

1957; Braun, 1950; Kuchler, 1964; and DeSelm and Schmalzer, 1982). In fact, these sites appear to be what Galloway (1919) referred to as "Hardwood Glades" occurring on outcrops of massive limestone in contrast to the thin bedded, platy limestone characteristic of the cedar glades.

Secondary succession and a discontinuous pattern of occurrence has evidently allowed these stands to form and maintain themselves in a individualistic manner, each under different pressures from human interference (Gleason, 1926; Whittaker, 1951). Quarterman (1959b) suggested a generalized succession from a cedar subclimax to an oak-hickory pre-climax, with a tendency toward a mixed mesophytic association on the favorable sites. Each of these stands exist on protected lands and, therefore, are expected to develop without disturbance. It will be interesting to follow the development of these forests over the next several decades.

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AMERICAN MISTLETOE (*PHORADENDRON SEROTINUM*) IN THE NORTHEASTERN CENTRAL BASIN AND ADJACENT DISSECTED HIGHLAND RIM OF MIDDLE TENNESSEE

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ABSTRACT

American mistletoe, a woody angiosperm, parasitizes a variety of North American deciduous trees. The hosts of this parasite vary in different localities. In this study, a total of 314 mistletoe-infested trees, representing twenty-five species and nineteen genera, was observed in the northeastern Central Basin and adjacent dissected portion of the Highland Rim of Middle Tennessee. The most frequently parasitized species were *Ulmus americana* (29.9%), *U. rubra* (15.6%), *Robinia pseudo-acacia* (11.9%), and *Fraxinus americana* (9.9%).

These results were compared to those completed in other parts of the Basin and the surrounding Highland Rim. Also, reasons for the differential infestation among host species were discussed. Some possible factors were: the availability of potential hosts; characteristics of tree species which could attract birds which disperse the seeds; mechanical or chemical barriers possessed by host trees; and the availability of nutrients and water.

INTRODUCTION

Phoradendron serotinum (Raf.) M. C. Johnston (Loranthaceae), synonym *P. flavescens* (Pursh.) Nutt. (Johnston, 1957), American mistletoe, is an obligate parasite which

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grows on the branches of deciduous trees. The plant is a nutrient and water parasite. The leaves have a chlorophyll content comparable to that of the host (York, 1909).

The parasite is dioecious. Anthesis is from October to December; twelve months are required for the development of the pearly white berries. Dissemination of the sticky seeds is accomplished by birds, wind and rain. Germination begins usually in early spring; the radicle grows along the surface and subsequently penetrates the host bark (Cannon, 1901).

The plant's geographic range embraces the eastern deciduous forest region from southeastern Oklahoma and Missouri, eastern Texas, the extreme southern portion of Illinois, Indiana, and Ohio, southeastern Pennsylvania and New Jersey, southward to the Gulf Coast (Weins, 1964).

American mistletoe infests many different angiosperm species throughout its area of distribution; however, it seems to parasitize only certain tree species in each locality (York 1907; Gleason, 1963). This phenomenon has been observed in various portions of its range. For example, Jones (1963) listed mistletoe on *Ulmus americana*, *Nyssa sylvatica*, and several *Quercus* species in Illinois. Deam (1970) in Indiana also observed mistletoe principally on *U. americana* and *N. sylvatica*. In a survey of Kentucky (Reed and Reed, 1951), five tree species were most often found infested with mistletoe: *Juglans nigra*, *Nyssa sylvatica*, *Ulmus americana*, *Robinia pseudo-acacia*, and *Gleditsia triacanthos*. James (1958) reported mistletoe in eastern Tennessee on *Carya* spp. and *Nyssa sylvatica*, *Platanus occidentalis*, *Acer rubrum*, and *Quercus* spp. (Stupka, 1964).

