May 23, 1958

To the Graduate Council:

I am submitting herewith a thesis written by Harry L. Sherman entitled "The Vegetation and Floristics of Five Gorges of the Cumberland Plateau." I recommend that it be accepted for twelve quarter hours of credit in partial fulfillment of the requirements for the degree of Master of Science, with a major in Botany.

Royal E. Shanks
Major Professor

We have read this thesis
and recommend its acceptance:

A. J. Sharp

Accepted for the Council:

Dale Brantley
Dean of the Graduate School

THE VEGETATION AND FLORISTICS OF FIVE GORGES OF THE CUMBERLAND PLATEAU

A THESIS

Submitted to
The Graduate Council
of
The University of Tennessee
in
Partial Fulfillment of the Requirements
for the Degree of
Master of Science

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by

Harry L. Sherman

June 1958

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I. INTRODUCTION

The unglaciated Appalachian Plateaus, as part of the more extensive Appalachian highlands, represent some of the oldest land area in North America with respect to continuous land masses suitable for occupancy by terrestrial plants. These plateaus, along with the Blue Ridge Province and the Ozark and Ouachita highlands, had long been above marine waters when the Coastal Plain emerged, probably during the Miocene Epoch (Fenneman 1938). With the formation and southward advance of the great ice sheets of the Pleistocene, the existing plant life of the glaciated region was destroyed, thereby drastically reducing the botanical age of the otherwise ancient land area north of the glacial boundary (Fernald 1931; Harshberger 1911).

The character of the forest which occupied the Southern Appalachian region (including the present Blue Ridge Province and the Cumberland Plateau) since Cretaceous time and the effect of the period of glaciation upon this forest have been of considerable interest to phytogeographers (Braun 1938, 1947, 1950, 1955; Core 1938; Harshberger 1911; Sharp 1941). Harshberger described the mixed forest south of the glacial border as a remnant of the Tertiary forest which persisted during the Pleistocene with its greatest density in the region drained by the Tennessee River and its tributaries. Braun (1950) considered the Tertiary forest to be the progenitor of the present-day Mixed Mesophytic Forest. She described this modern forest as coextensive with the unglaciated Appalachian Plateaus ". . . except the northeast arm of the Unglaciated Allegheny Plateau, and the southernmost end of the Cumberland Plateau." She further stated: "The Mixed Mesophytic association . . . is the most complex and the oldest association of the Deciduous Forest Formation . . . and from it or its ancestral progenitor, the mixed Tertiary forest, all other climaxes of the deciduous forest have arisen."

The ancestral nature of the Southern Appalachian flora and the unique characteristics of the Mixed Mesophytic Forest in general make this area exceedingly interesting to plant geographers. This interest may be indicated by the following quotation from Mohr (1901) concerning Lookout Mountain in northeast Alabama:

> . . . along the low, damp banks of Little River, there occurs a strong mingling of [Southern Appalachian] types . . . with plants of the lower ranges within the Carolinian area, giving rise to a varied flora, the like of which has not been observed in any other part of the mountainous region of Alabama. When the low elevation of this extremely limited spot is considered . . ., the suffusion of types from different life zones admits of no explanation on the ground of climate or local influences controlling plant distribution, but points clearly to a disjunction of floral conditions due to geological changes.

A number of papers concerning the composition of the forests of the unglaciated Appalachian Plateaus and the affinities of the species which occur in the region have been written by various authors. Perhaps the most thorough discussions are contained in a series of articles by Braun (1938, 1940, 1942, 1947) and in her book on the deciduous forests of eastern North America (1950). Work of a more intensive nature, but more limited in scope, has been completed by Caplenor (1954) and partial results have been published by him in a paper on the Fall Creek Falls system of gorges in Tennessee (1955).

Most of the work by Braun was done in the northern portion of the Cumberland Plateau (especially in Kentucky), in the Unglaciated Allegheny

Plateau and in the Cumberland Mountains. The work by Caplenor apparently represents the only systematic study of any of the gorges of the southern district of the Cumberland Plateau. However, several of the protected ravines of the plateau outlier section (Warrior Tablelands) of northern Alabama have received some attention in the literature (Harper 1919, 1937, 1943a; Harvill 1949, 1950, 1951; Segars et al., 1951), mostly because of the occurrence of hemlock at or near its southern limit in this region. Few of these papers provided a comprehensive list of the species occurring in the gorges. Rather, attention was focused on the dominant canopy and understory species and a few others of special interest.

This paper presents further information concerning the vegetation and floristics of the gorges of the Cumberland Plateau of Tennessee, Georgia, and Alabama. An attempt has been made to characterize the vegetation of five of these gorges, and to provide lists of woody species known to occur in each. Information concerning the continental affinities of the species involved is included, and a number of general distribution maps have been prepared with the help of the curators of various herbaria. A review of the history of the Southern Appalachian region in so far as it is pertinent to this study has been provided.

II. LITERATURE SURVEY

Early Development of the Deciduous Forest

The history of the vegetation within the Southern Appalachians, involving the origin and dispersal of species, has been discussed at length in the literature. The conclusions reached by the various authors have been based to a large degree upon the fossil evidence available and upon present distributions and affinities. Considerable speculation is necessarily involved, and differences of opinion are to be expected.

It is generally agreed that the modern deciduous forest had its beginning with the rise of the dicotyledonous angiosperms at some time during the Mesozoic era (Jurassic or earlier), and that these were becoming dominant over the primitive cycads and gymnosperms at least by Upper Cretaceous time. Just where and when the angiosperms arose, from what ancestral stock, and the direction of their subsequent dispersal are matters of debate (Axelrod 1952; Camp 1947; Fernald 1926; Just 1947, 1948; Stebbins 1940, 1947; Wulff 1950).

The origin and early dispersal of the flowering plants are of little importance in so far as this study is concerned. It is sufficient to say that the modern Cumberland Plateau forest had its origin in the evidently wide-spread and more or less ecologically undifferentiated Cretaceous forest, and is the result of climatic, topographic, and genetic changes since that time. When considered in the light of Braun's statement that the Tertiary forest was the "progenitor" of the Mixed Mesophytic forest of today (and all other deciduous forest climaxes), even the Cretaceous forest becomes of secondary importance.

It should be noted, however, that the Upper Cretaceous flora probably did present a somewhat modern aspect because of the presence of such deciduous genera as Acer, Celtis, Diospyros, Fagus, Juglans, Liriodendron, Magnolia, Populus, Quercus, and Salix (Braun 1950). Along with these were the modern gymnospermous genera Pinus, Picea, Thuja, Sequoia, Torreya (Tumion), Araucaria, and Podocarpus.

According to Schuchert and Dunbar (1941), most of eastern North America probably was reduced to a peneplain during the Jurassic and remained low and flat throughout the Cretaceous period. It was early in Late Cretaceous time that an inland sea filled the Rocky Mountain geosyncline from the Gulf of Mexico to the Arctic Ocean, dividing the continent into two land masses. Near the close of the period, the base-leveled eastern land mass was uplifted and the Schooley Cycle of erosion (discussed later) was initiated. It was during the succeeding Tertiary period (Miocene and later) that the Schooley peneplain was perfected, uplifted, and cut down again (in some parts). It was during this time, also, that much of the Coastal Plain emerged.

The Tertiary Forest

The Wilcox Flora, from the rich Lower Eocene deposits of the southeastern and south-central states, has provided considerable evidence concerning the early Tertiary forest of southeastern North America. This fossil flora was a part of the extensive Neotropical-Tertiary Flora which

Chaney (1947) described as extending northward to latitude 37 degrees in the Mississippi embayment region of Eocene time. According to Berry (1930), there was a gradual displacement of the temperate to warm-temperate Cretaceous flora by the Neotropical-Tertiary Flora during the Eocene. He noted the absence of such temperate genera as Betula, Acer, Cornus, Fagus, Liriodendron, Pinus, Salix, Sassafras, Juniperus, Viburnum, and Quercus. These genera had been present in the Upper Cretaceous holarctic flora, and most of them had ranged northward into Greenland and Alaska. Brown (1944, 1946) later revised Berry's original identifications to include Betula, Fagus, Sassafras, Populus, Staphylea and other genera in the Wilcox.

Sharp (1951) compared the modern southeastern flora with the Wilcox (as revised by Brown) and found that eighty-two of 137 genera still persist in this region.

Apparently, most of the members of the temperate Cretaceous flora became restricted to the higher latitudes (as part of the Arcto-Tertiary Flora) or to the higher elevations as a result of the warmer climate of the Eocene (Axelrod 1952; Chaney 1947). Berry (1937) stated that the climate of Middle Eocene evidently became progressively warmer and reached its thermal maximum during Upper Eocene or the succeeding Oligocene epoch. It was during this period that the greatest northward extension of the warm-temperate or subtropical elements of the Neotropical-Tertiary Flora occurred.

A trend toward a cooler and less humid climate became pronounced toward the close of the Oligocene epoch, and the Arcto-Tertiary flora of the higher latitudes and altitudes migrated southward and downward (Chaney 1947). Berry (1937) noted this shift in Miocene deposits in which subtropical trees apparently were being replaced by temperate species from the north. Most of the warm-temperate and subtropical species of the eastern United States apparently had been eliminated by the close of the Miocene. The Neotropical-Tertiary flora now survives in the Antilles, northern South America, Central America and Mexico, with relics in southern Florida and sparsely northward (Chaney 1947). The tropical element in the modern southeastern flora can be attributed partly to "relics" of this early Tertiary flora.

Chaney noted that the Arcto-Tertiary flora (which replaced the Neotropical-Tertiary) included ". . . a long list of angiosperms and gymnosperms of which the more common and widely distributed (were): *Acer*, *Alnus*, *Betula*, *Carpinus*, *Castanea*, *Cercidiphyllum*, *Cornus*, *Crataegus*, *Fagus*, *Fraxinus*, *Ginkgo*, *Juglans*, *Pinus*, *Platanus*, *Populus*, *Quercus*, *Salix*, *Sequoia*, *Taxodium*, *Tilia*, *Ulmus*, and *Zelkova*." The Arcto-Tertiary forest evidently was somewhat like the modern mixed mesophytic stands of the unglaciated Appalachian Plateau region and the cove forests of the Smoky Mountains. Cain (1943) pointed out that 27 per cent of the genera represented in the flora of the cove forests of the Smokies had been reported from Cretaceous or Tertiary deposits in the southeast, while another 54 per cent ". . . are probably as ancient as the middle or late Tertiary as shown by their modern areas."

During the Late Tertiary (Upper Miocene and Pliocene) the continental climate apparently was much the same as it is today, resulting from the expansion of dry interior regions and the appearance of sub-polar climates at high latitudes (Axelrod 1952). According to Axelrod and other writers, the final disruption of the transcontinental Tertiary flora was completed during this period, resulting in widely-separated forests of very similar composition in eastern Asia and southeastern North America. A number of Southern Appalachian species now have their closest living relatives in eastern Asia, and a large number of genera are restricted to the two regions.

The Effect of Changes in Topography

The effect of changing topography upon the distribution of plants during Tertiary time has been suggested as an important factor in the history of the southeastern flora. This has been given as a possible explanation of the present distribution of a large number of disjunct and endemic species within the Southern Appalachians. The following statements are summarized, for the most part, from Braun's discussions of topographic changes and their possible consequences (1947, 1950, 1955).

The area suitable for occupancy by the lowland flora of the Middle and Upper Eocene was greatly expanded during the Schooley cycle of erosion when much of the interior highland was base-leveled. At the same time, plant communities favored by diverse topography were restricted as the highlands gradually became smaller in area. The resulting topography (culminating in Miocene time) may be pictured as an expanse of flat to rolling lowland with slow-moving, meandering streams. Due to resistant rocks or great mass in headwater positions, some areas within the Southern

Appalachians were never reduced to base level, and their topography is diverse even today (*i.e.*, the Cumberland Mountains and the Blue Ridge and Unaka ranges).

During Late Tertiary (Miocene epoch), the Schooley peneplain was uplifted and a new cycle of erosion (the Harrisburg Cycle) was initiated. The mixed forest that had been restricted to regions of diverse topography expanded into new habitats afforded by the dissection of the uplifted tableland by rejuvenated streams (as in the gorges of the Cumberland Plateau). The present endemism and disjunctive distribution of some Southern Appalachian species perhaps can be attributed, in part, to genetic shifts in the character of their restricted populations. The lowland flora which had become widespread before the Miocene uplift began retreating before the changing environment, possibly leaving behind what are known today as relic colonies of Coastal Plain plants in the Cumberland Plateau and other Southern Appalachian regions.

