on the Gulf Coastal Plain and may appear similar at first sight. But *Agalinis filicaulis* is much more branched, and has less crowded flower stalks than *A. aphylla*. The two are readily distinguished from each other by floral characters. Unfortunately, little is known about this plant.



ANNUAL. STEMS: up to 0.3 m tall, very slender, irregularly branched, each branch terminated by two or three flowers. **LEAVES:** very small, reduced to bracts; which, unlike *A. aphylla*, are slightly divergent from the stem. **FLOWERS:** small, 1 cm at longest measurement, the two lateral lobes of the corolla parallel with the tube, the upper lobe reflexed over the mouth of the corolla, no yellow lines in throat.

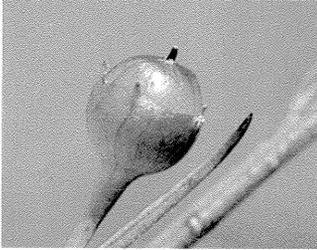


Flower showing prominent lateral corolla lobes.

Mottled stem with leaves.



Corolla.



Immature capsule with calyx.

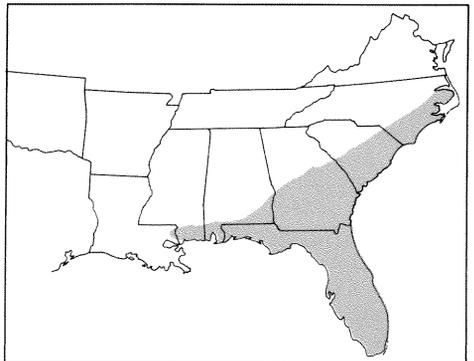
Agalinis linifolia on Blackgum.

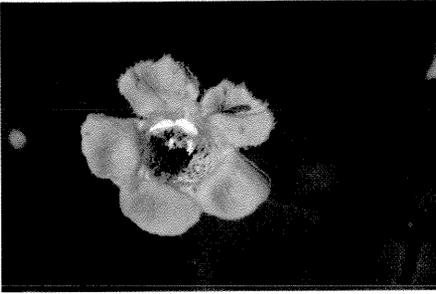
***Agalinis linifolia*/Perennial gerardia**

This parasite is restricted to moist sites on the Atlantic and Gulf Coastal Plains. It is most commonly found at the margins of cypress pools, in shallow ditches, and in depressions in pine savannas.

Data on hosts are preliminary but perennial gerardia appears to favor species such as baldcypress that grow in moist areas.

PERENNIAL: rhizome long and narrow. **STEM:** up to 10 cm tall, fleshy, mottled with purple. **LEAVES:** up to 4 cm long, 2 mm wide, fleshy. **FLOWERS:** have five lobes of approximately equal size and shape, at right angles to the corolla tube, no yellow guidelines in the corolla, purple dots abundant.

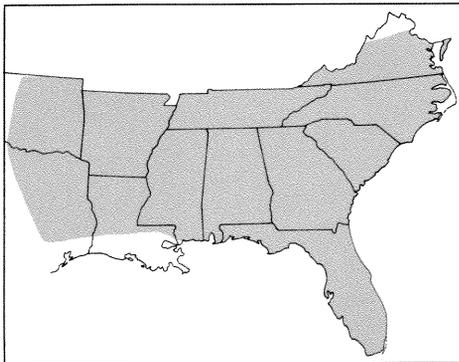




***Agalinis purpurea*/
Purple gerardia**

Agalinis purpurea is one of the most common gerardias in the South, and is found in large numbers along roads and in other open, disturbed sites. Superficially, it may be confused with *A. fasciculata*, particularly in flower structure. However, *A. purpurea* has broader leaves, poorly developed fascicles (if any), and typically is well branched.

In culture, individuals of the purple gerardia will flower and set seed without attachment to any host. Such plants are usually smaller than plants with hosts. This autotrophic behavior has not been reported from nature.



ANNUAL. STEMS: up to 1 m tall, usually much branched, older branches have distinct ridges. **LEAVES:** up to 3.5 cm long, 2 mm wide, scabrous. **FLOWERS:**



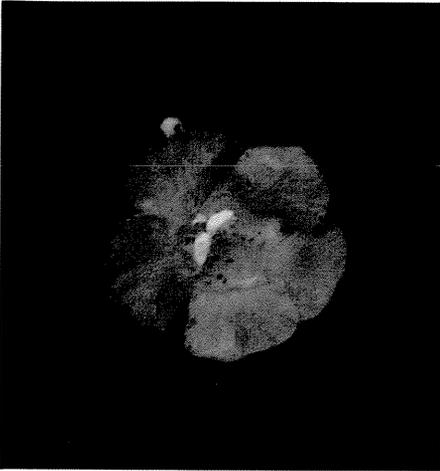
Agalinis purpurea on Green ash.

The host range of *A. purpurea* is one of the largest in the genus. In our pot studies, *A. purpurea* parasitized all 19 species (see Appendix III). Eight hosts had over 200 haustoria.



***Agalinis tenella*/Slenderleaf
gerardia**

Corolla



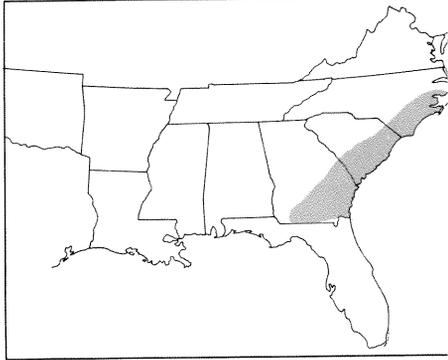
This species favors weedy habitats along the Atlantic Coastal Plain. It is often abundant in dry pinelands and on roadbanks. *Agalinis tenella* is one of three species that may be easily confused. *Agalinis setacea* is another Atlantic Coastal Plain species that prefers disturbed habitats. It has a range extending further north and west than *A. tenella*. The floral and vegetative features of these two species are very much alike. Both have bristle-like leaves and two prominent yellow guidelines in the corolla. But *A. setacea* is a larger plant overall, and has corollas twice as large as *A. tenella*.



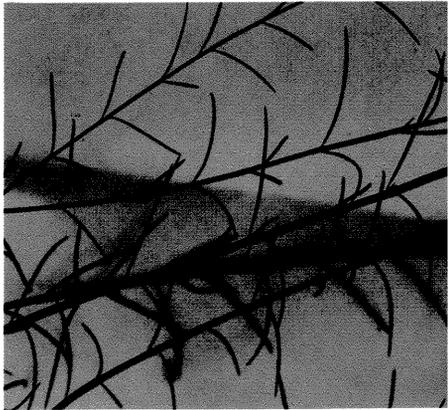
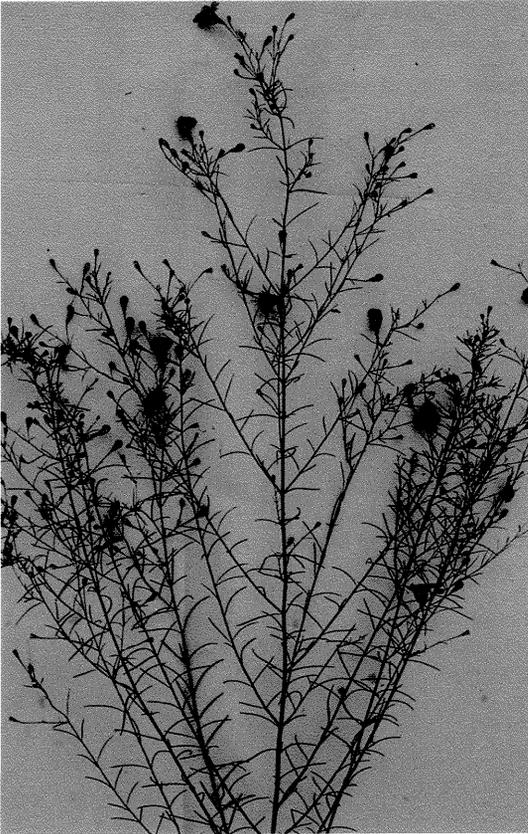
Group of *Agalinis tenella*

The third species, *A. obtusifolia*, grows in pine savannas, but may also be found in disturbed habitats. It is a small plant, like *A. tenella*, and seldom reaches over 60 cm in height. Its leaves are broad (up to 1.5 mm wide) relative to the size of the plant. *Agalinis obtusifolia* is distinguished from *A. tenella* by a sparse branching pattern, ridged stem, and lack of yellow guidelines in the corolla. A peculiar feature of *A. obtusifolia* is the occasional production of flowers directly on the lower stems of older plants.

We have experimental data on host selection for *A. setacea* only (Appendix III).



ANNUAL. STEMS: up to 0.5 m tall, profusely branched. **LEAVES:** up to 3 cm long, very narrow and bristle-like. **FLOWERS:** 1.2 cm wide, 1.5 cm long; lobes of approximately equal size and shape, at right angles to the corolla tube; upper throat of the tube hairy; throat has two yellow lines and numerous dark purple spots.