Middle Tennessee includes the Central Basin, an elliptical depression which is surrounded by the Highland Rim (Fig. 1). The inner edge of the Rim is known as the dissected Rim. Both the Basin, approximately 150 m above sea level, and the Rim, approximately 300 m above sea level, lie within Braun's (1950) Western Mesophytic Forest region. However, climatic and edaphic conditions vary in these areas, resulting in a mosaic of vegetation types.

In the central and southwestern portions of the Central Basin and adjacent dissected Rim, recent surveys including Rutherford County (Rucker and Hemmerly, 1976), Maury County (Ferguson and Hemmerly, 1976), Davidson County (McKinney and Hemmerly, 1977), Bedford County (Brown and Hemmerly, 1979), and Williamson County (Hemmerly, 1981) revealed that several *Ulmus* species along with *Carya ovata* and *Fraxinus americana* were the preferred mistletoe hosts. In contrast, in Lawrence County, located on the Highland Rim, *Nyssa sylvatica* was the predominant host (Hemmerly, Forsythe and Womack, 1979).

The Basin counties northeast of Rutherford and Davidson Counties had not been surveyed systematically. The purpose of this survey was to determine the host specificity of mistletoe in this northeastern portion of the Central Basin and adjacent dissected Highland Rim. This will permit a comparison of mistletoe specificity in a large portion of the Basin and dissected Rim to that of other parts of the Highland Rim and nearby areas. Also, hypotheses will be proposed to explain the varying host specificities of mistletoe in different portions of its range.

METHODS

During the months November, 1977 through March, 1978 and January, 1979 through February, 1979, the northeastern portion of the Central Basin and adjacent dissected Highland Rim of Middle Tennessee (Fig. 1) was surveyed by automobile and motorcycle for trees infested with mistletoe. Included was one entire Central Basin county: Wilson. Basin and/or dissected Rim portions of eight other counties: Sumner, Macon, Jackson, Putnam, Dekalb, Cannon, Smith and Trousdale were sampled.

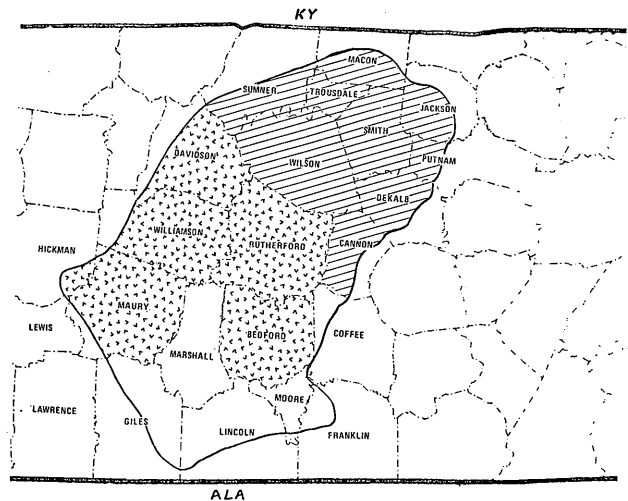


FIG. 1. Northeastern portions of the Central Basin and adjacent Highland Rim of Middle Tennessee surveyed in this study (shaded area). Stippled areas indicate previous surveys within the Basin and solid heavy line delineates Basin and dissected Rim area from surrounding un-dissected Highland Rim.

Wilson County was sampled along approximately 400 kilometers of roads. Other counties were sampled according to their proportional areas (Table 1). The portion of each county to be studied was divided into four quadrants and each was sampled equally as appropriate from the portion of the study area included.

Identifications of infested trees were made in the winter condition, using manuals, keys, and checklists by Brockman (1968), Harlow (1941), Harrar and Harrar (1946), and Shanks (1952).

RESULTS

A total of 314 mistletoe-infested trees were observed; nineteen genera and twenty-five species were represented. Over half (51.2%) of the infested trees were of the genus *Ulmus*, including *U. americana* (29.9%) and *U. rubra* (15.6%). Other trees in the northern Basin frequented with mistletoe included *Robinia pseudo-acacia* (11.9%), *Fraxinus americana* (9.9%), and *Juglans nigra* (4.5%). With the exception of *Maclura pomifera* which has long been naturalized, all are native to Tennessee (Shanks, 1952).