The effect of the changing topography seems to be evidenced by the occurrence of the most typical mixed mesophytic forest in places where the Schooley Peneplain was never perfected (the Cumberland Mountains, the western escarpment of the Cumberland and Allegheny Plateaus, and the coves of the eastern mountains). According to Braun (1950), many of the disjunct and endemic species of these unreduced areas (*Buckleya distichophylla*, *Shortia galacifolia*, *Diphylleia cymosa*, *Rhododendron catawbiense*, *Stewartia ovata*, *Clethra acuminata*, *Gaylussacia brachycera*, *Cladrastis lutea*, and *Conradina verticillata*) may be among those which were greatly restricted by the reduction of mountainous areas during the Schooley cycle. A number of these species have close relatives in eastern Asia, indicating that they are direct descendents from Arcto-Cretaceous or Arcto-Tertiary ancestry.

The Effect of Pleistocene Glaciation

According to Gleason (1922), the Arcto-Tertiary flora had little or no latitudinal differentiation (within the temperate unit), and segregation into a northern coniferous forest and a southern deciduous forest probably began only with the approach of the first glacial period. Braun (1950) made the following statement:

> The segregation of a northern spruce-fir forest came late in forest history. It may have been pre-Pleistocene, altitudinal or latitudinal, or both; it may have resulted from the climatic stress of glacial climate, and been aided by the vast expanse of area of raw soil material unsuited to invasion by broad-leaved species; it may have been perfected only in late Pleistocene time.

Fossil evidence related to the effect of Pleistocene glaciation south of the glacial fronts is meager and almost entirely from Coastal Plain or other lowland deposits. Such evidence as is available presents a somewhat confused picture of the distribution and composition of the vegetation of the Southern Appalachians during this period. According to a number of writers (Braun 1950, 1955; Gleason 1922; Harshberger 1911), mass displacement of the southern forest by migrating northern species was limited to a relatively narrow band of conifers just south of the ice fronts.

Braun (1950) made the following statements concerning the effects of glacial climate:

> That it did not cause pronounced shifts in the position of vegetation of the Cumberland Plateau and Southern Appalachian Mountains is indicated by the wealth of ancient relic endemics of Asiatic relationship which could not conceivably have migrated away from, and returned to the few areas retaining their Miocene topography . . . The deciduous forest did not, en masse, move far south, and there is nothing in the evidence . . . to indicate that it was ever completely displaced by more northern vegetation types except close to the ice front. How close may have depended upon the nature of the topography.

Wolfe (1942) has presented evidence that the effects of glaciation were not exceedingly severe just south of the ice front in southern Ohio. He cited the presence of a number of southern and southeastern species now present in the area and proposed that they had persisted there during the Pleistocene.

An opposing view was expressed by Core (1938) who maintained that ". . . a climate cool enough to have produced glaciers within 25 miles of the northern tip of West Virginia could not have but exerted a profound influence upon the vegetation . . ." He further suggested that West Virginia, southern Ohio, and southern Pennsylvania must have presented the aspect of an Arctic tundra, while many Canadian species were forced hundreds of miles farther south. Deevey (1949) has taken an even more extreme point of view, suggesting that the temperate species of the southeast were pushed south of the Rio Grande and deep into the Florida peninsular.

Just how much of the so-called "northern" element now evident in the Southern Appalachian flora is due to Pleistocene migrations is problematical. Sharp (1941) stated that the lower temperature of the glacial period probably extinguished some species previously present in the region, but the total number must have been substantially increased with the arrival of migrating forms. He further stated that:

> Aggressive northern species not previously present in the Southern Appalachians may have migrated southward and subsequently met one of three fates: (1) they may have later retreated northward, leaving no record in the south, (2) they may now have a continuous range to the north, (3) they may still be restricted or endemic to these mountains.

Some of the so-called "northern" species now present in the Southern Appalachians probably were present in the region before glaciation, and migrated northward for the first time in the late Pleistocene.

Modern Forests of the Plateau Tablelands

Some of the earliest descriptions of the forests of the Cumberland Plateau are contained in writings by Foley (1903), Hall (1910), Harper (1913), Harshberger (1911), Killebrew and Safford (1874), Mohr (1901) and Sargent (1884). These writers agreed, for the most part, that the forest of the tablelands, or plateau surface, was predominantly oak-hickory, with lesser amounts of other hardwoods. Sargent wrote of the plateau in Tennessee (and the eastern mountains) as being covered ". . . with a heavy forest of oak and other hardwoods . . . constituting one of the finest bodies of timber now standing in the United States."

Mohr (1901) described the tableland forest of Alabama as a xerophytic type consisting largely of chestnut oak (*Quercus prinus*), associated with post oak (*Q. stellata*), southern red or Spanish oak (*Q. falcata*), blackjack oak (*Q. marilandica*), black oak (*Q. velutina*), scarlet oak (*Q.* coccinea), white oak (*Q. alba*), mockernut hickory (*Carya tomentosa*), pignut (*C. glabra*) and blackgum (*Nyssa sylvatica*).

Writing of Sand Mountain, Mohr stated that ". . . the woodlands support from 25 to 35 timber trees of various species per acre, affording 5,000 to 6,000 feet B. M. of merchantable lumber of all grades, the largest amounts being derived from Spanish oak and the less valuable black oak . . ." Of Lookout Mountain, he wrote: ". . . this mountain was recently covered with a fine hard-wood forest, chiefly of oaks, and was noted for the abundance of white oak timber (*Quercus alba*) and tan-bark oak [*Q. prinus*] . . ."

Harper (1913) attached considerable importance to the role of pine in the original forest of the Alabama tablelands. He estimated the proportion of pines (and other evergreens) at 29 per cent, consisting largely of shortleaf (*Pinus echinata*) and loblolly (*P. taeda*), with Virginia pine (*P. virginiana*) and longleaf (*P. palustris*) in suitable habitats.

Hall (1910) divided the Tennessee portion of the plateau into coves, slopes, plateau ridges, and plateau swales. He listed chestnut oak or one of the black oaks as the dominant tree of the slopes, with scarlet oak, white oak, hickory, chestnut, blackgum, and occasionally shortleaf pine as associates. The forests of the plateau swales contained black oak, white oak, southern red oak, and scarlet oak (with varying amounts of hickory) as dominants, with blackgum, post oak, chestnut oak, chestnut, and shortleaf pine sometimes included. The dry woods were found on the plateau ridges, where stunted growths of post oak, blackjack oak, scarlet oak, chestnut oak, sand hickory (*Carya pallida*), blackgum and chestnut occurred.

The role which chestnut played in the original forests of the coves and uplands is indicated by the following quotation from Ashe (1912):

> It is common on the slopes of the Cumberland tableland, especially on the sandstone soils which have a sufficient depth and are not too rocky; in such situations it forms a large portion of the forest. Chestnut is always entirely absent, however, on the thin-soiled and stony portions of the tableland, especially near the southern end.

Braun (1950) more recently described the upland forest as being composed mostly of oak, oak-hickory, and oak-pine communities in which white oak, chestnut oak, scarlet oak, southern red oak, post oak, northern red oak, pignut and mockernut hickories, blackgum, sourwood, persimmon, dogwood, shortleaf and Virginia pines, and other xerophytic species are found.

The Forests of the Coves and Gorges

The unique character of the mixed mesophytic stands in the coves and gorges of the plateau was well recognized in early botanical literature for the region. Killebrew and Safford (1874) described the slopes, gorges, and ravines of the Tennessee portion as being very heavily timbered with chestnut, tuliptree, maple, walnut, buckeye, cherry, basswood, and beech. Hall (1910) listed these same trees for his "cove forest", but also included white oak, black oak, red oak, chestnut oak, hickories, ash, elm, hemlock, white pine, and cucumber tree (*Magnolia acuminata*).

Mohr (1901) described a mesophytic forest of the valleys and gorges of the Alabama plateau as containing beech, elm, butternut (*Juglans cinerea*), basswood, swamp chestnut oak (*Quercus michauxii*), and three species of magnolia (*Magnolia acuminata*, *M. macrophylla*, and *M. tripetala*) in addition to a number of the more xerophytic species previously mentioned.

The occurrence of eastern hemlock (*Tsuga canadensis*) in the gorges of the Alabama plateau (at the southern limit of its range) has stimulated much interest in these unique habitats, especially in the Warrior Tablelands (Harbison 1902; Harper 1919, 1937, 1943a; Harvill 1949, 1950, 1951; Mohr 1901; Segars *et al.*, 1951). The southernmost station for hemlock (Jefferson County) was reported by Harper in 1919, following earlier records by Mohr (Winston County) and Harbison (Jackson County). Segars, Crawford and Harvill (1951) added a number of new stations during the summer of 1949, including four new county records. One of these stations, Stuck's Creek in Lamar County, is only twelve miles from the Mississippi state boundary.

In his report on the occurrence of hemlock along Dismal Branch in Franklin County, Harper (1937) listed a number of associated woody species, including *Liriodendron tulipifera*, *Liquidambar styraciflua*, *Fagus grandifolia*, *Castanea dentata*, *Nyssa sylvatica*, *Quercus rubra*, *Oxydendrum arboreum*, *Ilex opaca*, *Magnolia macrophylla*, *Cornus florida*, *Carpinus caroliniana*, *Decumaria barbara*, *Xanthorhiza simplicissima*, *Kalmia latifolia*, *Hydrangea quercifolia*, *Symplocos tinctoria*, *Hamamelis virginiana*, *Asimina parviflora* (?), *Lindera benzoin*, *Euonymus americanus*, *Aralia spinosa*, *Viburnum nudum* (?), *Stewartia ovata*, *Gelsemium sempervirens*, *Vaccinium arboreum*, *Vaccinium vacillans*, *Pinus virginiana*, and *Amelanchier canadensis* (*A. arborea*).

Harvill (1951) wrote the following statement concerning King Cove, Lawrence County:

> The luxuriant forest which composes the cove is rich in species and it is impossible to designate any as especially characteristic. Among the most common trees are: *Tsuga canadensis* (L.) Carr., *Magnolia acuminata* L., *M. macrophylla* Michx., *M. tripetala* L., *Liriodendron tulipifera* L., *Betula lenta* L., *Juglans cinerea* L., *Fagus grandifolia* Ehrh., *Quercus alba* L., *Acer saccharum* Marsh., and *Tilia heterophylla* Vent.

Harbison (1902) made the following statement about Pisgah Gorge in Jackson County:

> In this gorge plants of the Alleghanian and Carolinian plant life areas intermingle. Here *Betula lenta* L. and *Tsuga canadensis* (L.) Carr. make trees of considerable size. *Rhododendron catawbiense* Michx. and *Hydrangea quercifolia* Bartr. grow side by side by side. . . *Ribes cynosbati* L. is common along the rocks throughout the gorge above the limestone formation. *Diervilla rivularis* Gattinger is common about the cascades, and on the rocks in dry situations *Philadelphus hirsutus* Nutt. and *Hypericum aureum* Bart. [*H. frondosum* Michx] are found. The latter usually found growing in calcareous soil, finds here a congenial habitat on the sandstone, growing luxuriantly and blooming profusely. Along the stream *Azalea arborescens* Pursh, *Ilex verticillata* (L.) Gray, *Viburnum cassinoides* L. and *Stuartia pentagyna* L'Her. [*Stewartia ovata* (Cav.) Weatherby] are common shrubs.

One of the few notes on the vegetation of Cloudland Canyon (Dade County, Georgia) was published by Cronquist (1949), who mentioned a well-developed beech-maple-hemlock forest and noted the presence of *Spiraea virginiana*. This rare shrub also was listed by Caplenor (1954) as occurring in the Fall Creek Falls system. A much earlier collection was made by Ruth at Lula Falls on Lookout Mountain (Dade County).

The Mixed Mesophytic Forest

Braun (1950) is credited with the development of the concept of the Mixed Mesophytic Forest as the climatic climax of the unglaciated Appalachian Plateaus, including the southern or Cliff Section of the Cumberland Plateau. In general, the Mixed Mesophytic Forest may be defined as a climax association in which dominance is shared by a number of species growing in various combinations, with beech (Fagus grandifolia), yellow buckeye (Aesculus octandra), cucumber tree (Magnolia acuminata), basswood (Tilia heterophylla), tuliptree (Liriodendron tulipifera), sugar maple (Acer saccharum), white oak (Quercus alba), and hemlock (Tsuga canadensis) as the most frequent dominants. The exact composition and the relative abundance of the included species may vary with the association-segregates, but the most characteristic canopy trees are considered by Braun to be Tilia heterophylla and Aesculus octandra.