Leaves

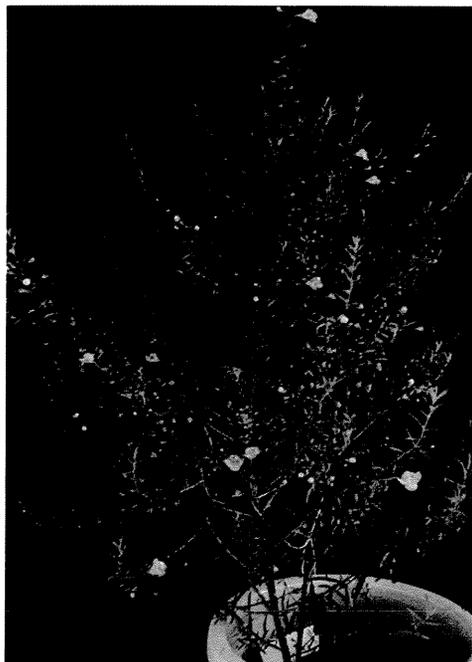
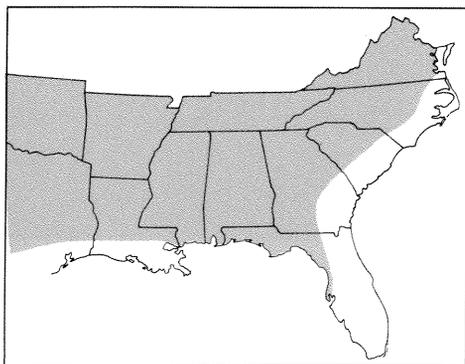
Agalinis tenella

Agalinis tenuifolia/ Slender gerardia

Agalinis filicaulis, *A. tenuifolia*, and *A. divaricata* have distinctive flowers in which the upper lobes of the corolla are arched forward, partially closing the throat. Of these, *A. tenuifolia* is the most widely distributed, being found throughout eastern North America. It is usually a much-branched plant, and quite variable in size. *Agalinis tenuifolia* and *A. setacea* may appear similar in growth form, but *A. setacea* has very narrow leaves and a conspicuously hairy corolla throat.

Slender gerardia commonly grows in disturbed sites, including clearcut areas. Large populations may also be found growing at the margins of ditches and in other wet or moist habitats.

This species is a vigorous parasite. It formed haustoria on all 19 commercial species (Appendix III). Of these, three plants formed over 1,000 haustoria on their hosts. No clear host preference was shown, although hardwood species supported more parasitic attachments than pines.



Agalinis tenuifolia on sycamore.



Corolla showing upper two lobes shorter than the remaining three.

ANNUAL. STEMS: up to 1 m tall, profusely branched. **LEAVES:** up to 1.5 mm wide, largest leaves at right angles to stem. **FLOWERS:** corolla lobes not equal, the lower three at right angles to the tube, the upper arched forward partially covering the stamens, yellow lines in throat.

***Aureolaria*/False foxglove**

The false foxgloves are some of the most widely distributed root parasites in the South. The common name derives from the resemblance of the flower shape to that of the common garden foxglove (genus *Digitalis*). All species have large showy flowers similar in size and shape, which open early in the morning and usually drop from the plant by late afternoon. Like *Agalinis*, the flowers are borne with only two open per flowering branch at one time. Except for occasional populations of *Aureolaria pedicularia*, all species flower from late summer to mid-fall. The leaves are opposite and some are deeply lobed in all species but *A. laevigata*. False foxgloves prefer open, sunny areas. The haustoria of these plants are large and numerous, and often form self-attachments.

Corolla



***Aureolaria flava*/Large false foxglove**

This is the tallest of all members of the genus and the most widespread of the perennial species. It usually flowers in mid-autumn throughout most of its range, but may occasionally flower in late October in parts of Florida. Large false foxglove grows in various open, dry habitat including disturbed sites. Large populations are often found at the margins of oak stands. In Georgia and Florida it is sometimes found

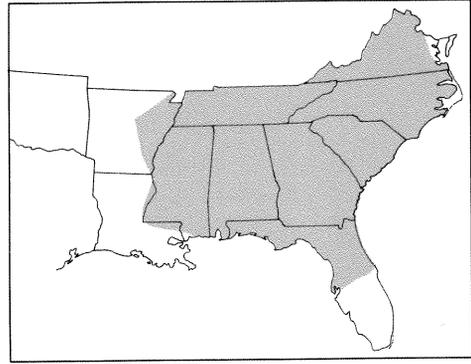
Aureolaria flava on Shumard oak.



in open areas in scrub oak-palmetto stands.

The haustoria of *A. flava* are up to 10 mm across (the largest in the Scrophulariaceae), and will readily kill young roots and stunt older roots. Previous researchers have considered this parasite to be restricted almost exclusively to the white oak group (Pennell 1935). In our study, *A. flava* formed large haustoria on 18 of 19 commercial species (Appendix III).

PERENNIAL. STEMS: 1 to 2.5 m tall, sparsely branched, glabrous, hollow.
LEAVES: basal, 7 to 15 cm long, 1.5 to 5 cm wide, lower deeply lobed, the upper (including the reduced leaves of the inflorescence) entire.



Silhouettes of various leaf forms.

Left—Basal leaf

Right—Reduced leaves associated with flowers



Larger plants of *Aureolaria grandiflora* have spreading branches.

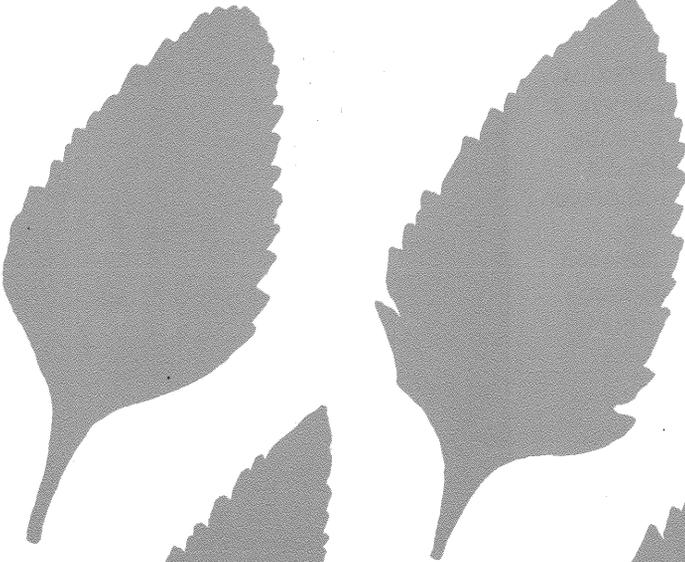
***Aureolaria grandiflora*/Showy false foxglove, big-leaf oakleech**

Aureolaria grandiflora is common in the Ozark and Ouachita Mountains. The selection of hosts, like those of all perennial species, was once thought to be very narrow and restricted to white oaks. However, our work indicates that *A. grandiflora* will parasitize many woody and herbaceous species. It grows in open oak woods on rocky or sandy soils.



Flower

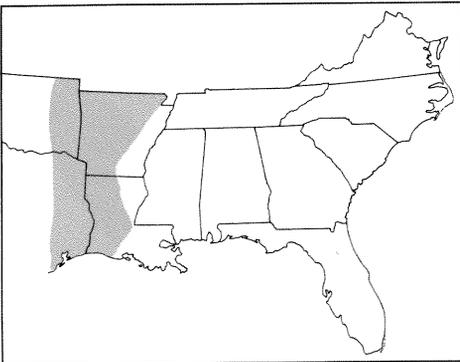
Basal Leaves



Silhouettes of various leaf forms.



Upper Leaves

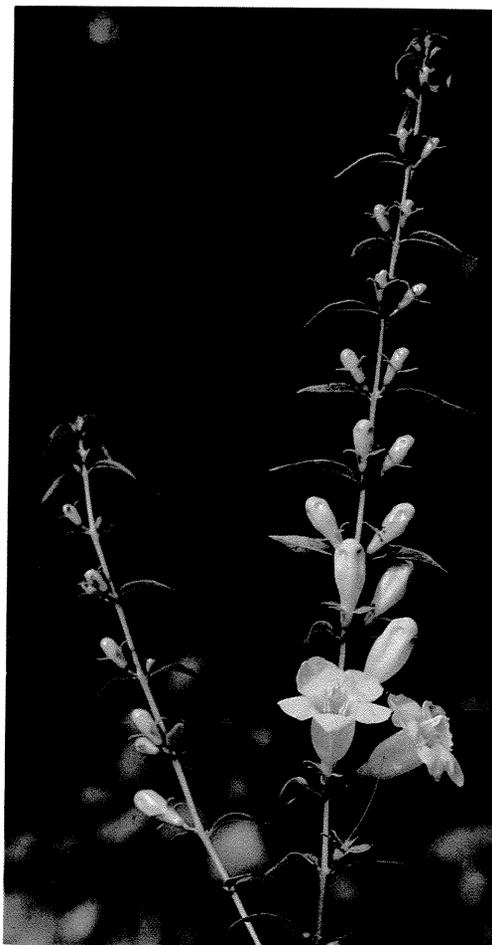
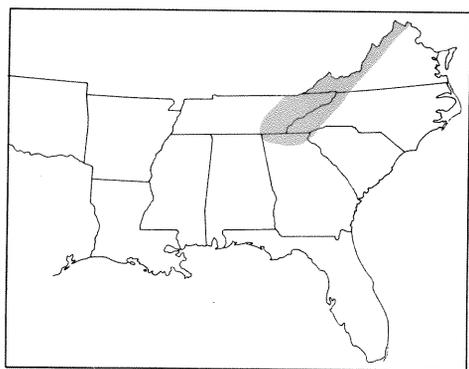


PERENNIAL. STEMS: 1 to 2 m tall, profusely branched, lateral branches often as long as the main stem, hollow. **LEAVES:** basal, 5 to 12 cm long, 1.5 to 4 cm wide, with scattered stiff hairs; those of westernmost plants (Ouachita Mountains) tend to be deeply lobed; those of more easterly plants are not; upper leaves of all plants have prominent lobes.