The degree of infestation ranged from a single small shoot to more than thirty masses per tree. The number of infested trees per road kilometer varied (Table 1) from 0.06 (Wilson and Sumner) to 0.72 (Trousdale).

TABLE 1. Numbers of mistletoe-infested trees in nine counties of the northeastern Central Basin and adjacent Rim of Middle Tennessee.

County	Kilometers Traveled	No. of Mistletoe-infested Trees	No. of Mistletoe-infested Trees per Kilometer
Wilson	434.0	26	0.06
Sumner	236.6	15	0.06
Smith	243.0	63	0.26
Trousdale	139.4	102	0.72
Macon	102.6	9	0.08
Jackson	94.6	64	0.66
Dekalb	104.2	21	0.20
Cannon	97.4	9	0.09
Putnam	46.0	5	0.10
TOTALS	1497.8	314	Mean 0.21

In Wilson, Smith and Putnam Counties, *Ulmus americana* and *Robinia pseudo-acacia* were the most common host species; *U. americana* comprised half of the total infested trees (Table 2). In Sumner County, *Ulmus americana* (26.7%) was also the tree species most often parasitized; however, *Carya ovata* was as prevalent as *Robinia pseudo-acacia* (20.0% each). Surveys of Macon and Dekalb Counties revealed that *Ulmus americana* (33.4% and 33.3%, respectively) was the most common host species. In Macon County, 22.2% of the trees were *Liriodendron tulipifera*, and in Dekalb County, 14.1% were *Nyssa sylvatica*. Trousdale County had the largest number of infested trees (102) and also the largest number of host species represented (15). In this county, *Fraxinus americana* (27.0%), *Ulmus americana* (16.7%), and *U. rubra* (15.7%) were found to be the most frequently parasitized tree species. In Jackson County, *Ulmus rubra* (40.5%) and *U. americana* (31.2%), or a total of nearly three-fourths of the infested tree species, were *Ulmus*. Cannon County was represented almost entirely by *Ulmus serotina* (77.8%); trees of only two other species were observed with infestations, *U. americana* (11.1%) and *Maclura pomifera* (11.1%).

DISCUSSION

There is a similarity between the results obtained in this survey of the northeastern Basin and those obtained in previous studies in the central and southern portion of the Basin. As in this study, all five central and southern Basin counties (Maury, Davidson, Rutherford, Bedford, and Williamson) previously surveyed included *Ulmus americana*, *Carya ovata*, *Fraxinus americana*, and *U. serotina* as common mistletoe hosts (references cited in "Introduction"). The tree species in the Basin found to be parasitized contrast with those of Lawrence County on the undissected Rim where *Nyssa sylvatica* constituted almost 90 percent of the total.

Considerable county to county differences exist in the numbers of mistletoe-infested trees. One explanation for the small number in Wilson County is that much of the area consists of cedar glades. According to Quarterman (1950), over half of Wilson County is composed of glades

which, at least during the warmer months, are xeric (Hemmerly, 1976). American mistletoe, dependent upon its host for water and nutrients, is apparently more common in those areas that have an abundance of water. This hypothesis is supported by the generally greater density of mistletoe towards the southeastern portion of its range where rainfall is greater (Cole and Hemmerly, 1981). Another factor to be considered is that some Counties, including Wilson, have a greater proportion of land area in agriculture, thus reducing the number of potentially infested trees.

In considering possible explanations for the host specificity and density phenomena displayed by the parasite, the basic requirements of the plant must be considered. Mistletoe depends on water and mineral salts absorbed from the host xylem through the haustoria. Therefore, one of the most important factors determining the success of this parasite is the dispersal of the seed onto a substrate suitable for germination.