Whittaker (1956) has stated that the mixed mesophytic stands of the Cumberland Mountains (the center of the association, according to Braun) may best be compared with the cove forest transition of the Smoky Mountains. Braun (1950) also noted the similarity of the mixed mesophytic stands in the plateau and the cove forests of the mountains and considered the latter to be advanced disjuncts from the main body of the Mixed Mesophytic Forest association.

Concerning the climax vegetation of the Cliff Section of the Cumberland Plateau, Braun (1950) stated:

> There is no doubt that oak or oak-hickory forest prevails over the large area of submaturely dissected plateau . . . in Tennessee and Alabama. But a submature topography does not support the regional

> climax. This forest type, although areally dominant, no more represents the climatic climax than do the small patches of this same community on the ridge-tops of the plateau farther north. It is a physiographic climax maintained by topography (old) and soil (sandy and leached or lithosol) and frequently affected by fire. Where the plateau is dissected, on the slopes of valleys cut into the plateau and of ravines indenting it, even along the bold west facing escarpment of the Cumberland Plateau, mixed mesophytic forests are seen. If the whole plateau were dissected, as it is farther north, mixed mesophytic forest would be the prevailing type. Although areally limited, it is the climax of this area; hence, almost all of the Cumberland Plateau is included in the Mixed Mesophytic Forest region.

Caplenor (1954) concluded that the climax community of the Fall Creek Falls system of gorges is mixed mesophytic and that the slight changes that are occurring in other communities are in the direction of the mixed mesophytic type.

Continental Affinities

The continental affinities of the flora of the Cumberland Plateau and the Southern Appalachians in general have been discussed by Cain (1930) and Braun (1937b).

Working with 248 woody species within the Great Smoky Mountains and vicinity, Cain found that the area fell well within the range of 69 per cent (intraneous flora), while the remaining 31 per cent reached the northern or southern limit of their ranges within the area (extraneous flora).

Braun summarized her work as follows:

> . . . the flora of the Cumberland Plateau and the Cumberland Mountains in Kentucky displays strong southern affinities, indicated by (1) the large proportion of species of southern range in the intraneous flora, (2) the Southern Appalachian species, and (3) the Coastal Plain species. Northern species are present and are interpreted as representing survival from the undifferentiated Tertiary flora.

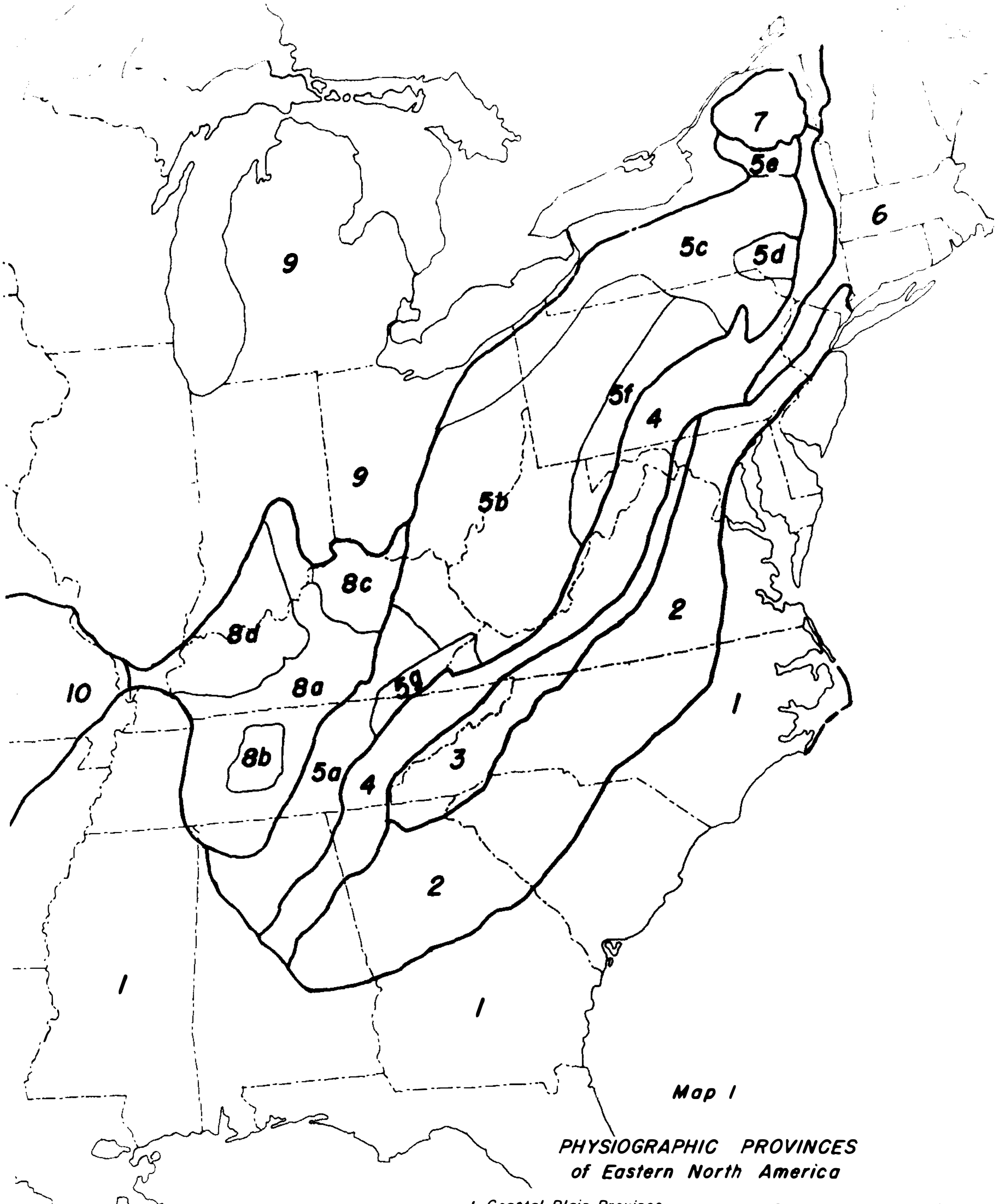
III. GENERAL DESCRIPTION OF THE STUDY AREA

Geology and Topography

The Appalachian Plateaus, as defined by Fenneman (1938), are composed of seven sections which differ in the character of their underlying rocks, in altitude, in degree of dissection, and in the presence or absence of glaciation. The largest and, according to Fenneman, most typical section is the Unglaciated Allegheny Plateau of western Pennsylvania, western Virginia, eastern Ohio, and eastern Kentucky (see Map 1). The Cumberland Plateau is a southern extension of the Allegheny, with the arbitrary boundary placed within the drainage basin of the Kentucky River. In general, the rocks of the Cumberland section are more resistant than those to the north, and the plateau surface is much less dissected (Fenneman 1938).

Of the seven sections of the Appalachian Plateau Province, as recognized by Fenneman, the Cumberland Plateau section is the only one considered in this report. The tablelands which comprise the plateau should not be confused with the much more rugged Cumberland Mountains which embrace an area some 150 miles long and twenty-five miles wide in Virginia, Kentucky, and Tennessee. These maturely dissected highlands represent a separate section of the Appalachian Plateau Province, although the two sections were sometimes combined by earlier authors and collectively referred to as the "Cumberland Mountains."

In the less dissected portions, which represent the prevailing topography of the region, the Cumberland Plateau is flat to rolling up-



Map 1

PHYSIOGRAPHIC PROVINCES
of Eastern North America

1. Coastal Plain Province
2. Piedmont Province
3. Blue Ridge Province
4. Ridge & Valley Province
5. Appalachian Plateaus Province
   a. Cumberland Plateau
   b. Unglaciated Allegheny Plateau
   c. Glaciated Allegheny Plateau
   d. Catskill Mountains
   e. Mohawk Section
   f. Allegheny Mountains
   g. Cumberland Mountains
6. New England Province
7. Adirondack Province
8. Interior Low Plateau
   a. Highland Rim Section
   b. Nashville Basin
   c. Bluegrass Section
   d. Shawnee Section
9. Central Lowland
10. Ozark Plateaus Province

(Map redrawn from Braun, 1950)

land underlain by the resistant sandstones of the Pottsville formation (Pennsylvanian system). The plateau surface represents a remnant of the Schooley Peneplain which was perfected in Miocene time (Fenneman, 1938). The Pennsylvania rocks are coextensive with the coal fields of the entire Plateau Province, and are often called the coal measures by geologists. They are chiefly sandstones, conglomerates and shales, with intermingled beds of coal and fire clay.

The resistant nature of the Pottsville sandstones and their great thickness (sometimes as much as 700 feet) maintain the dominant immature topography of the plateau. Sapping occurs only at the edges (escarpments) where the weaker, underlying Mississippian limestones are exposed. The escarpments (Figure 1) form prominent boundaries where the plateau adjoins the Ridge and Valley Province to the east and the Interior Lowland Plateau (Highland Rim) to the west. The western portion of the plateau in Tennessee rises gradually from 1,800 feet above sea level near the Kentucky line to more than 2,000 feet in the southern part of the state. The elevation declines to 1,400 feet before reaching the Tennessee River, and the plateau gradually dips beneath the Coastal Plain sediments in northwest Alabama (Fenneman, 1938).

Where streams flowing off the plateau surface have eroded through the resistant sandstones and into the weaker limestones and shales below, deep and rugged gorges have been formed. It is in these gorges that many species of the Tertiary forest evidently were able to survive during diverse climatic periods. The mixed mesophytic vegetation that exists in these protected habitats provides a basis for classifying the climax vegetation of the entire plateau as Mixed Mesophytic (Braun 1950).

Figure 1. View of the eastern escarpment of the main Cumberland Plateau from the Sequatchie Valley near Whitwell, Tennessee.