Aureolaria laevigata/Smooth false foxglove

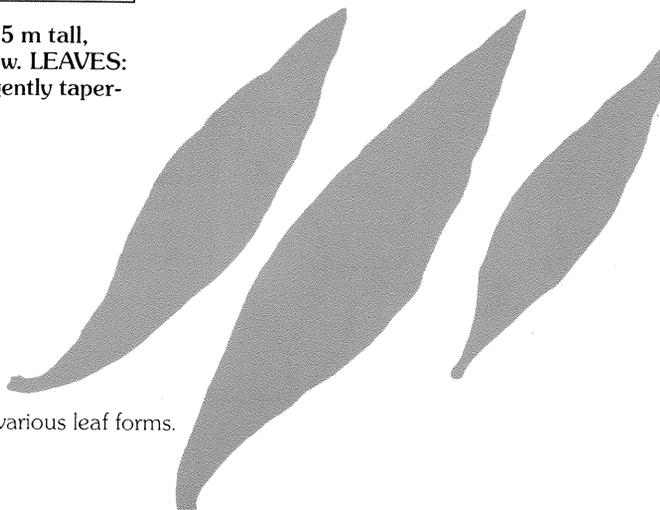
Aureolaria laevigata is restricted to the southern Appalachians where it may form large populations at the margins of oak woods and in disturbed sites such as road and power line rights-of-way. Superficially, it can be confused with *A. flava* but is readily distinguished by its much smaller size and narrower, unlobed leaves.

Little information was available on the host selection of this species except for the early observations of Pennell (1935), who stated that it parasitizes white oaks. In our tests it formed haustoria on 13 of 19 species (Appendix III).



Aureolaria laevigata

PERENNIAL. STEM: up to 0.5 m tall, very sparsely branched, hollow. **LEAVES:** up to 6 cm long, 2 cm wide, gently tapering to a narrow point.



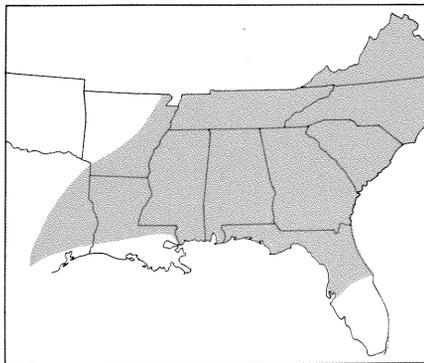
Silhouettes of various leaf forms.

Aureolaria pedicularia

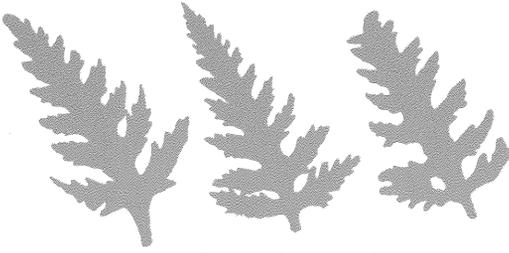


***Aureolaria pedicularia*/
Fernleaf false foxglove**

There is disagreement among botanists as to how these plants should be treated taxonomically. According to some, those plants with pectinate (comb-like) divisions of the leaves, and abundant glandular hairs on the upper portions of the plant, should be treated as a distinct species, *A. pectinata*. In our work, we have found that there is a more or less continuous range of variation in regard to these characters. More northerly plants resemble *A. pedicularia*. These plants have broader leaves and



ANNUAL or BIENNIAL: entire plant covered with glandular hairs. **STEMS:** 1.5 to 2 m tall, solid, much branched (especially when growing in full sunlight), lateral stems arch upward. **LEAVES:** up to 6 cm long, 2.5 cm wide, with four to six lobes or prominent teeth.



Leaves from southern plants

fewer glands, although plants fitting both descriptions may be found throughout the East. Consequently we consider these plants one species, *A. pedicularia*, until a more thorough taxonomic study is completed.

Glands are a distinctive feature of this species. They are especially active on hot, sunny days. Handling the plants at this time will leave a fragrant yellow resin on the hands that soon oxidizes to a black gum. The secretion of the glands may aid the parasite in its transpirational pull on host tissue. Only this species and *Seymeria cassioides* have abundant glandular hairs.

Aureolaria pedicularia occurs throughout eastern North America and may be found in almost any open, dry habitat. It is most abundant in the sand hills of the

Flowering branch showing glands.



Rosette



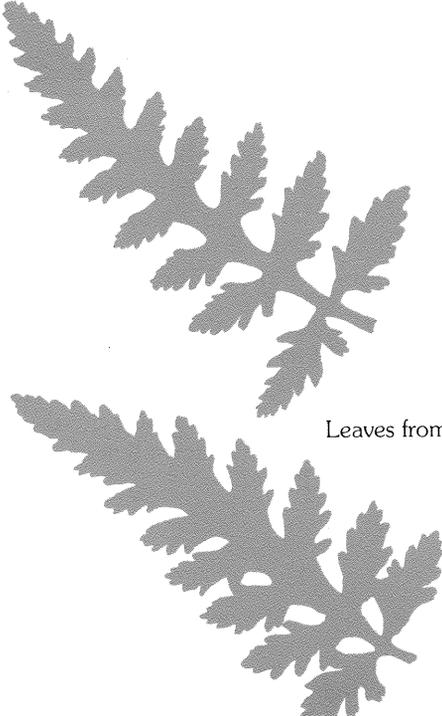
Carolinas and the sandy flatwoods of northern Florida.

The activities of man have contributed to its spread. It is often found in large numbers on road banks and power line rights-of-way and other disturbed areas. Because of its preference for such habitats and its prolific seed production, it has great biological potential as a forest plantation pathogen.

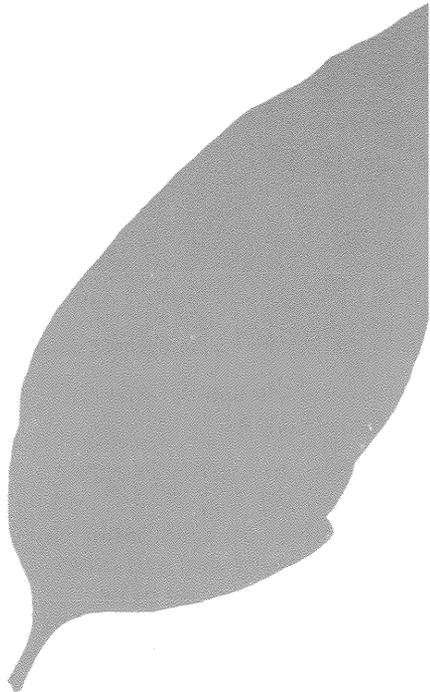
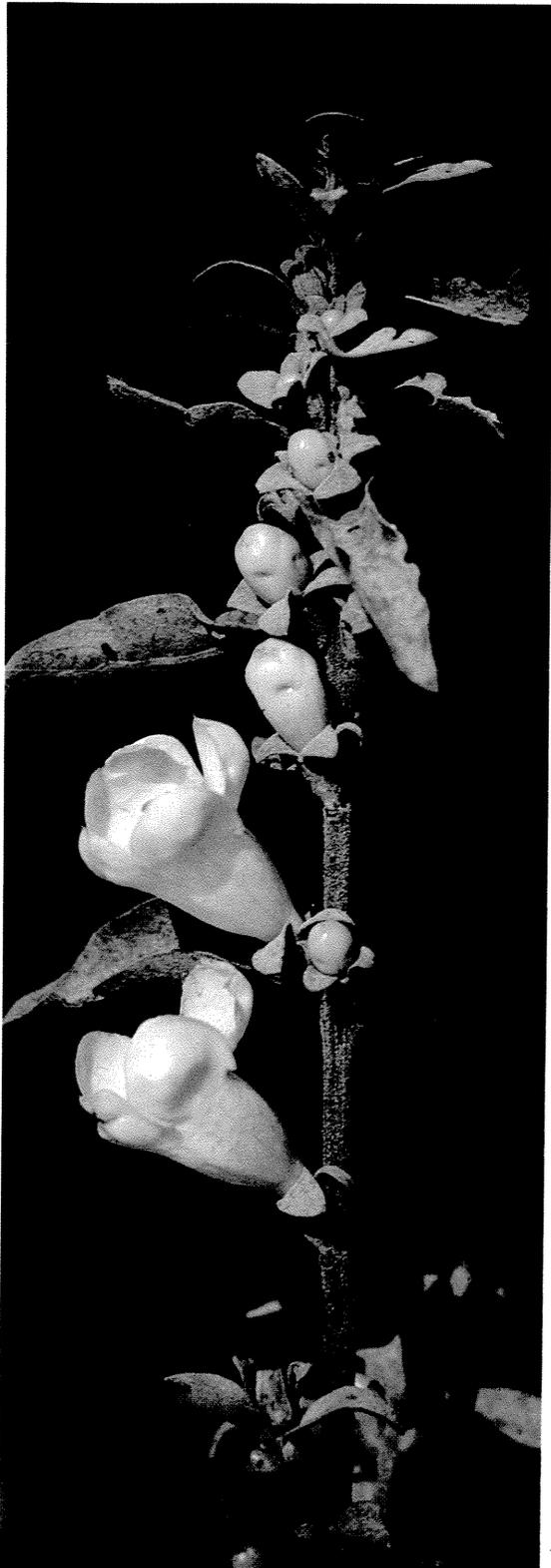
The life history of *A. pedicularia* is variable depending on where it is growing. In the North, it is a biennial which produces a rosette in late summer, overwinters in this stage, and bolts the following spring. In central Florida and perhaps elsewhere in the Deep South, it is an annual. When this occurs, *A. pedicularia* flowers around May.

Like all species in the genus, the flowers of *A. pedicularia* are large, showy, and last for only one day. The flowers have a distinct fragrance, noticeable early in the morning.

The host selection of *A. pedicularia* has been studied extensively (Pennell 1935). It was once thought to have a narrow host selection, and to require attachments to trees of the black oak group for maturation. In nature, haustoria will sometimes form on non-oak species but not without some haustoria of the same plant being attached to a black oak. In pot studies, *A. pedicularia* formed 41 haustoria on water tupelo as well as 198 on eastern cottonwood. One thousand two hundred ninety-two haustoria were found on shumard oak and 402 on southern red oak, both of which are in the black oak group.



Leaves from northern plants.