The dissemination of seeds is accomplished primarily by birds, including the Cedar waxwing, Robin, and the Eastern bluebird (York, 1909; Martin, 1951). Surrounded by sticky viscin, the berries are appealing to birds; they attach to beaks, feathers, and feet or pass undigested through the alimentary tract. This mode of seed dispersal results in a clustered (Daubenmire, 1968) type of population distribution advantageous to mistletoe, a dioecious plant. The branching patterns of certain tree species could be related to the roosting preferences of birds which disperse the seed; thus the selection of particular tree species.

When temperature and moisture conditions are suitable, germination of the mistletoe seed is initiated. Haustorial penetration is accomplished as the tip or the radicle forms a flattened disc. Primary haustoria originate on the underside of the radicular disc and penetrate the bark, aided by the secretion of a digestive enzyme.

It is likely that various tree species possess a bark texture of different degrees of suitability for the adherence of the seed and the subsequent establishment of the radicular disc. The initial penetration of the bark may be related to bark thickness; it has been recognized (York, 1909) that trees such as *Ulmus* and *Celtis* possess a thin corky bark which is easily penetrated. It is also possible that a chemical inhibitor exists in the bark of those tree species which are not characteristically infested with mistletoe; a chemical could inhibit the digestive enzyme secreted by the primary haustoria. Studies have revealed also that the pH of the bark, which can be altered by air pollution, inhibits the growth of epiphytic plants such as lichens (Gilbert, 1970). The scarcity of mistletoe observed in urban areas of the Central Basin such as Nashville (McKinney and Hemmerly, 1977) could be related to this factor.

After dissolving through the bark, the haustoria spread out in the host cortex. Secondary haustoria, originating from the cortical haustoria, follow the path of the medullary rays, and penetrate the woody fibers into the xylem of the host. The ease with which these latitudinally-oriented haustoria penetrate the host xylem depends upon the distance between the woody fibers; thus, the occurrence of mistletoe on certain tree species may be due partly to the nature of the woody fibers. In addition, chemicals present in the host system could discourage the establishment of mistletoe.

TABLE 2. Occurrence of mistletoe-infested trees in nine counties of the northeastern Central Basin of Middle Tennessee.