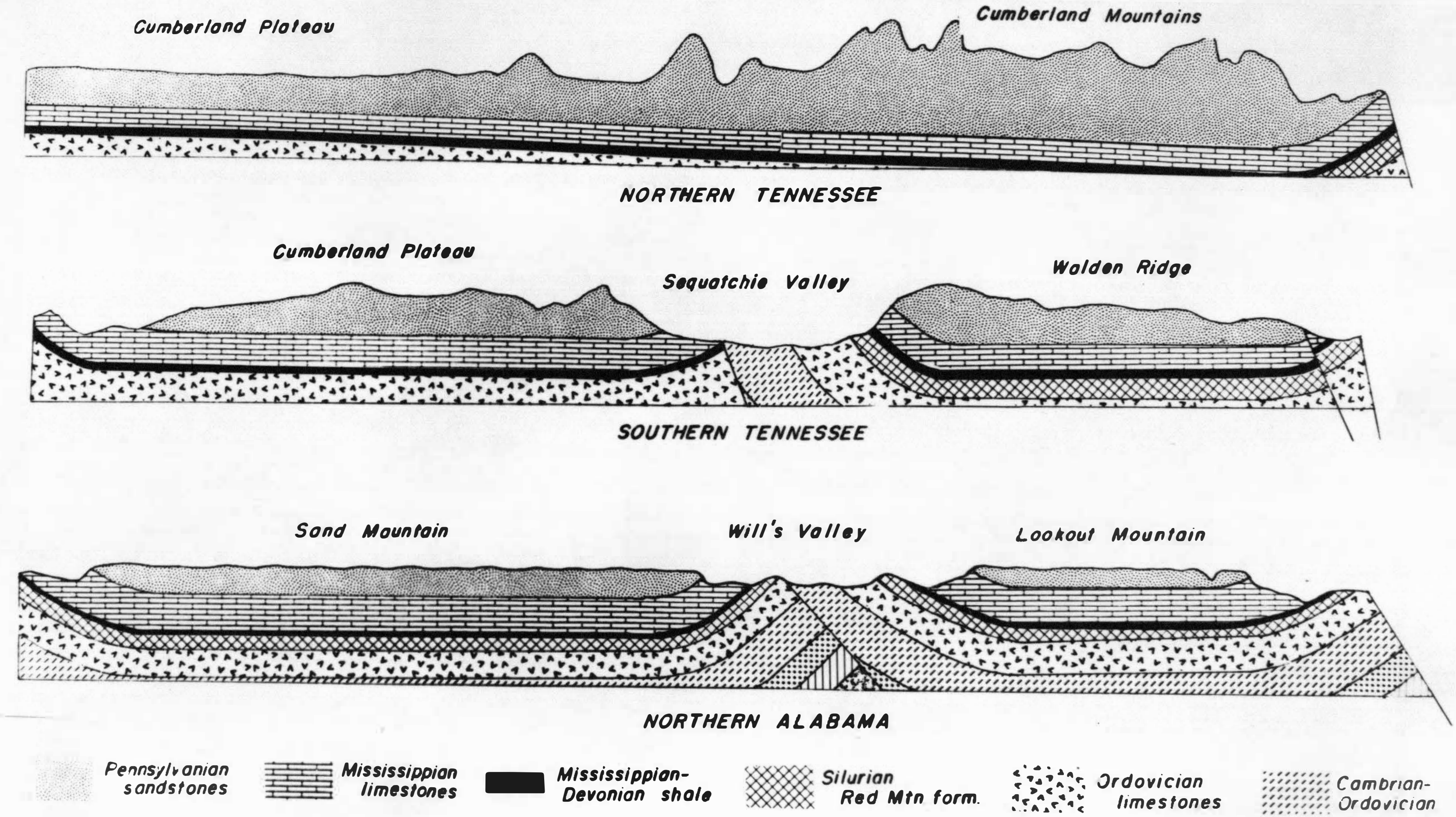
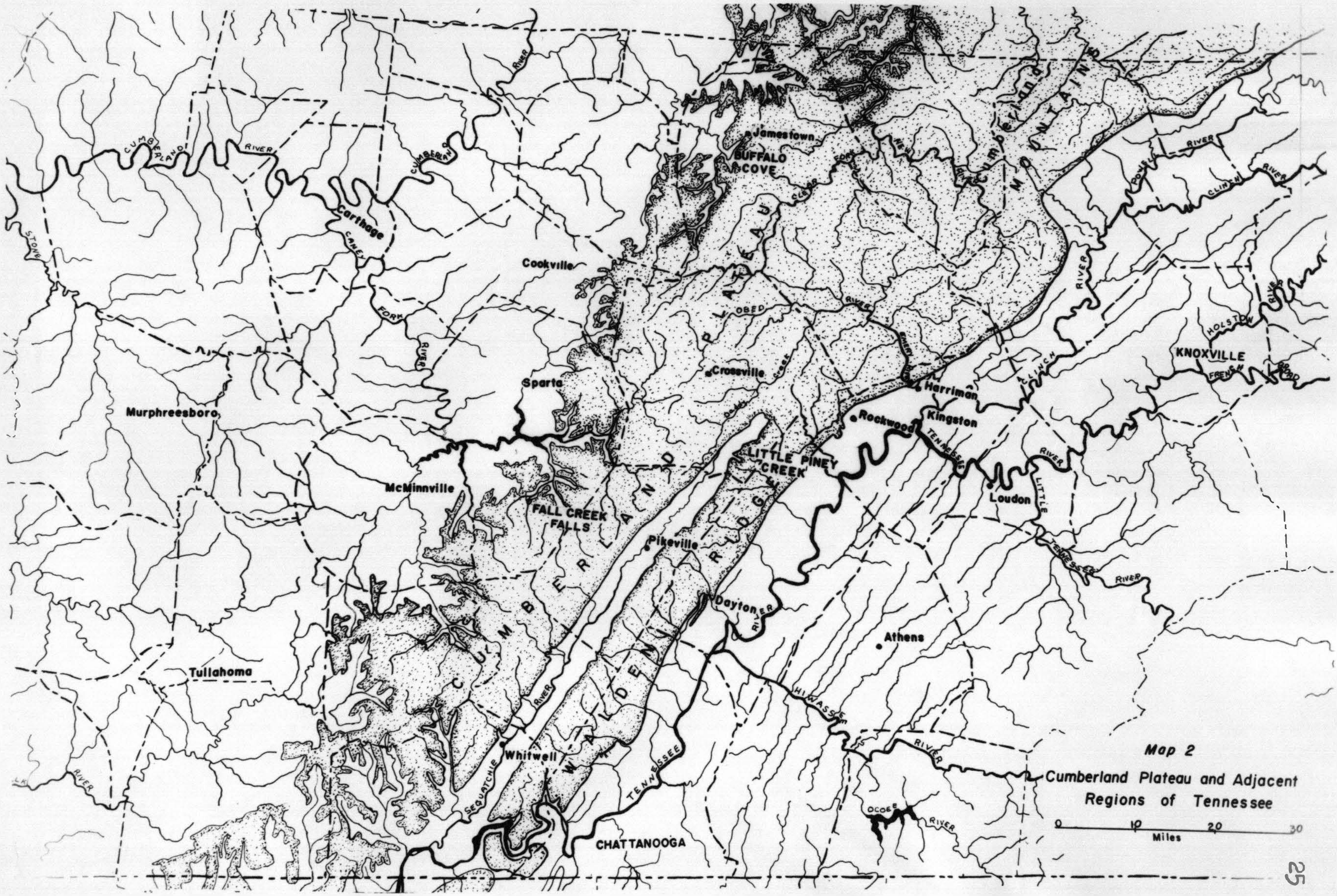


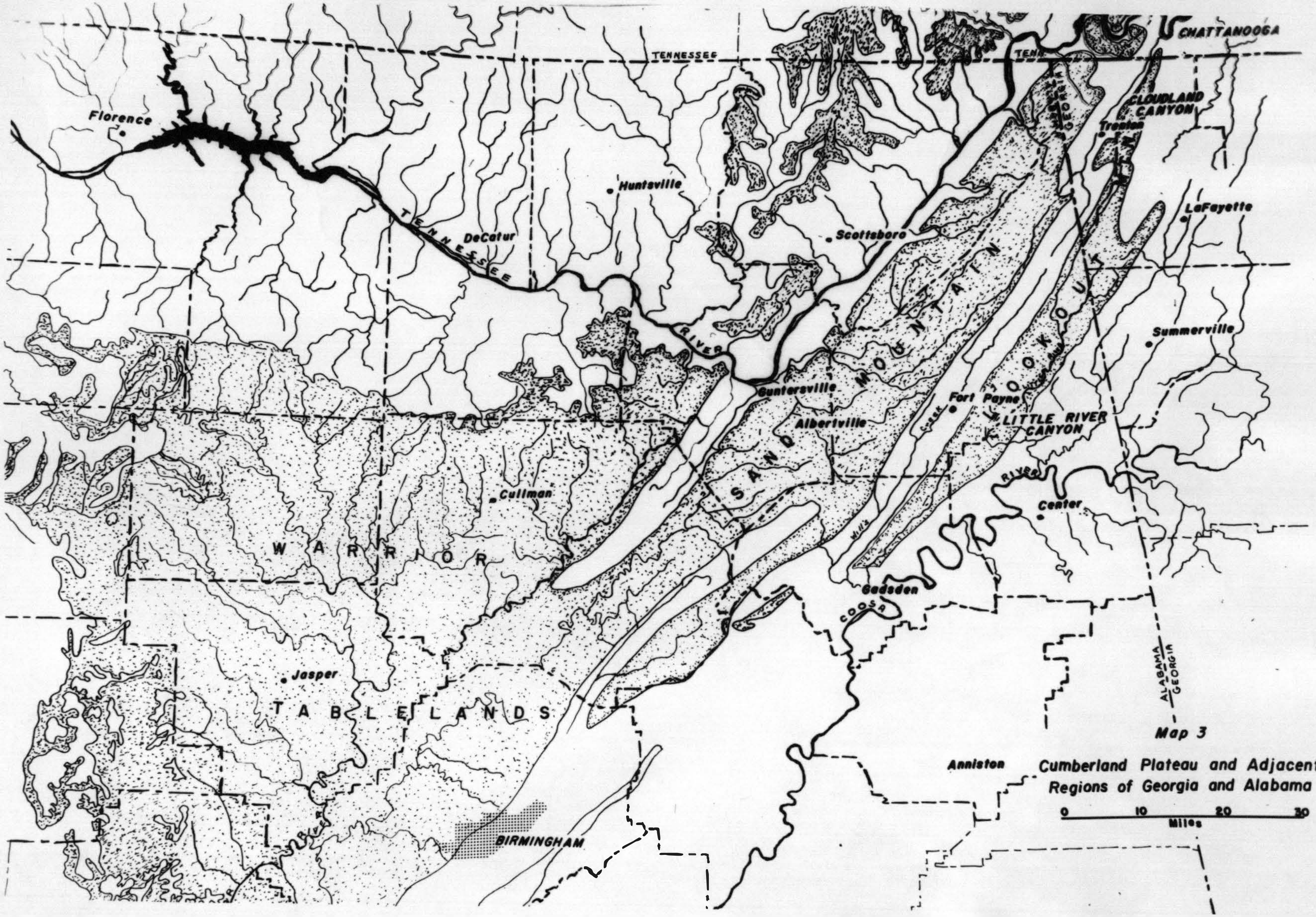
Figure 2. Representative Vertical Sections of the Cumberland Plateau

The Cumberland Plateau may be more or less arbitrarily divided into five sections, each section with rather definite physical boundaries (see Maps 2 and 3). The Tennessee portion is divided by the Sequatchie Valley into two distinct sections, the main Cumberland Plateau and Walden Ridge. The narrow, anticlinal Sequatchie Valley was formed by the erosion of folded rocks, and extends some two hundred miles from the southern part of Cumberland County, Tennessee, southward into Alabama. To the southwest of Walden Ridge is Sand Mountain, a broad tableland extending from the Tennessee River through the northwest corner of Georgia and into Alabama. To the east of Sand Mountain, and separated from it by Will's Valley is Lookout Mountain, extending from Chattanooga southwestward to Gadsden, Alabama. Each of these four sections present the same general appearance, with rolling upland abruptly terminated by steep escarpments (except Sand Mountain, where the escarpments gradually decrease in height and are mostly lost in the tablelands of Alabama).

The fifth section differs from the first four in being generally lower and without the pronounced escarpments typical of most of the plateau. The topography of this section has been described by Harper (1943b) as being moderately hilly with no extensive flat uplands. The region is composed mostly of the Warrior Tablelands of Alabama and is included in what Harper (1913, 1943b) has termed the Basin Region of the plateau. It is in the transition zone of the southwestern portion of the tablelands that the Pennsylvania sandstones of the plateau dip gradually under the Cretaceous deposits of the Coastal Plain. The more recent strata cap the hills, while the typical plateau rocks are exposed only in the valleys and gorges (Harper 1937).



Map 2
Cumberland Plateau and Adjacent
Regions of Tennessee



Map 3

Cumberland Plateau and Adjacent Regions of Georgia and Alabama

More extensive information concerning the geology, stratigraphy, and topography of the plateau in Tennessee, Georgia, and Alabama may be found in writings by Butts (1926), Butts and Gildersleeve (1948), Glenn (1925), and Nelson (1925).

Soils

The Cumberland Plateau is included in the Hartsells-Muskingum soils area of the more extensive lithosol and shallow soil group by the Soil Survey Division of the Department of Agriculture (Yearbook of Agriculture, 1938). These soils are dominantly fine sandy loams to silt loams which are low in mineral plant nutrients and organic matter, and medium to strongly acid in reaction. The Hartsells soils, derived from the sandstone and shale of the surface rocks, are the most extensive members of the group. They are gray to grayish-yellow at the surface, with pale-yellow to grayish-yellow subsurface layers and yellow to brownish-yellow, friable, fine sandy clay to silty clay loan subsoils, extending to a depth of about twenty-eight to thirty inches.

Soil surveys available for a number of counties in the plateau region classify the soil of the gorges as "Rough stony land (Muskingum soil material)" and describe this as the prevailing land class on steep and broken land in which sandstone boulders and outcrops of sandstone bedrock are numerous over the surface. The soil among the boulders and rocks is classified as Muskingum stony fine sandy loam, with rapid to very rapid surface drainage and medium to rapid internal drainage. Local variations in the soils of the gorges are evident, depending primarily upon the character of the vegetation and parent materials (usually sandstone or shale). There is some local evidence of calcareous soil materials in a few of the gorges, especially in the wider and deeper portions.

Climate

The plateau region of Tennessee and Alabama often is credited with a higher yearly rainfall than adjacent regions. Examination of climatic data contained in Weather Bureau and Tennessee Valley Authority publications reveals that this conclusion is generally true for many, but not for all, plateau stations.

The most abundant rainfall on the plateau usually is in the winter months from December to March, with a second peak in July and August. There is moderate rainfall from April through June, and the driest season occurs from September through November.

Temperature data contained in the 1941 Yearbook of Agriculture and Weather Bureau publications indicate a consistently lower mean temperature for most plateau stations than for stations of the same general latitude in adjacent provinces.

Information provided by the Tennessee Valley Authority Division of Forestry Relations reveals that during 1956, the total rainfall in the Sequatchie and Emory Rivers watershed area (Cumberland Plateau) amounted to fifty-six inches. This amount was equaled only by the Hiwassee and Little Tennessee watershed area which includes much of the mountainous area of the eastern part of Tennessee. The amount of water retained in the shallow, sandy plateau soils amounted to only six inches at the beginning of the growing season in April.