***Aureolaria virginica*/
Downy false foxglove**

A wide-ranging species found throughout the South. It is the most distinctive of all the perennial species and is identifiable any time of year by its densely hairy stems and leaves and is the only species with hairy fruits. It grows on dry, open, sunny margins of oak wood road banks, and clearings.

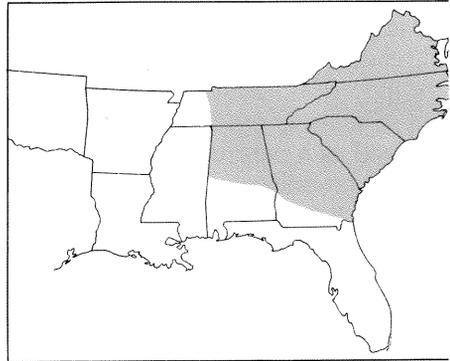
Like other perennials in this genus it is thought to parasitize trees of the white oak group, but pot studies showed haustoria formation on all but one of the 19 species tested (Appendix III).



Silhouettes of various leaf forms

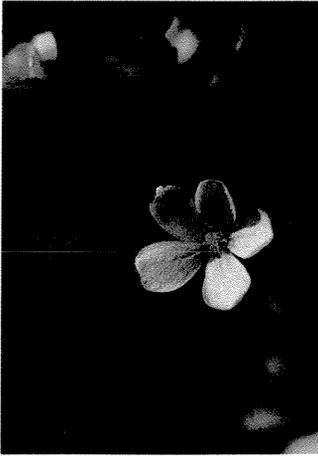


Open capsule with persistent hairs.



PERENNIAL. STEMS: up to 1.5 m high, rarely branched. **LEAVES:** up to 10.5 cm long and 4 cm wide, basal leaves usually have two prominent lobes.

Flowers are nearly symmetrical.



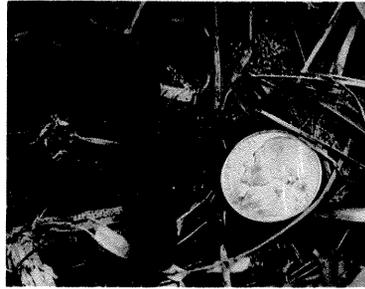
Buchnera americana/Bluehearts

Bluehearts is found throughout most of the southern and central United States but is most abundant in central and southern Florida. It prefers moist, sandy soils and full sun and may occur in large numbers after logging of low flatwoods. This and related species will mature without ever attaching to a host plant. *Buchnera americana* is often described as a perennial, but our field and greenhouse studies clearly show that it is a rosette-forming biennial. In this booklet we recognize only one species, but other workers treat an additional species, *B. floridana* based on slight differences in the venation of the basal leaves. Plants of southern Florida tend to have three veins in the larger leaves and corollas that are larger and redder than those of northern plants.

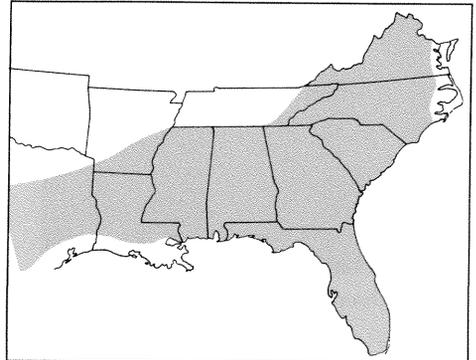
BIENNIAL. STEM: up to 1 m tall,
LEAVES: clustered near the base, rough to the touch, usually three-veined.
FLOWERS: reddish-purple to blue.
CAPSULES: 1 cm long, cylindrical with very thick compartments. **SEEDS:** less than 1 mm long, shiny, black.



Buchnera americana



Rosette



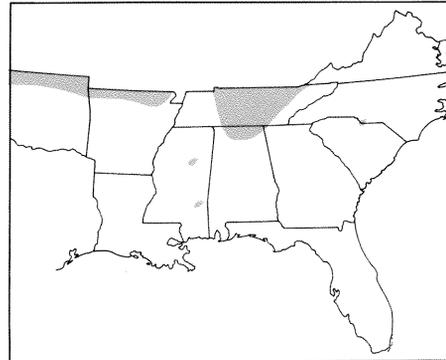
***Dasistoma macrophylla*/
Mullein foxglove**

The common name of this limestone-loving plant is appropriate because the small, bright yellow flowers resemble the flowers of the common mullein, *Verbascum thapsus*. *Dasistoma* has a broad geographic range, but is most common on the Cumberland Plateau, in central Missouri, and other limestone areas. It is often found on stream banks and in openings in alluvial forests. Our studies show that *Dasistoma* is a rosette-forming biennial. Seedling establishment takes place in late summer. One plant produces several hundred capsules or more and is capable of supplying thousands, perhaps millions of seeds. In terms of numbers and size of haustoria, this species is the most vigorous in the family. When the roots of a mature

Intertwined roots of host and parasite with numerous haustoria.

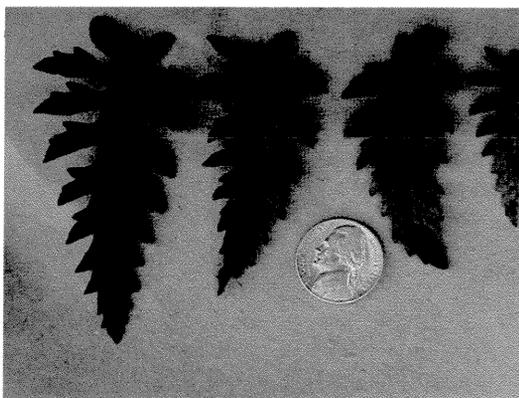


parasite are excavated, one finds hundreds of short roots, each terminated by a haustorium that penetrates the host.



BIENNIAL. STEM: up to 1.5 m tall, profusely branched. **LEAVES:** large, up to 20 cm long, 5 cm wide, the lowest leaves have a few deep lobes, upper leaves tend to be entire. **FLOWERS:** up to 1 cm long, about as wide, inside of the flower densely hairy.

A large specimen of *Dasistoma macrophylla* with fruit.



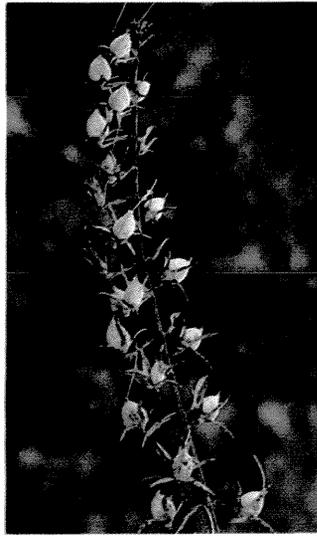
***Macranthera flammae*/
Macranthera, orange blackherb**

This is perhaps the most beautiful of all southern root parasites, and one of the largest. *Macranthera* is a rosette-forming biennial. The seeds germinate in the spring to form a rosette that bolts the following year. Abundant, bright orange flowers, which are reportedly pollinated by

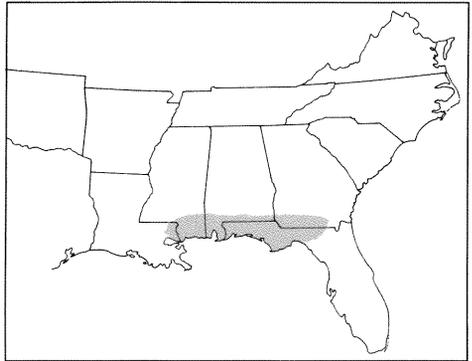
hummingbirds, are produced at the ends of the abundant branches in fall. *Macranthera* is a Gulf Coast endemic and prefers the open, sunny margins of gum swamps. Like *Dasistoma*, this species is a particularly vigorous parasite. At one excavation in northern Florida, hundreds of haustoria were formed on a single young blackgum root.



Young fruits with persistent styles.



BIENNIAL. STEM: up to 3 m tall, much branched. **LEAVES:** deeply divided, up to 8.5 cm long, 3 cm wide, falling from older portions of stem. **FLOWERS:** bright yellow-orange, tubular, 4 cm long. **CAPSULE:** hairy with persistent style.



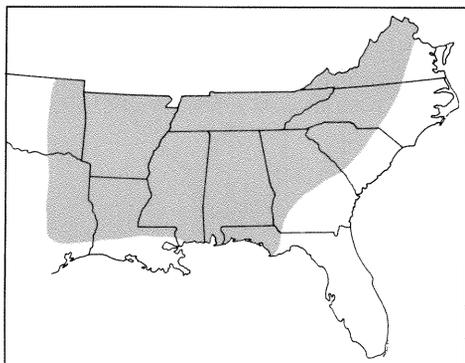
Macranthera flammea on yellow - poplar.



In our pot studies, *Macranthera* formed haustoria on white pine and other trees with which it is not associated in nature (Appendix III). Thus, it has the potential of parasitizing a large number of species.



Pedicularis canadensis



PERENNIAL: spreads by whitish rhizomes. **STEMS:** unbranched, up to 20 cm tall. **LEAVES:** deeply dissected, 10 cm long, 4 cm wide, most of the leaves clustered at the base of the stem. **FLOWERS:** borne in dense heads, two-lipped, 2 cm long, 0.5 cm wide. **CAP-SULE:** 1 cm long, enclosed by green sepals. **SEEDS:** about 10 per capsule, 5 mm long, brown.

***Pedicularis canadensis*/
Common lousewort, wood betony**

All above-ground parts of this plant are covered with broad hairs that were once thought to harbor lice, hence the name, lousewort. This is one of the more common plants of the southern Appalachian forests, but it is found throughout the South. Few parasitic figworts tolerate as much shade as wood betony, although it apparently needs an open canopy to become established. There is considerable variation in the color of the flowers. They range from yellow to reddish-brown.