TREE SPECIES	WILSON		SMITH		PUTNAM		SUMNER		MACON		DEKALB		TROUS-DALE		JACKSON		CANNON		TOTAL		
	#	%	#	%	#	%	#	%	#	%	#	%	#	%	#	%	#	%	#	%	
1. <i>Acer rubrum</i> L.			1	1.6	1	20.0							1	1.0	2	3.0			5	1.6	
2. <i>Carya ovata</i> (Mill.) K. Koch	1	3.9	2	3.2			3	20.0			1	4.8	3	3.0	1	1.6			11	3.5	
3. <i>Castanea dentata</i> (Marsh.) Borkh.			2	3.2															2	0.6	
4. <i>Celtis laevigata</i> Willd.	2	7.7	3	4.7			1	6.7					5	5.0	1	1.6			12	3.8	
5. <i>Fagus grandifolia</i> Ehrh.															1	1.6			1	0.3	
6. <i>Fraxinus americana</i> L.			2	3.2						1	4.8	28	27.0						31	9.9	
7. <i>F. pennsylvanica</i> Marsh.												4	4.0						4	1.3	
8. <i>Gleditsia triacanthos</i> L.			3	4.7						2	9.5	1	1.0	5	7.9				11	3.5	
9. <i>Juglans nigra</i> L.	2	7.7	5	8.0			2	13.3	1	11.1	1	4.8	2	2.0	1	1.6			14	4.5	
10. <i>Liquidambar styraciflua</i> L.														1	1.6				1	0.3	
11. <i>Liriodendron tulipifera</i> L.			1	1.6					2	22.2				1	1.6				4	1.3	
12. <i>Maclura pomifera</i> (Raf.) Schneid	1	3.9	4	6.4									1	1.0	1	1.6	1	11.1	8	2.5	
13. <i>Nyssa sylvatica</i> Marsh.										3	14.1			1	1.0				3	1.0	
14. <i>Ostrya virginiana</i> (Mill.) K. Kock.													1	1.0					1	0.3	
15. <i>Platanus occidentalis</i> L.									1	11.1					1	1.6			2	0.6	
16. <i>Prunus serotina</i> Ehrh.										1	4.8								1	0.3	
17. <i>Quercus alba</i> L.	1	3.9											1	1.0	1	1.6			3	1.0	
18. <i>Q. prinus</i> L.											1	4.8							1	0.3	
19. <i>Robinia pseudo-acacia</i> L.	5	19.0	9	14.0	2	40.0	3	20.0	1	11.1	1	4.8	14	13.7	2	3.0			37	11.9	
20. <i>Sassafras albidum</i> (Nutt.) Nees.											1	4.8							1	0.3	
21. <i>Ulmus alata</i> Michx.													1	1.0					1	0.3	
22. <i>U. americana</i> L.	13	50.0	27	43.0	2	40.0	4	26.7	3	33.4	7	33.3	17	16.7	20	31.2	1	11.1	94	29.9	
23. <i>U. rubra</i> Muhl.			4	6.4					1	11.1	2	9.5	16	15.7	26	40.5			49	15.6	
24. <i>U. serotina</i> Sarg.	1	3.9											7	6.9				7	77.8	8	2.5
25. <i>U. thomasi</i> Sarg.							2	13.3											2	0.6	
TOTALS	26	100.0	63	100.0	5	100.0	15	100.0	9	100.0	21	100.0	102	100.0	64	100.0	9	100.0	314	100.0	

There is a conspicuous scarcity or absence of mistletoe hosts of the genus *Acer* (particularly *A. saccharinum*), and also species of the Salicaceae and Fagaceae. There is no quantified information available concerning occurrences of tree species within the Basin by species and county. There may be, for example, fewer trees of *Quercus* spp. in the Basin than those of *Ulmus* spp., but the oaks are certainly represented, and presumably would be attacked more often by mistletoe if they did not possess some type of defense mechanism.

CONCLUSIONS

Phoradendron serotinum has demonstrated an ability to parasitize a variety of deciduous trees throughout its range. However, there is considerable selectivity exhibited by the parasite; the host species affected often varies from the relative abundance of potential hosts.

A survey of the northeastern portion of the Central Basin revealed (Table 2) *Ulmus* spp. (*U. americana* 29.9% and *U. rubra* 15.6%) to be, along with several other species, common hosts of American mistletoe: *Robinia pseudo-acacia* (11.9%), *Fraxinus americana* (9.9%), and *Juglans nigra* (4.5%). Surveys conducted in the central and southern portions of the Basin listed *Ulmus* spp. (*U. americana* 34.5% and *U. serotina* 12.5%) and also *Carya ovata* (18.8%), *Fraxinus americana* (5.9%), and *Juglans nigra* (3.9%). These results contrast with those of Lawrence County, located on the Highland Rim, which listed *Nyssa sylvatica* (89.9%) as the predominant host.

Reasons for the occurrence of mistletoe on various host species in different portions of Middle Tennessee (or other areas) are not presently fully understood. Among the possible factors suggested are: (1) Availability of potential host trees, (2) Air pollution which could alter the pH of the

bark and thereby inhibit germination or haustorial penetration, (3) Soil nutrients and pH in which host trees are growing, (4) The availability of water to the host, and thereby to the parasite.

To have a complete understanding of the host specificity of American mistletoe in Middle Tennessee, surveys of the remainder of the area need to be concluded. Also, experimental germination studies should be conducted regarding the selective parasitism exhibited by the plant in relationship to various potential hosts, and in all regions of its geographical distribution.

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