These and other data indicate that most of the precipitation which falls on the plateau may be lost due to runoff and evaporation before the beginning of the growing season. During the growing season, from April through September, much of the water that falls is lost through a high rate of evaporation and transpiration.

Wiesehuegel (1958) made the following statement concerning Southern Appalachian forests:

> . . . almost all years will show (water) deficits and . . . the forest will consume practically all of the available water within the root zone in any given year. This means that especially dry years may become limiting to tree species distribution, both good and poor sites being affected. Since species vary in their water requirements, the water economy becomes an important factor in determining their distribution and growth.

This statement becomes of special interest when the apparent differences between the microclimates of the gorges and the general climate of the plateau are considered. Unfortunately, few data concerning microclimates are now available, but these may be inferred from studies made in other portions of the Plateau Province, or in somewhat similar situations in the Piedmont.

Evaporation studies conducted by Segars, et al. (1951) in King Cove (Lawrence County, Alabama) revealed an average daily loss of 4.6 cubic centimeters of water from atmometers placed in the shade of hemlock within the protected cove, compared with a loss of 10.3 cubic centimeters in the shade of oaks and pines on a nearby ridge. The high humidity and relatively low evapo-transpiration rate in the area where hemlock grows in the

Warrior Tablelands of Alabama has been considered an important factor in the persistence of the species in these disjunct localities (Harper 1952; Segars, et al. 1951).

Wolfe, et al. (1949) published extensive data concerning microclimatic studies in the Neotoma Valley of Hocking County, Ohio (Unglaciated Alleghany Plateau). These data indicate differences in microclimate due to exposure, and also provide a comparison of the climate of the valley with the general climate of the region as shown by records of a nearby Weather Bureau station at Lancaster, Ohio (see Table I). Similar differences must exist among the habitats within the gorges of the Cumberland Plateau, and between the microclimates of these gorges and the general climate of the plateau region.

A recent study of a disjunct stand of hemlock in Wake County, North Carolina (lower Piedmont), by Oosting and Hess (1956), also is indicative of local variation in climate. This study revealed a consistently lower temperature and higher humidity for the hemlock stand on a bluff face than for an adjacent mixed hardwoods-pine stand on the bluff top.

TABLE I

TEMPERATURE AND EVAPORATION DATA FOR SOME STATIONS IN NEOTOMA VALLEY (HOCKING COUNTY, OHIO) AND LANCASTER, OHIO[a]

STATION	Temperature Data[b]		Evaporation in Liters		
	Maximum	Minimum	1940	1941	1942
Lancaster, Ohio (Weather Bureau)	87-90	21-24			
Neotoma Valley					
Cliff Top	91-112	15-26	4.0	3.9	3.0
Southwest-Facing Slope	79-93	21-28	2.2	2.1	1.7
Upper Northeast-Facing Slope	74-93	21-29			
Lower Northeast-Facing Slope	77-90	19-25	1.8	1.7	1.2
Cove	67-80	23-33	.4	.7	.4

[a]From Wolfe *et al*. (1949).

[b]Weekly reports, 1940-1944.

IV. METHODS

In order to provide information concerning the occurrence of species within gorges from northern Tennessee to Alabama, collections and field notes were made in selected areas of Buffalo Cove (Fentress County, Tennessee), Cloudland Canyon (Dade County, Georgia), and Little River Canyon (DeKalb-Cherokee Counties, Alabama). The locations of all of the gorges discussed in this paper are indicated on Maps 2 and 3. No systematic sampling of the vegetation in the study areas was attempted, but field notes concerning the character and composition of the various communities observed were made in each. The general descriptions of the gorge vegetation contained herein are based upon these notes.

No effort was made toward a further study of the Fall Creek Falls area (VanBuren County, Tennessee) or of Little Piney Creek (Rhea County, Tennessee), which have received attention from other workers. Special thanks are due Dr. Donald Caplenor of Millsaps College (Jackson, Mississippi) for information concerning Fall Creek, and to Mrs. Lou Woughter of Bryan University (Dayton, Tennessee) for the list of woody plants and notes concerning the vegetation of Little Piney gorge.

Field work was begun in the summer of 1956 and continued during the spring, summer and early fall of 1957. Except for some of the common species which were easily recognized in the field, collections were made in a variety of habitats in Buffalo Cove, Cloudland Canyon, and Little River Canyon. These specimens have been deposited in the University of Tennessee Herbarium at Knoxville.

The species lists included herein are limited to the woody plants which have been collected or reported to occur within the limits of the gorges. In each case, the study area was limited to the area enclosed by steep, overhanging cliffs or the upper limits of talus slopes. Species which are known to occur in other gorges of the plateau (viz., Decumaria barbara L., Symplocos tinctoria (L.) L'Her., and Diervilla sessilifolia Buckl.) have been excluded.

Botanical names listed herein are, for the most part, those used in Gray's Manual of Botany, Eighth Edition (Fernald, 1950). The exceptions are names of species which do not occur in the manual range and names which are not recognized as valid by Little in his Checklist of Native and Naturalized Trees of the United States (1953).

All species collected or reported from the five gorges have been assigned to distributional categories according to a system modified from that used by Cain (1930) in his work with the woody plants of the Great Smoky Mountains and vicinity. The species have been divided into two major categories, including those which do not reach a range limit within the Cumberland Plateau (intraneous flora) and those which do reach a geographical limit within this region (extraneous flora).

Information concerning the general distribution of species was obtained from range descriptions in manuals (Fernald 1950; Small 1933) or from published or unpublished maps by Little (1949) and others. Maps for all of the extraneous species, except Fothergilla major, have been prepared from information contained in published floras and checklists or furnished by the curators of a number of herbaria. These maps (see Appendix) are based chiefly upon herbarium specimens. The sources of the information utilized in their preparation are indicated in the Appendix of this paper.

V. RESULTS

The Vegetation of the Gorges

Brief descriptions of each of the five study areas and the major communities involved are included in the following paragraphs. Except for Fall Creek Falls, the descriptions are not based upon systematic sampling, and only the major community types or others of special interest are considered.

Fall Creek Falls

The Fall Creek Falls system of gorges has been described in detail by Caplenor (1954), and the description which follows is principally based upon his study. The system is located in the northern portion of the Fall Creek Falls State Park in VanBuren County, Tennessee, and is composed of a wide central gorge (Cane Creek Gulf) and three narrow, steep-sided tributary gorges (Fall Creek Gulf, Piney Creek Gulf, and Johnny Creek Gulf).

The Fall Creek system undoubtedly provides a much greater variety of habitats than does any other study area included in this report. This fact may be indicated by a lengthy list of woody plants (Table III) rich in extraneous species. Some communities within the system (especially Fall Creek Gulf) were considered to be virgin by Caplenor, but most of the area had been subjected to one large-scale logging as late as 1921 and 1922.

As a result of extensive study during the spring and summer of 1952 and 1953, Caplenor listed three principal community types as occurring within the system. By far the largest area was included within the limits of the mixed mesophytic community (see Figure 3) and its segregates (i. e., the hemlock, hemlock-yellow birch, and hemlock-basswood communities). Mixed mesophytic stands were described as prevalent in habitats with deep soil, an absence or paucity of boulders, and an exposure toward the north and/or east. The main body of the community was restricted to gentle, dissected slopes exposed to sunlight for a considerable part of the day. In contrast, the hemlock-segregates were found mostly in the narrow gorges or in other areas which were shaded for a part of the afternoon. The hemlock community (in which hemlock was the sole dominant) was confined to the narrow, upper portion of Johnny Branch Gulf.

The oak-hickory and chestnut oak "pre-climax" communities (Figure 4) were found on the southwest-facing talus slope of Cane Creek Gulf. The oak-hickory was situated on the undissected middle slope just above the limits of the mixed mesophytic community, while chestnut oak dominated the dry, upper talus.

Buffalo Cove

Buffalo Cove is located two and one-half miles south of Jamestown along the western escarpment of the plateau in Fentress County, Tennessee. That part of the cove studied for this report is not extensive, but it possesses a number of features that are not common to the other gorges described herein. The study area is part of the original Gernt property and is now utilized as a private park for guests of a local motel. It extends a little more than 3,000 feet into the plateau tableland and opens to the southwest.

Figure 3. View along Fall Creek (Fall Creek Falls State Park), showing a mixed mesophytic forest mostly of hemlock and yellow birch.

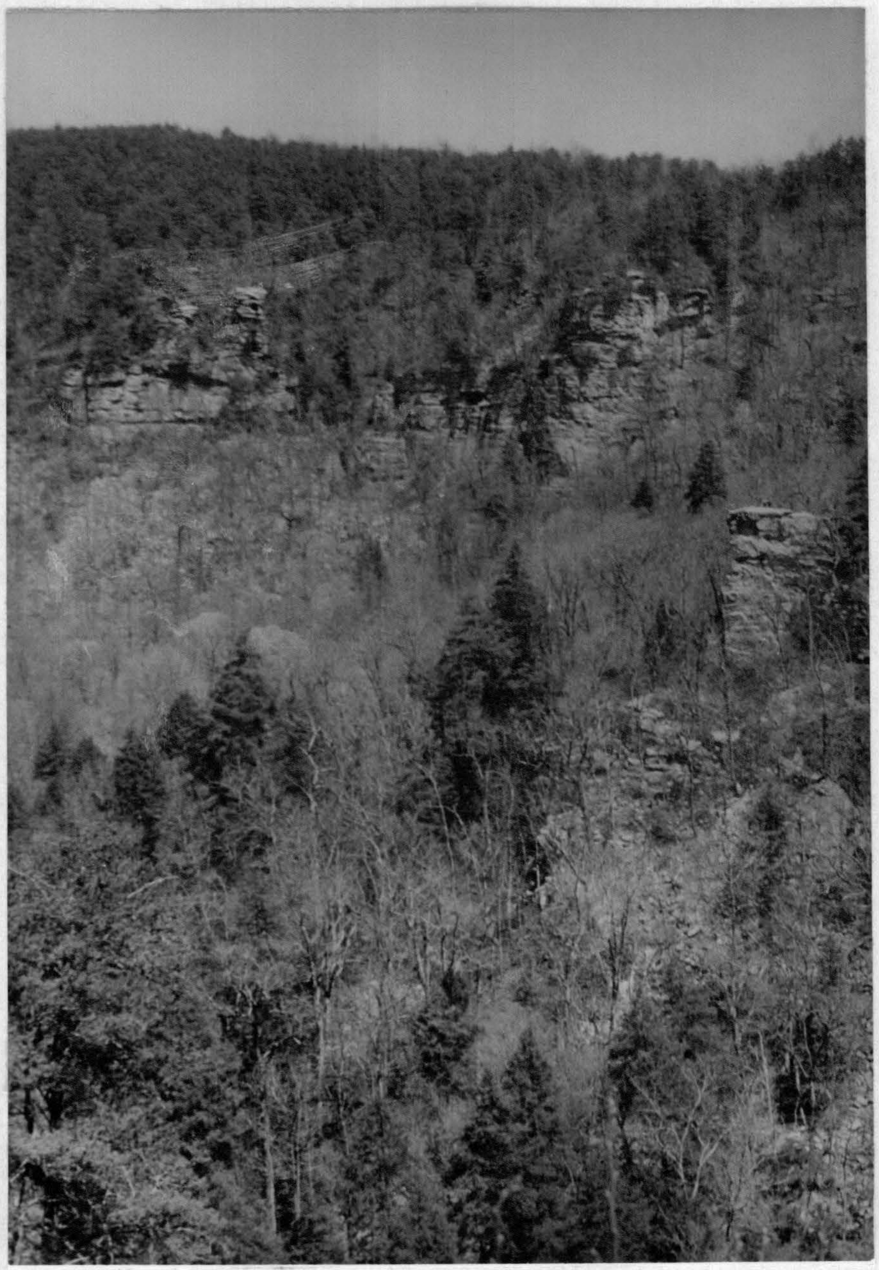


Figure 4. View of the south-facing talus slope of Cane Creek Gulf (Fall Creek Falls State Park), showing a transition in community types from stream side to cliff top. The coniferous evergreens along the stream are hemlocks within a mixed mesophytic stand. The evergreens on the cliff top are Virginia pines. An oak-hickory community occupies the middle slope and a chestnut oak community is found on the upper talus.

The cove is wide and relatively open for most of its extent, expanding from approximately 1,500 feet at the head to 3,500 feet at the mouth. The terraced talus slopes extend from the relatively low cliffs to the small stream which traverses the center of the cove. They slope gently for the most part, but are dissected by drainage channels at places, especially on the south side. Exposure is predominantly to the northwest and southeast.