Piehl (1963) studied the host selection of *P. canadensis* in Michigan and recorded attachments to 80 species of vascular plants in 35 families. Many of these hosts were trees

Schwalbea americana/Chaffseed

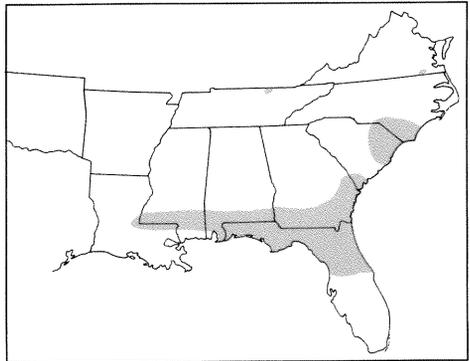
Chaffseed is the rarest parasitic seed plant in the South and is currently known from two populations in South Carolina (each with less than 25 plants) and one population in the New Jersey pine barrens. It grows in pine savannas and other open, sunny habitats. Its rarity is not caused by its preference for a specialized host. We have been able to grow it with several tree species. Because of this rarity, there is little chance that chaffseed could become a serious problem. *Schwalbea* flowers in the spring and produces seed in the early summer. Each seed is long and narrow and enclosed in a loose-fitting sac-like structure that provides the basis for the common name, chaffseed.



Flowers



Schwalbea americana



PERENNIAL: entire plant copiously covered with soft hairs. **STEMS:** up to 8 dm tall, unbranched. **LEAVES:** alternate, without a leaf stalk, up to 4 cm long, 1 mm wide. **FLOWERS:** borne in the axil of reduced upper leaves, 15 mm long, 7 mm wide, yellow to purple. **CAPSULE:** enclosed by the persistent sepals, cylindrical, up to 10 mm long. **SEEDS:** 6 mm long, yellowish, narrow.

Seymeria/*Seymeria*

In terms of damage to commercial species, this is the most important genus of native root parasites in the South. Damage to pines by *S. cassioides* is well documented, although Mann and others (1969) were the first to report damage to any commercial species by a native root parasite. Two sympatric species occur in the South but are distinctive and easily recognized. Both produce abundant, small, yellow flowers in late summer and early fall. Each flower lasts for only one day before falling from the plant. The flowers of this genus have an unusual type of anther opening, a small pore rather than a long slit.

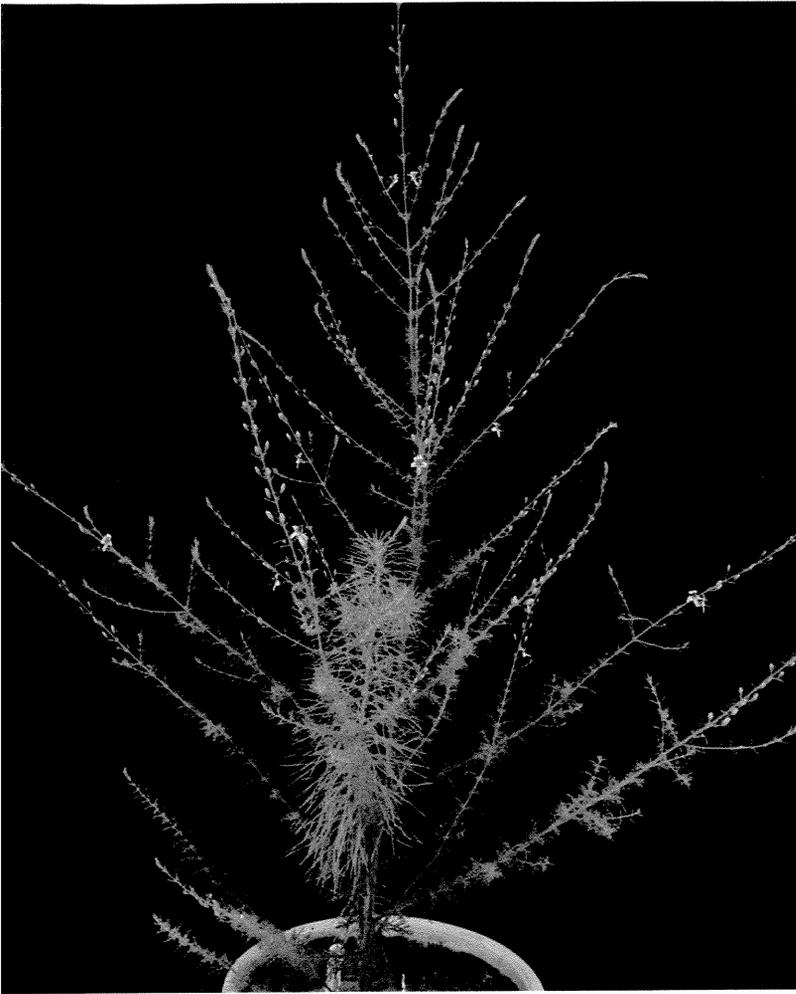
Leaves showing arrange



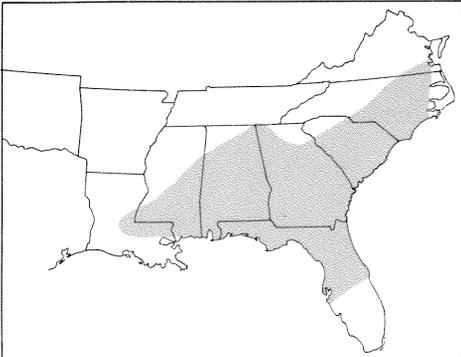
Fl

Seymeria cassioides/*Senna seymeria*

This is one of the few root parasites which exhibits any host specificity. It will produce normal-sized plants only when grown with pines. This host requirement enhances its pathogenic effect because there is no sharing of the parasitic impact by other species nearby. *Senna seymeria* is readily grown from seed without any pretreatment.



Seymeria cassioides on Ocala sand pine



ANNUAL. **STEMS:** up to 1 m tall, much branched, entire plant covered with glandular hairs. **LEAVES:** finely divided into linear segments; in the field each segment gives the impression of being an individual leaf. **FLOWERS:** 1 mm long, bright yellow with brown marks near the ovary, outside of flower not hairy. **CAPSULES:** 5 mm long, shiny brown when mature.



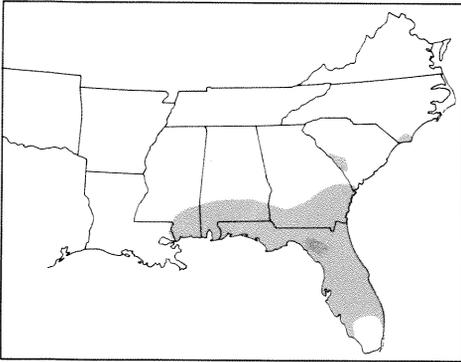
Flower



Seymeria pectinata/Combleaf seymeria

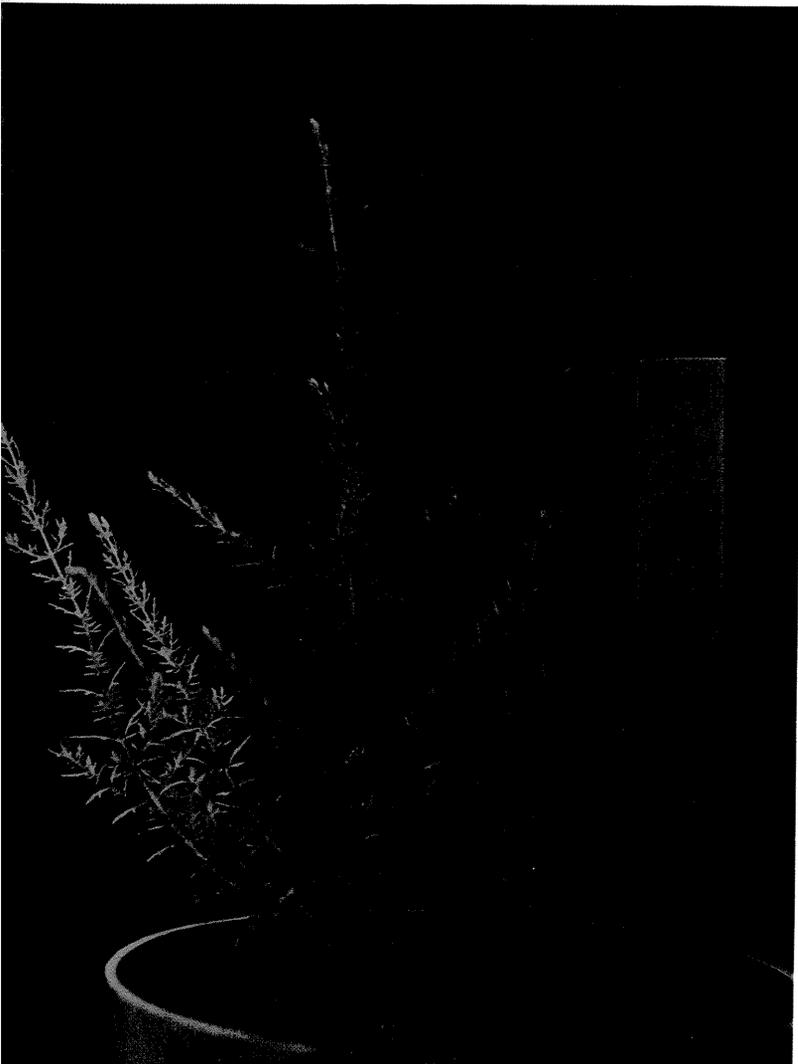
Combleaf seymeria is much more restricted in its distribution than senna seymeria and also has a much broader host range. It prefers drier sites (such as turkey oak-scrub oak woods) than *S. cassioides*, but on rare occasions both may be found growing together. We have found no evidence of hybridization between the two species. In our previous studies *S. pectinata* parasitized yellow poplar, blackgum, water tupelo, pecan, sweetgum, green american sycamore, and four different pines (Appendix III). These species are not present in the communities where *S. pectinata* grows, which indicates a pathogen potential, especially on drier sites in the Deep South.