Severe disturbance during early logging and more recent mining operations has resulted in a marked change in the vegetation in some parts of the cove. According to reports of persons familiar with the history of the area, intensive logging during the years just prior to 1900 removed practically all of the big timber trees then present (especially oaks and tuliptree). Evidence of logging debris (said to have been abundant) is still apparent in some parts, and a number of old logging roads remain well defined. The present vegetation is patchy, with areas of near-climax growth alternating with areas still in early stages of secondary succession.

It is possible to distinguish four principal vegetation types within the cove, although the pattern is somewhat obscured because of disturbance. A mixed mesophytic community prevails along the main stream in the center of the cove, and partly along two tributary streams flowing over the southern escarpment. The community is not extensive, being restricted almost to streamside on the south-facing talus and extending up the north-facing slope only a short distance.

The dominant trees are _Tilia heterophylla_ (basswood), _Acer saccharum_ (sugar maple), _Fagus grandifolia_ (beech), and _Liriodendron tulipifera_ (tuliptree). Principal associates are Quercus alba (white oak), Liquidambar styraciflua (sweetgum), Quercus rubra (red oak), Acer rubrum (red maple), Carya ovata (shagbark hickory), Tsuga canadensis (hemlock), Magnolia acuminata (cucumber tree), Platanus occidentalis (sycamore), Aesculus octandra (yellow buckeye), Ulmus americana (American elm), Cladrastis lutea (yellowwood) and Juglans cinerea (butternut).

The principal vegetation type over most of the area is oak-hickory, extending almost to streamside on the south-facing slope, with a somewhat narrower band between the mixed mesophytic community and the escarpment on the north-facing slope. The dominant trees are Quercus alba, Carya glabra (pignut hickory), Quercus rubra, Liriodendron tulipifera, and Carya ovata. Carya ovalis (red hickory), Quercus prinus (chestnut oak), Nyssa sylvatica (blackgum), Fraxinus americana (white ash), Acer rubrum, and Acer saccharum are important associates.

A chestnut oak community is restricted to a narrow band above the oak-hickory on the south-facing talus. Here the dominant tree is Quercus prinus, with Nyssa sylvatica, Carya glabra, Quercus alba, and Pinus virginiana (Virginia pine) as principal associates.

The fourth community type includes the scattered areas which were highly disturbed or denuded during logging and mining operations. The most abundant species are Robinia pseudo-acacia (black locust), Rhus glabra (smooth sumac), Rhus copallina (shining sumac), Cercis canadensis (redbud), Nyssa sylvatica, Pinus virginiana, Sassafras albidum, and blackberries (Rubus spp.).

Little Piney Creek

This narrow, S-shaped gorge eroded into Walden Ridge by Little Piney Creek represents the only study area on the eastern escarpment of the plateau in Tennessee. It is located above Spring City (Rhea County) and, although private property, it has not been subjected to any severe disturbance by logging or recent fires.

The study area extends approximately 5,000 feet from the falls at the upper end to the mouth, where it opens into a wider gorge formed by Soak Creek. It is narrow in the upper portion but widens to about 1,200 feet at the lower end. Slope exposures vary from north and south to east and west.

A study involving an analysis of the vegetation in Little Piney gorge is now being made by Mrs. Lou Woughter of Bryan University (Dayton, Tennessee), and the discussion which follows is based primarily upon information furnished by her.

A hemlock-dominated segregate of the mixed mesophytic forest occupies the narrow upper portion of the gorge between the upper and lower falls. White basswood (*Tilia heterophylla*), beech (*Fagus grandifolia*), tuliptree (*Liriodendron tulipifera*), white pine (*Pinus strobus*), yellow birch (*Betula alleghaniensis*), red maple (*Acer rubrum*), cucumber tree (*Magnolia acuminata*), black oak (*Quercus velutina*), sycamore (*Platanus occidentalis*), and white oak (*Quercus alba*) are among the other tree species included. This community is the only one in the five study areas in which white pine is included as a dominant species.

A second community type, in which chestnut oak (*Quercus prinus*) is the dominant, occupies the upper talus adjacent to the mixed mesophytic stand. Associated species include white oak, black gum (*Nyssa sylvatica*), red oak (*Quercus rubra*), Virginia pine (*Pinus virginiana*), and black oak.

In the wider portions of the gorge, the mixed mesophytic community is found on the lower slopes and an oak-hickory community similar to those found in other gorges occupies the upper talus.

Cloudland Canyon

This gorge system is the principal attraction of Cloudland Canyon State Park which is located near the northern end of Lookout Mountain in Dade County, Georgia. It consists of the deep, but wide, Sitton Gulch (Figure 5) and two narrow, steep-sided tributary gorges formed by Daniel and Bear Creeks. The Gulch opens northward into a wide cove indenting the western escarpment of the mountain above Trenton, Georgia. The tributaries form the arms of the Y-shaped system, extending into the plateau to the southeast and southwest.

A well-developed mixed mesophytic forest is found in the deeper and narrower portions of the tributary gorges. Here the dominant trees are white basswood (*Tilia heterophylla*), tuliptree (*Liriodendron tulipifera*), sweet birch (*Betula lenta*), beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), hemlock (*Tsuga canadensis*), white oak (*Quercus alba*), red oak oak (*Quercus rubra*), cucumber tree (*Magnolia acuminata*) and yellow buckeye (*Aesculus octandra*).

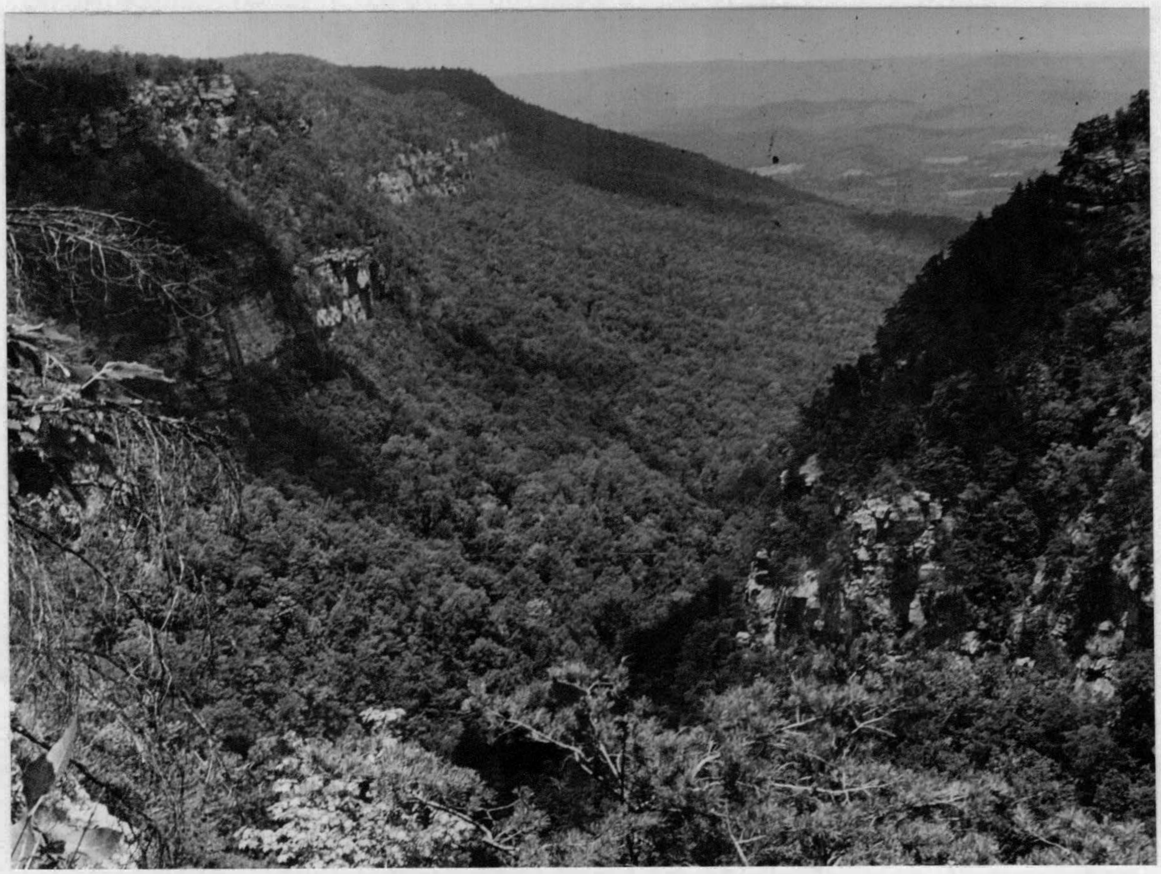


Figure 5. View of Sitton Gulch in Cloudland Canyon State Park in northwest Georgia (Dade County).

Common understory species include *Alnus serrulata*, *Xanthorhiza simplicissima*, *Magnolia tripetala*, *Hydrangea arborescens*, *Rhus radicans*, *Parthenocissus quinquefolia*, *Cornus florida*, *Rhododendron catawbiense*, *Kalmia latifolia*, *Cephalanthus occidentalis*, and *Viburnum acerifolium*.

A drier forest exists on the slopes of the main portion of the gorge and on the upper talus of the tributaries. This community is essentially oak-hickory and includes such species as pignut hickory (*Carya glabra*), chestnut oak (*Quercus prinus*), white oak (*Quercus alba*), white ash (*Fraxinus americana*), and blackgum (*Nyssa sylvatica*).

The more exposed habitats (including the upper west- or south-facing slopes and the numerous rock ledges) are covered with chestnut oak and Virginia pine (*Pinus virginiana*).

Little River Canyon

One of the most extensive gorge systems in the Cumberland Plateau has been cut into Lookout Mountain in northeastern Alabama. This deep, steep-sided "canyon" is the result of the erosive action of Little River which rises in northwest Georgia and winds some twenty-five miles southwestward before leaving the mountain and eventually emptying into the Coosa River. For much of its distance, the river forms the boundary between DeKalb and Cherokee counties, Alabama.

Little River Canyon begins with a cascade near where State Route 35 crosses the river about seven miles east of Fort Payne. From this point to its mouth, the gorge is relatively narrow with precipitous sandstone cliffs for much of its eighteen-mile length. Several small streams (especially Bear Creek) have eroded deep tributary gorges which contribute to the total area of the system. A considerable diversity of habitats results from differences in slope exposure in the winding "canyon" and its tributaries. For the most part, however, the narrow and steep talus slopes face either to the northeast or to the southwest.

The "canyon" is administered by the Alabama Parks Department as a part of DeSoto State Park, located several miles upstream. Both of these areas had been Federal property until they were ceded to the state in 1937. The only known logging operation in the "canyon" occurred in 1922 or 1923, and fire disturbance in recent years apparently has not been severe.

In certain respects, this southernmost of the five study areas has been the most interesting to botanists. It is included within the area which has received considerable attention in the writings of Mohr (1901), Harper (1913, 1943b) and others, mostly because of the occurrence of species which are more characteristic of other physiographic regions. The Coastal Plain element is especially conspicuous, representing over 10 per cent of the total number of woody species known to occur in the gorge.

The vegetation within Little River Canyon differs somewhat from that of the other study areas, either because of the absence of species which are characteristic of certain common community types or because of the presence of species which are not known to occur in the other gorges. Although there is a mesophytic forest on a portion of the north-facing slopes, two of the usual species - Tsuga canadensis and Aesculus octandra - are missing. Included among the prominent members of this community are basswood (Tilia heterophylla), sweet birch (Betula lenta), tuliptree (Liriodendron tulipifera), white oak (Quercus alba), beech (Fagus grandifolia), shagbark hickory (Carya ovata), and red oak (Quercus rubra). This is the only community within the five study areas in which silverbell (Halesia carolina) was found.

The oak-hickory community found on the south-facing slopes of Little River Canyon also differs from the oak-hickory types found in the other four gorges, chiefly because of the occurrence of sand hickory (Carya pallida), chalk maple (Acer leucoderme), and oak-leaved hydrangea (Hydrangea quercifolia) as prominent members of the tree layer or the understory. These three Coastal Plain and Piedmont species were not found in any of the other gorges. Many of the more characteristic species of the oak-hickory communities of the other gorges are present, including chestnut oak, white oak, red oak, pignut hickory, red hickory, blackgum and white ash.

A chestnut oak community, in which Quercus prinus is the dominant species, is found on the upper south-facing slopes directly beneath the sandstone cliffs. Some of the major associates here are blackgum, sand hickory, Virginia pine, pignut hickory, and white ash. In parts of the gorge the oak-hickory or chestnut oak communities grade into other community types which include shortleaf pine (Pinus echinata) or loblolly pine (Pinus taeda) as dominants.

One of the most conspicuous features of Little River Canyon is the flood plain which is found in the wider portions of the gorge. This flat area immediately adjacent to the main stream is characterized by an accumulation of sandstone boulders alternating with sandy soil. It is by no means extensive, due to the narrowness of the gorge, but no similar feature was noted in any other gorge observed in the course of this study. The woody vegetation of this rather unique habitat is composed mostly of shrubs or small trees, with scattered larger trees such as loblolly pine, sweetgum (Liquidambar styraciflua), Virginia pine, white oak, and others. The shrubs and small trees include several species of Vaccinium (V. arboreum, V. elliottii), Viburnum (V. acerifolium, V. cassinoides, V. dentatum, V. rufidulum), and Ilex (I. opaca, I. verticillata), along with Alnus serrulata, Cephalanthus occidentalis, Fothergilla major, Celtis tenuifolia var. georgiana, Rhododendron catawbiense, Kalmia latifolia, Calycanthus floridus, and Chionanthus virginicus.

General Distribution of Species

A total of 126 species of woody plants (excluding adventives and questionable identifications) was found in the five gorges utilized for this study. These represent forty-four families (twenty-one with one species each) and seventy-seven genera (fifty-five with one species each). A composite list of all woody species known to occur in the five gorges is presented in Table III.

Each of the 126 species herein reported for the five study areas has been assigned to a certain category according to distribution. One hundred and five (83.3 per cent) are included within the intraneous flora, comprised of species which do not reach a range limit within the Cumberland Plateau. Twenty-one (16.7 per cent) do reach a range limit (mostly to the south and/or west) within the plateau, and are here included in the extraneous flora.

Intraneous Flora

I. Species Generally Distributed Over Much of Eastern North America From the Gulf of Mexico North to the Great Lakes and Canada.

Of the 105 species included in the intraneous flora, fifty-six (53.3 per cent) are widely distributed from the Gulf region to the Great Lakes and Canada (see Maps 4 and 5). The total area included within the ranges of the individual species of this group varies considerably. For example, the range of *Ulmus americana* (American elm) extends from southern Florida to well north of the Canadian border, and from the Atlantic coast westward to the Dakotas, Kansas and mid-Texas; whereas *Liriodendron tulipifera* (tuliptree) is chiefly restricted to the states east of the Mississippi River. A number of the species included here also occur as disjuncts (*) in Mexico and Central America.

Juniperus virginiana L.
**Smilax glauca* Walt.
Smilax rotundifolia L.
**Smilax tamnoides* L. var. *hispida* (Muhl.) Fern.
**Salix nigra* Marsh.

Juglans nigra L.
Carya cordiformis (Wang.) K. Koch
Carya glabra (Mill.) Sweet
Carya ovalis (Wang.) Sarg.
**Carya ovata* (Hill) K. Koch

Carya tomentosa Nutt.
**Ostrya virginiana* (Mill.) K. Koch
**Carpinus caroliniana* Walt.
Alnus serrulata (Ait.) Willd.
Fagus grandifolia Ehrh. (Map 4)

Quercus alba L.
Quercus rubra L.
Quercus velutina Lam.
Ulmus americana L.
Ulmus rubra Muhl.

Celtis occidentalis L.
Morus rubra L.
Liriodendron tulipifera L. (Map 5)
Asimina triloba (L.) Dunal
Lindera benzoin (L.) Blume

Sassafras albidum (Nutt.) Nees
Hydrangea arborescens L.
*Hamamelis virginiana L.
Platanus occidentalis L.
Amelanchier arborea (Michx. f.) Fern.

Rubus occidentalis L.
*Prunus serotina Ehrh.
*Cercis canadensis L.
*Ptelea trifoliata L.
Rhus copallina L.

*Rhus glabra L.
Rhus radicans L.
Ilex verticillata (L.) Gray
Euonymus americanus L.
Staphylea trifolia L.

Acer rubrum L.
Ceanothus americanus L.
*Parthenocissus quinquefolia (L.) Planch.
Vitis aestivalis L.
*Nyssa sylvatica Marsh.

Aralia spinosa L.
Cornus alternifolia L. f.
*Cornus florida L.
Lyonia ligustrina (L.) DC.
Kalmia latifolia L.
Vaccinium stamineum L.

Fraxinus americana L.
Cephalanthus occidentalis L.
Viburnum acerifolium L.
Viburnum dentatum L.
*Sambucus canadensis L.

II. Species Generally Distributed Over Much of Eastern North America From Canada and the Great Lakes South to the Northern Portions of the Gulf States.

Eight species of the intraneous flora (7.6 per cent) have ranges similar to those of the preceding category, except that they do not extend as far south (see Map 6). The geographical center of distribution for the group is near the glacial boundary and the species may, perhaps, be best considered as "northern."

Smilax ecirrhata (Engelm.) S. Wats.
Juglans cinerea L. (Map 6)
Corylus americana Walt.
Rubus pensilvanicus Poir.

Amelanchier laevis Wieg.
Acer saccharum Marsh.
Vaccinium vacillans Torr.
Viburnum cassinoides L.

III. Species Generally Distributed Over Much of the Eastern United States South of the Glacial Boundary.

A third group of widely-distributed species is more or less restricted to the area south of the glacial boundary (Map 7), and is best considered to be a part of the "southern" element which is prominent in the flora of the Cumberland Plateau. The group includes twenty-one species (20.0 per cent of the intraneous flora), many of which are especially characteristic of the Piedmont and Coastal Plain regions.

Pinus echinata Mill.
Smilax bona-nox L.
Salix caroliniana Michx.
Quercus falcata Michx.
Ulmus alata Michx. (Map 7)

Celtis tenuifolia Nutt.
var. georgiana (Small) Fern. & Schub.
Itea virginica L.
Liquidambar styraciflua L.
Ilex opaca Ait.

Rhamnus caroliniana Walt.
Vitis rotundifolia Michx.
Hypericum frondosum Michx.
Oxydendrum arboreum (L.) DC.
Vaccinium arboreum Marsh.

Diospyros virginiana L.
Halesia carolina L.
Chionanthus virginicus L.
Callicarpa americana L.
Campsis radicans (L.) Seem.
Bignonia capreolata L.
Viburnum rufidulum Raf.

IV. Species Chiefly of the Piedmont and Coastal Plain of the Southern States.

Nine members of the intraneous flora (8.6 per cent) are found chiefly in the Piedmont and Coastal Plain of the south, with only limited extensions inland (Map 8). Half of these species - Smilax laurifolia, Acer leucoderme Small, Vaccinium elliottii, and Gelsemium sempervirens - are either rare or missing in Tennessee. Three others, Pinus taeda, Hydrangea quercifolia, and Ilex longipes, have been reported only for the southern tier of counties in Tennessee.

The ranges of most of the species of this group extend from Texas to Virginia or New Jersey in the Coastal Plain region, except Ilex longipes which is found from Louisiana to North Carolina. Berchemia scandens and Gelsemium sempervirens are found inland in the Mississippi embayment region as far as Missouri. Berchemia and Gelsemium also occur in Mexico.

Pinus taeda L.
Smilax laurifolia L.
Carya pallida (Ashe) Engl. & Graebn.
Hydrangea quercifolia Bartr.

Ilex longipes Chapm.
Acer leucoderme Small
Berchemia scandens (Hill) K. Koch (Map 8)
Vaccinium elliottii Chapm.
Gelsemium sempervirens (L.) Ait. f.

V. Species With Centers of Distribution in the Appalachian Region of the Eastern United States.

The four species included here (3.8 per cent of the intraneous flora) are especially characteristic of the Appalachian region from New York or Pennsylvania to Alabama (Map 9). All are trees which are prominent in the forests of the Cumberland Plateau and one, Aesculus octandra, is considered by Braun (1950) to be indicative of the Mixed Mesophytic forest. The importance of chestnut (Castanea dentata) in the deciduous forest has, of course, been greatly reduced by disease.

Pinus virginiana Mill.
Castanea dentata (Marsh.) Borkh.
Quercus prinus L. (Map 9)
Aesculus octandra Marsh.

VI. Appalachian-centered Species With Disjunct Populations to the West (Chiefly in the Ozark and Ouachita Highlands).

This group of seven species (6.7 per cent of the intraneous flora) is much like the preceding group, except for the disjunct populations which occur in the Ozark and Ouachita highlands and other scattered areas west of the Mississippi River (Maps 10 and 11). All of the species except Magnolia macrophylla are found as disjuncts in the highlands of Missouri or

Arkansas. However, this species is found in Mexico, where it is known as *Magnolia dealbata* (according to Dr. A. J. Sharp, University of Tennessee). *Tilia heterophylla* (white basswood) is rather widespread east of the Mississippi River, extending from southern New York to northern Florida and to the Atlantic coast in the middle part of this range. This species also is considered by Braun (1950) to be especially indicative of the Mixed Mesophytic forest.

Magnolia acuminata L.
Magnolia macrophylla Michx. (Map 10)
Magnolia tripetala L. (Map 11)
Philadelphus hirsutus Nutt.
Robinia pseudo-acacia L.
Cladrastis lutea (Michx. f.) K. Koch
Tilia heterophylla Vent.

Extraneous Flora

I. Canadian-transcontinental Species With Southern Appalachian Extensions.

Sambucus pubens, the only species considered here, has been reported for the plateau only from the Fall Creek Falls area. It is otherwise restricted to the eastern mountains in the southern part of its range, and reaches a southern limit in the Blue Ridge of Towns County, Georgia.

Sambucus pubens Michx. (Map 12)

II. Species Characteristic of the Great Lakes Region, New England and Southern Canada (With Southern Appalachian Extensions).

All of the seven species included here (33.3 per cent of the extraneous flora) are rather common in the northern United States from the Lakes to New England, and three of them (*Tsuga canadensis*, *Pinus strobus*, and *Betula alleghaniensis*) are dominant trees in the Hemlock-White Pine-Northern Hardwoods region.

Hemlock (*Tsuga canadensis*) is found in most of the gorges of the Cumberland Plateau, at least in Tennessee, and plays a dominant role in the Mixed Mesophytic forest in these protected habitats. This species reaches its southern limit in the tablelands of Alabama. White pine (*Pinus strobus*) is missing in the plateau section of Alabama, but it is found as a disjunct in the highlands of Mexico. Northern white cedar (*Thuja occidentalis*), mostly limited to calcareous soils, has a disjunct station in the Fall Creek Falls area where several small trees are growing in a crevice near Cane Creek Falls. Otherwise, the species reaches its southern limit on the bluffs of the Emory River near Harriman in Roane County, Tennessee.

Gaylussacia baccata has a somewhat atypical distribution (when compared with other members of this group) because of its wide northern range (west to Saskatchewan) and scattered occurrence in the Piedmont and Coastal Plain of Virginia, North Carolina, and Georgia.

Tsuga canadensis (L.) Carr. (Map 13)
Pinus strobus L. (Map 14)
Thuja occidentalis L. (Map 15)
Betula alleghaniensis Britt. (Map 16)
Ribes cynosbati L. (Map 17)
Acer pensylvanicum L. (Map 18)
Gaylussacia baccata (Wang.) K. Koch (Map 19)

III. *Species of the Northeastern United States and Canada, With Southern Appalachian Extensions.*

This group includes only two species (9.5 per cent of the extraneous flora) which extend from southern Canada and New England southward in the

Appalachians to Georgia or Alabama. Rhododendron maximum reaches its southern limit in the Blue Ridge section of northeast Georgia, and is not found in Alabama. Sweet birch (Betula lenta) has been reported as far south as the Blue Ridge foothills of Talladega and Clay counties, Alabama (Cheaha State Park).

Betula lenta L. (Map 20)
Rhododendron maximum L. (Map 21)

IV. Species Chiefly of the Appalachian Region, With Extensions Into the Piedmont and Coastal Plain of the South.

The five species included here (23.8 per cent of the extraneous flora) are primarily centered in the Southern Appalachian region from West Virginia to Alabama, with varying degrees of extension into the Piedmont and Coastal Plain.

Two species, Xanthorhiza simplicissima and Calycanthus floridus, are rather widely distributed in many of the southeastern states, but are unknown or very rare west of the Plateau in Tennessee and Kentucky. Although Xanthorhiza is essentially a southeastern species, extending for the most part from West Virginia to the Gulf in Alabama, it occurs as a disjunct in southern New York and in eastern Texas.

Calycanthus floridus, a pubescent-leaved species, undoubtedly is confused with Calycanthus fertilis (with glabrous leaves) because of variations which are evident in some populations. It is certainly the common species of the plateau, while the latter is found mostly in the mountainous regions.