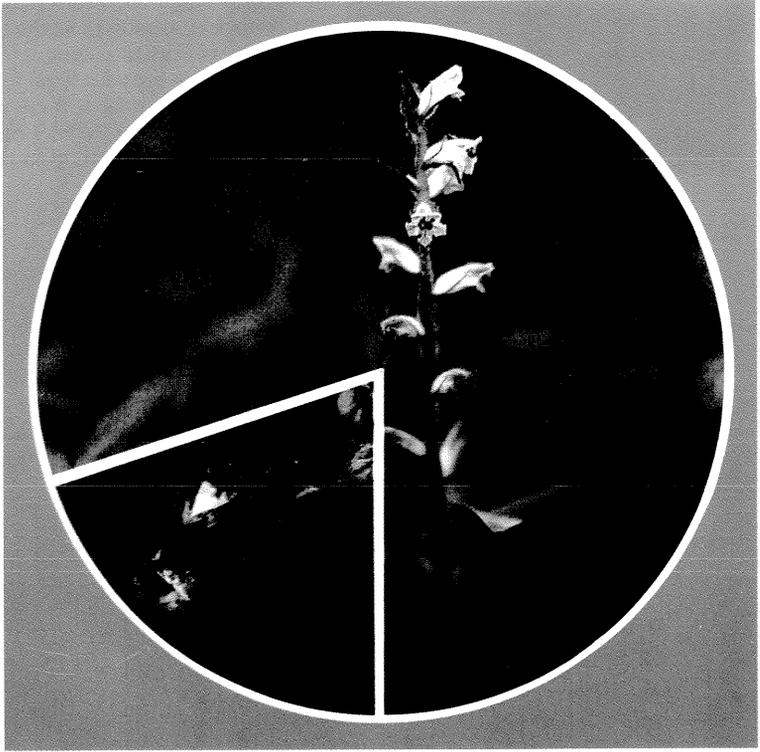
Young fruits covered with hairs.



ANNUAL: entire plant covered with stiff nonglandular hairs. **STEM:** up to 75 cm tall, widely and stiffly branched, the longest branches arising near the base of the plant. **LEAVES:** deeply divided with segments broader than 1 mm. **FLOWERS:** solid yellow, 1 cm long, hairy on the exterior. **CAPSULE:** ovoid, 5 mm long, covered with glandular hairs.

Seymeria pectinata on pecan.





Orobanchaceae
(Broomrape Family)

Orobanchaceae (Broomrape family)

Unlike all the other families considered so far, broomrapes would be recognized as parasites at first glance. They lack chlorophyll entirely and are usually succulent and herbaceous with the above-ground parts lasting only one growing season. Several species are serious pathogens on a variety of food crops in the Mediterranean region, the Middle East, and central Asia, where they cause great economic losses. The species of the South are rather benign although careful studies of the effect of these plants on their hosts have not been carried out.

There are three genera in the eastern United States: *Orobanche*, *Conopholis*, and *Epifagus*. Species of *Orobanche* are rather rare and difficult to locate. They were not included in our culture study at the request of USDA Plant Protection and Quarantine because

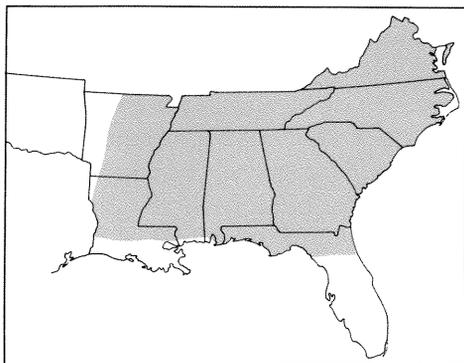
some have the potential of becoming serious parasites of crop plants such as tobacco and tomato.

Both *Epifagus* and *Conopholis* (each with a single species in our region) are widespread and are good examples of parasites very selective for hosts. We were unable to germinate seed of either *Epifagus* or *Conopholis*. *Epifagus*, as the name implies, will grow only on the roots of the American beech, *Fagus grandifolia*. *Conopholis* has been found only on the roots of members of the red oak group. Because both attack forest species, they are included in this study even though no experimental data are available.



Plant in fruit.

ANNUAL: arising from a swollen, bulb-like base from which short, stiff hook-like roots arise. **STEM:** up to 0.5 m tall, usually much branched. **LEAVES:** absent, represented by minute scales. **FLOWERS:** 6 mm long, 2 mm wide, white with brown; cleistogamous flowers are often present, most commonly at the base of the plant. **CAPSULE:** 5 mm long, 2 mm wide.



Epifagus virginiana/Beechdrops

Epifagus may be found anywhere American beech grows. While the ranges of host and parasite are sympatric, not all beech trees in a given stand are parasitized by beechdrops. The entire plant is pale brown with purple stripes and blotches. Beechdrops flowers in the autumn. The flowers, like the plants, are inconspicuous. Within a few weeks of flowering, the capsules split open to release dust-like seeds. They apparently open in such a way as to form a splashcup for dispersal of seeds by rainwater. We have determined that there are about 14 million beechdrops seeds in one pound.



Ripe fruit showing numerous dust-like seeds



A large population of *Epifagus virginiana* at base of old beech



Conopholis americana, just past flowering.

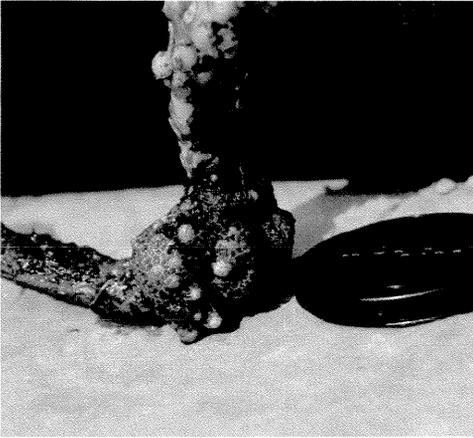
***Conopholis americana*/
Squawroot, cancer root**

Conopholis is widespread throughout the South but is less common in the western regions of the South. It is distinctive and is easily recognized at almost any time of year. Very little is known about its life history. The seeds apparently take several years to germinate. In one of the few instances where *Conopholis americana* has been grown from seed, at the University Botanic Garden in Copenhagen, 8 years elapsed between sowing of the seeds and emergence of the flowering stalks. We found the first recognizable stage to be a swollen white growth on small oak roots. As the



Seedlings

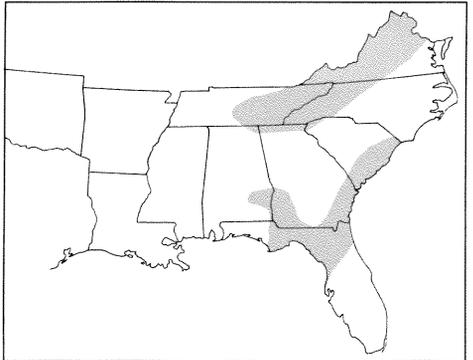
parasite develops it apparently stimulates host tissue growth until a gall-like mass of host-parasite tissue develops. When examined microscopically, it is difficult to distinguish between host and parasite tissue because the two tissues are so intermingled. The host root usually dies back to the gall-like growth. In spite of this damage, it has not been possible to determine growth loss or damage to the host tree. From the underground perennating structure, fleshy, yellow shoots covered with large brown scales arise in spring. Small flowers are borne from the fleshy stem. The stems and fruits are apparently an important part of the diet of bears in some areas of the southern Appalachians. The fruit is usually described as a dry capsule when mature, but the seeds appear to be ripe while the capsule is fleshy. This fleshy structure may be a means of dispersal by animals.



Host root.

Parasite and host tissue.

PERENNIAL: arising from an underground swollen mass on oak roots.
STEMS: up to 16 cm tall, yellow, fleshy.
LEAVES: absent, represented by large brown scales. **FLOWERS:** small, 2 cm long, two-lipped, yellowish with some purple. **FRUIT:** a capsule with numerous yellowish-brown, shiny seeds.

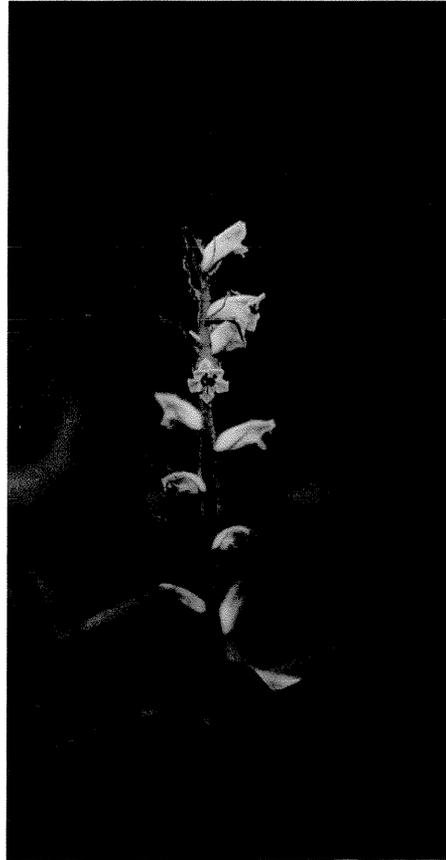


Orobanche minor/Small broomrape

This species is very rare and is apparently known in the South only from a few locations in Virginia and North Carolina. However, it could easily be overlooked since it is a very small and inconspicuous plant. It is also shade-tolerant and may grow unnoticed beneath dense vegetation. Its selection of hosts is apparently broad. Small broomrape have been recorded on legumes and other crops in Europe and the Middle East. For several years at one site in Virginia, a population has been observed parasitizing the roots of ornamental shrubs.

Unlike many of its relatives, small broomrape is not presently known to cause any serious damage al-

though it could be considered potentially harmful. *Orobanche minor* could easily spread throughout a planting, because like all species in this genus it produces thousands of seeds per plant. Damage from such a holoparasite would be considerably greater than from an equal number of hemi-



Flowering stalk.

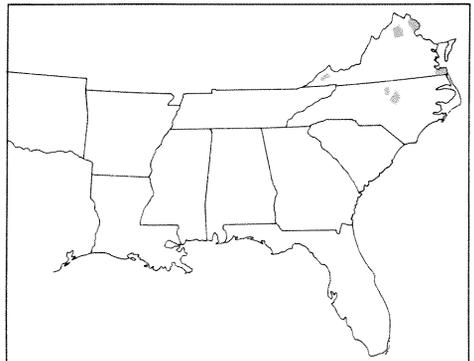
Aspect and young plant of *Orobanche minor*.

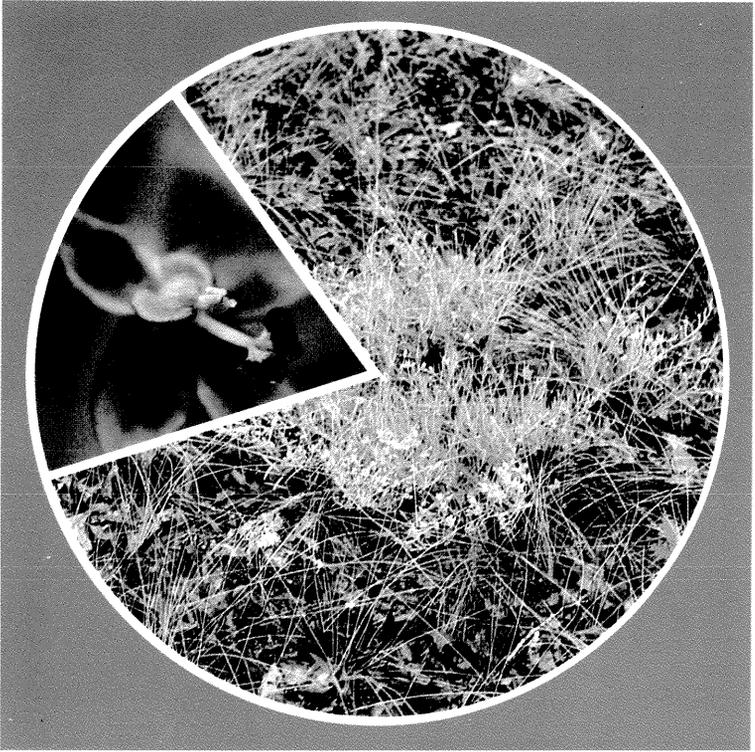


parasites because of the total dependence of these parasites on their host.

Small broomrape is easily distinguished from the more widespread native species, *Orobanche uniflora*, which has bluish-white, densely hairy stems, and solitary flowers.

ANNUAL: seeds apparently germinating in early spring to form small, round, white seedlings on host roots. **STEMS:** up to 15 cm tall, fleshy, unbranched, brown. **LEAVES:** absent, represented by small scales. **FLOWERS:** up to 2 cm long, 0.5 cm wide, whitish. **CAPSULE:** 1 cm long, 0.5 cm wide with numerous dust-like seeds.





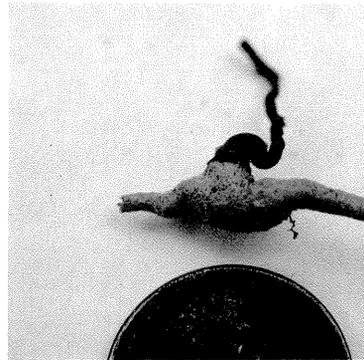
Krameriaceae
(Rattany Family)

Krameriaceae (Rattany family)

The rattany family is small (a single genus). Most species are found in the deserts of the Southwestern United States. Only one species, *Krameria lanceolata*, occurs in the Southeast, where it is restricted to deep sand ridges of the coastal rivers of Georgia and sandy flatwoods in northern and central Florida.



Flower



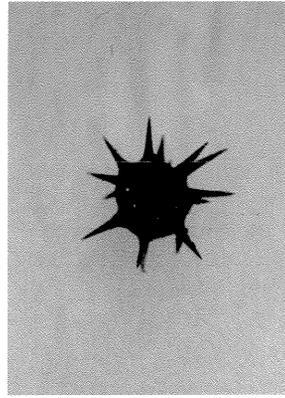
Haustrorium on host root.

Krameria lanceolata/Sandspur

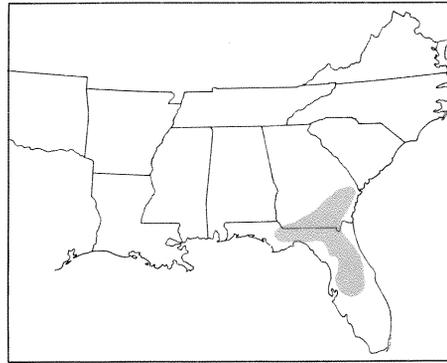
Sometimes called sandspur because of the resemblance of its fruit to a sandbur, *Krameria lanceolata* is visually unimpressive. It forms an extensive network of wiry rhizomes from which the stems arise. Large, fleshy taproots are present. The leaves are small and grayish green. Attractive purple flowers are produced in May.

Recent studies have shown that *K. lanceolata* attacks many hosts including longleaf pine, persimmon, turkey oak, prickly pear, and various grasses and forbs (Musselman 1975).

PERENNIAL: arising from stout taproots.
STEMS: up to 2 dm long, lying on the ground.
LEAVES: alternate, up to 1.7 mm long, 2.5 mm wide, widest at tip, covered with long, silvery hairs, deciduous.
FLOWERS: 2 cm long, purple, irregular in shape.
FRUIT: 1 cm in diameter, armed with sharp prickles, resembling a sandbur, containing one seed.



Fruit

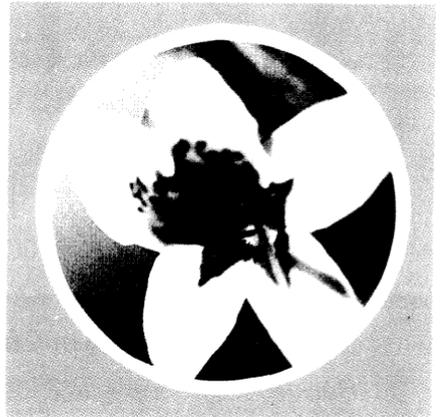


A single specimen of *Krameria lanceolata* growing with wiregrass.



Literature Cited

- Cook, C. E., L. B. Whiard, M. E. Wall, G. H. Egley, P. Coggan, P. A. Luhan, and A. T. McPhail.
1972. Germination stimulants. 2. The structure of strigol—a potent seed germination stimulant for witchweed (*Striga lutea* Lour.). *J. Am. Chem. Soc.* 94:6198-6199.
- DeFilipps, R. A.
1968. A revision of *Ximenia* (Plum.) L. (Olacaceae). Doctoral dissertation. South. Ill. Univ., Carbondale. 139 p. Univ. Microfilm.
- Johnson A. W., G. Rosebery, and C. Parker.
1976. A novel approach to *Striga* and *Orobanche* control using synthetic germination stimulants. *Weed Res.* 16:223-227.
- Kuijt, J.
1969. The biology of parasitic flowering plants. 246 p. Univ. Calif. Press, Berkeley.
- Mann, W. F., Jr., H. E. Grelen, and B. C. Williamson.
1969. *Seymeria cassioides*, a parasitic weed on slash pine. *For. Sci.* 15:318-319.
- Musselman, L. J.
1975. Parasitism and haustorial structure in *Krameria lanceolata* (Krameriaceae) a preliminary study. *Phytomorphology* 25:416-422.
- Pennell, F. W.
1935. The Scrophulariaceae of eastern temperate North America. Academy of Natural Sciences of Philadelphia Monograph No. 1, 650 p.
- Piehl, M. A.
1963. Mode of attachment, haustorium structure, and hosts of *Pedicularis canadensis*. *Am. J. Bot.* 50:978-985.
- Piehl, M. A.
1965. The natural history and taxonomy of *Comandra* (Santalaceae). *Mem. Torrey Bot. Club* 22:1-97.
- Radford, A. E., H. E. Ahles, and C. R. Bell.
1968. Manual of the vascular flora of the Carolinas. Univ. N.C. Press, Chapel Hill.



Appendix

Appendix I

Root parasites of the Southeast

This is a list of all native root parasites that are known to occur in the states of Virginia, Tennessee, Arkansas, Louisiana, Mississippi, Alabama, Georgia, Florida, South Carolina, and North Carolina. The list is based on field work, published floras, and herbarium data. Taxonomic synonyms are not included. Witchweed, *Striga asiatica* (L.) Kuntze, is an introduced pathogen found in a few counties of North and South Carolina.

Name and Author	Common Name
Krameriaceae (Rattany family)	
<i>Krameria lanceolata</i> Torr.	Sandspur
Olacaceae (Olax family)	
<i>Schoepfia schreberi</i> J. F. Gmel.	Whitewood
<i>Ximenia americana</i> L.	Hog plum, tallowwood
Orobanchaceae (Broomrape family)	
<i>Conopholis americana</i> (L.) Wallr.	Squawroot, cancer root
<i>Epifagus virginiana</i> (L.) Barton	Beechdrops
Orobanche	
<i>O. uniflora</i> L.	One-flowered cancer root
<i>O. minor</i> Sm.	Small broomrape
<i>O. ludoviciana</i> Nutt.	Louisiana broomrape
Santalaceae (Sandalwood family)	
<i>Buckleya distichophylla</i> (Nutt.) Torr.	Buckleya, piratebush
<i>Comandra umbellata</i> (L.) Nutt.	Comandra, bastard toadflax
<i>Nestronia umbellula</i> Raf.	Nestronia
<i>Pyrolaria pubera</i> Michx.	Buffalo nut, oilnut
Scrophulariaceae (Figwort family)	
Agalinis	
<i>A. aphylla</i> (Nutt.) Raf.	Leafless gerardia
<i>A. divaricata</i> (Chapm.) Penn.	Gulf gerardia
<i>A. fasciculata</i> (Ell.) Raf.	Fascicled gerardia, beach gerardia

<i>A. filicaulis</i> (Benth.) Penn.	Slender-stemmed gerardia
<i>A. gattingeri</i> (Sm.) Sm.	Gattinger's gerardia
<i>A. georgiana</i> (Boynton) Penn.	Georgia gerardia
<i>A. heterophylla</i> (Nutt.) Sm.	Variable-leaf gerardia
<i>A. linifolia</i> (Nutt.) Britt.	Perennial gerardia
<i>A. maritima</i> (Raf.) Raf.	Seaside gerardia
<i>A. microphylla</i> (Gray) Sm.	Small-leaf gerardia
<i>A. obtusifolia</i> Raf.	Bluntleaf gerardia
<i>A. purpurea</i> (L.) Penn.	Purple gerardia
<i>A. setacea</i> (Walt.) J. F. Gmel.	Bristleleaf gerardia
<i>A. tenella</i> Penn.	Slenderleaf gerardia
<i>A. tenuifolia</i> (Vahl) Raf.	Slender gerardia
<i>A. virgata</i> Raf.	Stiff gerardia
Aureolaria	
<i>A. flava</i> (L.) Farw.	Large false foxglove
<i>A. grandiflora</i> (Benth.) Penn.	Showy false foxglove, big-leaf oakleech
<i>A. laevigata</i> (Raf.) Raf.	Smooth false foxglove
<i>A. pedicularia</i> (L.) Raf.	Fernleaf false foxglove
<i>A. virginica</i> (L.) Penn.	Downy false foxglove
<i>Buchnera americana</i> L.	
<i>Castilleja coccinea</i> (L.) Spreng.	Indian paintbrush
<i>Dasistoma macrophylla</i> (Nutt.) Raf.	Mullein foxglove
<i>Macranthera flammea</i> (Bartr.) Penn.	Macranthera, orange blackherb
<i>Melampyrum lineare</i> Desr.	
Pedicularis	
<i>P. canadensis</i> L.	Common lousewort, wood betony
<i>P. lanceolata</i> Michx.	Lousewort
<i>Schwalbea americana</i> L.	
Seymeria	
<i>S. cassioides</i> (J. F. Gmel.) Blake	Senna seymeria
<i>S. pectinata</i> Pursh	Combleaf seymeria
<i>Tomanthera auriculata</i> (Michx.) Raf.	
	Tomanthera

Appendix II

Commercial tree species used in pot studies

Scientific Name	Common Name
<i>Carya illinoensis</i> (Wang.) K. Koch	Pecan
<i>Celtis laevigata</i> Willd.	Sugarberry
<i>Fraxinus pennsylvanica</i> Marsh.	Green ash
<i>Liquidambar styraciflua</i> L.	Sweetgum
<i>Liriodendron tulipifera</i> L.	Yellow-poplar
<i>Nyssa aquatica</i> L.	Water tupelo
<i>Nyssa sylvatica</i> Marsh.	Blackgum
<i>Pinus clausa</i> (Engelm.) Vasey	Sand pine
<i>Pinus echinata</i> Mill.	Shortleaf pine
<i>Pinus elliottii</i> Engelm.	Slash pine
<i>Pinus palustris</i> Mill.	Longleaf pine
<i>Pinus strobus</i> L.	White pine
<i>Pinus taeda</i> L.	Loblolly pine
<i>Platanus occidentalis</i> L.	American sycamore
<i>Populus deltoides</i> Marsh.	Eastern cottonwood
<i>Quercus alba</i> L.	White oak
<i>Quercus falcata</i> Walt.	Southern red oak
<i>Quercus shumardii</i> Buckl.	Shumard oak
<i>Taxodium distichum</i> (L.) Rich.	Baldcypress

Appendix III

Haustorial attachments by 19 root parasites on commercial tree species

Host species	Parasites																		
	<i>Agalinis</i> <i>aphylla</i>	<i>Agalinis</i> <i>fasciculata</i>	<i>Agalinis</i> <i>linifolia</i>	<i>Agalinis</i> <i>purpurea</i>	<i>Agalinis</i> <i>setacea</i>	<i>Agalinis</i> <i>tenuifolia</i>	<i>Aureolaria</i> <i>flava</i>	<i>Aureolaria</i> <i>grandiflora</i>	<i>Aureolaria</i> <i>laevigata</i>	<i>Aureolaria</i> <i>pedicularia</i>	<i>Aureolaria</i> <i>virginica</i>	<i>Buchnera</i> <i>americana</i>	<i>Buckleya</i> <i>districhophylla</i>	<i>Dasistoma</i> <i>macrophylla</i>	<i>Macranthera</i> <i>flammea</i>	<i>Schwalbea</i> <i>americana</i>	<i>Seymeria</i> <i>cassioides</i>	<i>Seymeria</i> <i>peccinata</i>	<i>Ximena</i> <i>americana</i>
<i>Carya illinoensis</i>	X	X	O	X	X	X	X	X	X	X	X	O	X	X	X	O	X	X	X
<i>Celtis laevigata</i>	X	X	X	X	–	X	X	X	O	X	X	X	X	X	X	X	O	X	X
<i>Fraxinus pennsylvanica</i>	X	X	X	X	–	X	X	X	X	X	X	X	X	X	X	X	O	X	X
<i>Liquidambar styraciflua</i>	O	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Liriodendron tulipifera</i>	O	X	X	X	–	X	O	X	X	X	X	X	O	X	X	X	X	X	X
<i>Nyssa aquatica</i>	X	X	X	X	–	X	X	X	X	X	X	X	X	X	X	X	O	X	X
<i>Nyssa sylvatica</i>	O	X	X	X	–	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Pinus clausa</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	O	X	X	X	X
<i>Pinus echinata</i>	X	X	X	X	–	X	X	X	X	O	X	X	X	X	X	X	X	O	X
<i>Pinus elliotii</i>	X	X	X	X	–	X	X	X	O	X	X	X	X	X	X	X	X	X	X
<i>Pinus palustris</i>	X	X	X	X	–	X	X	O	O	X	O	X	X	X	X	O	X	X	X
<i>Pinus strobus</i>	X	X	X	X	–	X	X	O	X	X	X	X	X	O	X	X	X	O	X
<i>Pinus taeda</i>	X	X	X	X	–	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Platanus occidentalis</i>	X	X	X	X	X	X	X	X	O	X	X	X	X	X	X	X	X	X	O
<i>Populus deltoides</i>	X	X	X	X	–	X	X	X	O	X	X	X	X	X	X	O	X	X	X
<i>Quercus alba</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	O	X	X
<i>Quercus falcata</i>	O	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Quercus shumardii</i>	X	X	O	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Taxodium distichum</i>	X	X	X	X	X	X	X	X	O	X	X	X	X	X	X	X	X	X	X

Legend

X haustoria present

O grew in height, no haustoria

– no data

Appendix IV

Glossary

- ANTHER—The pollen sac of a flower, usually borne on a filament.
- AUTOTROPHIC—A plant that produces its own food.
- AXIL—Angle between the point of attachment of a leaf and the stem.
- BRACT—A reduced leaf.
- CALYX—Collective term for the sepals.
- CAPSULE—A fruit that contains many seeds and splits open at maturity.
- CLEISTOGAMOUS FLOWERS—Flowers that do not open, and are self-fertilized.
- COROLLA—Collective term for the petals.
- DIOECIOUS—Having male (staminate) and female (pistillate) flowers on separate plants.
- ENDEMIC—Confined to a restricted area or region.
- FASCICLE—Bundle.
- FRUIT—A mature ovary containing seeds.
- HAUSTORIUM—A modified root that penetrates a host root to form a physiological and morphological bridge between host and parasite.
- HOLOPARASITE—A parasitic angiosperm that lacks chlorophyll.
- INFLORESCENCE—A group of flowers and the manner in which they are arranged on an axis.
- OVARY—The part of the flower containing embryonic seeds.

PERENNATING—Over-wintering, renewing growth each year .

PERFECT—A flower containing both male and female parts.

PETAL—Typically the colored portion of the flower, though some flowers have colored sepals.

RACEME—An inflorescence with stalked flowers on an elongated axis.

RHIZOME—Underground stem.

ROOT PARASITE—A seed plant that parasitizes the roots of neighboring plants, usually via haustoria.

SCABROUS—Rough, sandpaper-like to the touch.

SCALE—Small, dry leaves or leaf-like structures.

SEMIPARASITE—A parasitic seed plant that contains chlorophyll.

SEPAL—The external part of the flower bud usually persistent at the base of the corolla. Typically green but sometimes colored and showy (As in *Comandra*).

STAMEN—Male reproductive structure with a stalk (filament) and pollen sac (anther).

STYLE—The elongated terminal portion of the ovary.

SYMPATRIC—Overlapping, as in having overlapping ranges.

UNISEXUAL—One sex.

Musselman, L. J. and W. F. Mann, Jr.

1978. Root parasites of southern forests. U.S. Dep. Agric. For. Serv.
Gen. Tech. Rep. SO-20, 76 p. South. For. Exp. Stn., New Orleans, La.

The five families of root parasites of the South are discussed relative to selection of hosts, ecology, and potential for damage to commercial species. An identification key to all genera of root parasites is included. Plants and flowers of 29 species are illustrated and their distribution in the South mapped.