Both Calycanthus fertilis and Rhododendron catawbiense have at times been considered as Southern Appalachian endemics by other writers. However, both are known to occur in scattered stations in the lower Piedmont of North Carolina. They have essentially the same distribution pattern (extending from West Virginia to Alabama), although the Calycanthus is less common.

Rhododendron arborescens has been reported to occur in several counties of the Coastal Plain in Virginia and North Carolina, but the species is otherwise primarily limited to the Appalachian region from Pennsylvania to Alabama.

Xanthorhiza simplicissima Marsh. (Map 22)
Calycanthus floridus L. (Map 23)
Calycanthus fertilis Walt. (Map 24)
Rhododendron arborescens (Pursh) Torr. (Map 25)
Rhododendron catawbiense Michx. (Map 26)

V. Southern Appalachian Endemics.

The six species included here (28.6 per cent of the extraneous flora) are almost entirely restricted to the Appalachian region from southern Pennsylvania to northern Alabama. Two species, Spiraea virginiana and Diervilla rivularis, occur very locally and have been reported from only a few counties. Diervilla is primarily a plateau endemic occurring in northeast Alabama and northwest Georgia, with an isolated station in Unicoi County, Tennessee. The type locality for the species is Lulu Falls on Lookout Mountain (Dade County, Georgia). Spiraea has been reported for scattered stations in West Virginia (including the type locality), North Carolina, Tennessee, and Georgia. Two of these stations are Fall Creek Falls and Cloudland Canyon.

Pyrularia pubera and *Aristolochia durior* are relatively wide-ranging species in the Appalachians, extending down the mountains and the plateau from Pennsylvania to Georgia or Alabama. Mohr (1901) listed *Aristolochia* are occurring in Winston County, Alabama (the only report for the state), but apparently no collections have been made since the beginning of the century.

Stewartia ovata is found from Kentucky and Virginia south to Alabama, and extends into the upper Piedmont of northern Georgia. *Fothergilla major* is not included among the species which were mapped for this study, but range descriptions in the manuals indicate that it is a Southern Appalachian species of very limited range.

Pyrularia pubera Michx. (Map 27)
Aristolochia durior Hill (Map 28)
Fothergilla major Lodd.
Spiraea virginiana Britt. (Map 29)
Stewartia ovata (Cav.) Weatherby (Map 30)
Diervilla rivularis Gattinger (Map 31)

VI. DISCUSSION OF RESULTS

The Vegetation

When the information presented in preceding portions of this paper are examined, it becomes apparent that the gorges of the Cumberland Plateau are, to a large extent, similar with respect to the major community types present in each. In general, these major types are represented by (1) the mixed mesophytic stands occupying what seem to be the most favorable habitats with respect to moisture relations, (2) a chestnut oak community which is found on some of the drier south-facing or upper talus slopes, and (3) an oak-hickory type which occupies more or less intermediate habitats.

Perhaps the most significant of these three types is the mixed mesophytic community, which is often described as the modern forest most closely resembling the rich Tertiary forests. It is the occurrence of mixed mesophytic communities in the gorges of the Cumberland Plateau that is the basis for the contention that the climatic climax of the entire region is Mixed Mesophytic (Braun 1950).

The area covered by mixed mesophytic forest varies considerably, depending upon the character of the individual gorges. It apparently occupies most of the area within the gorges of the Fall Creek Falls area, and it is well developed in the narrower and deeper portions of Little Piney Creek gorge and Cloudland Canyon. However, the community occupies a relatively small per cent of the total area included in Buffalo Cove and Little River Canyon. The restricted nature of the mixed mesophytic stands in Buffalo Cove may be due to the severe disturbances caused by logging and mining. In Little River Canyon, the relative scarcity of suitable habitats probably is the limiting factor, since the community seems to be limited mostly to certain portions of north-facing slopes.

Such species as white basswood (Tilia heterophylla), tuliptree (Liriodendron tulipifera), beech (Fagus grandifolia), white oak (Quercus alba), sugar maple (Acer saccharum), red maple (Acer rubrum), northern red oak (Quercus rubra), blackgum (Nyssa sylvatica), chestnut oak (Quercus prinus), and shagbark hickory (Carya ovata) are present in the mixed mesophytic stands of all five gorges, and may be among the dominant trees in the community. Yellow buckeye (Aesculus octandra), considered by Braun (1950) to be especially indicative of the mixed mesophytic forest, has not been reported for Little Piney Creek gorge or Little River Canyon. Hemlock (Tsuga canadensis) also is missing in the Little River area, where the mixed mesophytic community is all-deciduous.

Generally, the oak-hickory community of the gorges may include such tree species as chestnut oak, white oak, pignut hickory (Carya glabra), red hickory (Carya ovalis), tuliptree, blackgum, and white ash (Fraxinus americana) among the dominants. Sand hickory (Carya pallida), primarily a Piedmont and Coastal Plain species, may also assume a dominant role in the oak-hickory community of Little River canyon.

The composition of the chestnut oak community, in which Quercus prinus is the lone dominant, is much the same for all of the five gorges. The major associates involved usually are blackgum, pignut hickory, white oak, and Virginia pine (Pinus virginiana).

Several other distinct community types merit discussion here, although each of them occurs in only one of the five gorges. The rather common occurrence of shortleaf and loblolly pines in Little River Canyon results in pine communities in which one or the other of the two species may be the dominant tree. Communities in which pine is either the sole dominant or one of the major associates occur at intervals on both slopes and in the flood plain at the bottom of the gorge.

The shrubby flood-plain vegetation is another distinctive feature of Little River Canyon. This community is composed primarily of several species of Vaccinium, Viburnum, and Ilex, together with Cephalanthus occidentalis, Alnus serrulata, Kalmia latifolia, Rhododendron catawbiense, Fothergilla major, and other shrubs. A similar community was not observed in any of the other four gorges.

Still another community type is of special interest here, although it is not included within the limits of any of the gorges. It is composed mostly of herbaceous species and occurs on the partially bare sandstone outcrops along the rims of the gorges, especially in the Little River Canyon area. Apparently there is a close relation between this community and similar types occurring on granite outcrops in parts of Georgia and Alabama (McVaugh 1943), since a number of taxa are common to both.

If the data presented by Wolfe et al. (1949) for the Neotoma Valley in the plateau region of Ohio are indicative of microclimatic differences existing in the gorges of the Cumberland Plateau, then some of the principal factors involved in the distribution of community types within these gorges become apparent. Table I (microclimatic data for Neotoma Valley) reveals a significant difference in temperature and humidity among various habitats, grading from the rather severe microclimate of the cliff top to the cool, humid habitats of the cove and lower northwest-facing slope. In Neotoma Valley, the cove and lower northeast-facing slope are covered with a mixed mesophytic forest; an oak-hickory community occupies the lower southwest-facing slope; and chestnut oak is dominant on the upper southwest-facing slope. These three communities occupy essentially the same positions in the gorges of the Cumberland Plateau.

Floristics

The woody species occurring in the gorges of the plateau represent only a portion of a rich flora that is of general interest to plant geographers. Within this region there occur endemic species and disjunct patterns that can be explained only in relation to past geologic or climatic events. The complexity of the gorge flora is evident, even when the woody species alone are considered. In addition to the presence of endemics and disjuncts, there is a mingling of characteristically northern and Coastal Plain species with others which are essentially Appalachian-centered.

A number of theories have been advanced to explain the occurrence of certain species within the Southern Appalachians, as well as the distribution patterns that are involved. Some of these theories are outlined in the following paragraphs, and discussed in relation to the results obtained from this study.

The various species groups presented in the preceding section of this paper offer a basis for dividing the woody flora of the gorges into a number of more or less distinct floristic elements (Table II). When the widespread species of the intraneous flora (Groups I, II, and III) are excluded[1], those remaining may be considered as belonging to the following floristic groups: (1) the northern element; (2) the Coastal Plain and Piedmont element; (3) the Appalachian-centered element; (4) the Appalchian-Ozarkian element; and (5) the Southern Appalachian endemics.

The Northern Element

Included here are species which are especially characteristic of the northern portion of the United States (from the Great Lakes to New England) and of parts of Canada. These species (viz. Tsuga canadensis, Thuja occidentalis, Betula alleghaniensis, Ribes cynosbati, Acer pennsylvanicum, and Gaylussacia baccata) extend southward chiefly along the mountains and plateaus of the Appalachian highlands. To these may be added the Canadian-transcontinental species, Sambucus pubens, which exhibits much the same distribution pattern in the southern portion of its range.

The most common explanation for the presence of these "northern" species in the southeastern United States is based upon the effects of climatic conditions associated with glaciation, presumably resulting in a southward migration. It should be noted that none of the genera involved, except Betula, was reported from the Wilcox Flora (Berry 1930;

[1]According to Wulff (1950), such wide-spread species should be excluded since they cannot give any clues to the origin and history of a flora unless their centers of origin and time of dispersal have been determined.

TABLE II

CONTINENTAL AFFINITIES OF THE WOODY FLORA OF FIVE GORGES OF THE CUMBERLAND PLATEAU

Affinities	Buffalo Cove	Fall Creek	Little Piney	Cloudl. Canyon	Little River
Northern Element	2 spp. 2.7%	7 spp. 7.7%	4 spp. 6.6%	2 spp. 3.2%	1 spp. 1.2%
Coastal Plain and Piedmont Element	- -	- -	1 sp. 1.6%	- -	9 spp. 10.9%
Appalachian-Centered Element	8 spp. 10.7%	9 spp. 9.9%	6 spp. 9.8%	9 spp. 14.5%	8 spp. 9.8%
Appalachian-Ozarkian Element	5 spp. 6.7%	7 spp. 7.7%	4 spp. 6.6%	4 spp. 6.5%	4 spp. 4.9%
Southern Appalachian Endemics	2 spp. 2.7%	3 spp. 3.2%	3 spp. 4.9%	3 spp. 4.8%	4 spp. 4.9%
Species of Wide Distribution					
Canada to Gulf of Mexico	41 spp. 54.7%	47 spp. 51.7%	33 spp. 54.1%	34 spp. 54.8%	38 spp. 46.3%
North of the Gulf States	6 spp. 8.0%	6 spp. 6.6%	3 spp. 4.9%	4 spp. 6.5%	4 spp. 4.9%
South of the Glacial Boundary	11 spp. 14.7%	12 spp. 13.2%	7 spp. 11.5%	6 spp. 9.7%	14 spp. 17.1%

Brown 1944, 1946; Sharp 1951), although some others are known from more recent pre-Pleistocene deposits in the south. There remains the possibility that other genera within this group did exist on unreduced southern areas and that no evidence of their occurrence was recorded in the lowland deposits.

The occurrence of white pine (Pinus strobus) in the highlands of Mexico and Guatemala poses an interesting question of migrational history. Dressler (1954) and Sharp (1953) suggest that this and other temperate mesophytic species may have reached Mexico as a result of migration during the Pleistocene. An opposing view is taken by Braun (1955) and Martin and Harrell (1957), who suggest that white pine in these disjunct stations probably predates the period of glaciation.

The presence of the hemlock root parasite, Buckleya distichophylla, as an endemic in the southern mountains raises still another interesting problem in distr bution (Braun 1950). The nearest living relatives of this highly restricted species occur in eastern Asia. If the assumption that hemlock in the south is a result of Pleistocene migration is accepted, it follows that Buckleya also migrated southward during this period, but without a subsequent reinvasion of the glaciated region.

It would appear that the occurrence of "northern" species in the Southern Appalachians may be the result of either (1) southward migration during the Pleistocene, or (2) continuous existence in the region since before the onset of the ice age. In either case, these species are now restricted, for the most part, to protected and/or humid habitats in the southern portion of their ranges.

The Coastal Plain and Piedmont Element

Included within the intraneous flora are nine species (*Pinus taeda*, *Smilax laurifolia*, *Carya pallida*, *Hydrangea quercifolia*, *Ilex longipes*, *Acer leucoderme*, *Berchemia scandens*, *Vaccinium elliottii*, and *Gelsemium sempervirens*) which are essentially characteristic of the Coastal Plain and, to a lesser extent, the Piedmont Province. With only one exception, *Berchemia scandens*, these were found only in Little River Canyon, the southernmost gorge included in this report.

Braun (1937a, 1955) suggested that certain Coastal Plain species which occur as disjuncts on the Cumberland Plateau are relics which were isolated from main populations as a result of migration during the uplift of the plateau. However, none of the species listed above have distributions similar to those of relics discussed by Braun.

Sharp (1955) listed three possible explanations for the tropical element in the flora of Tennessee, including (1) continuous persistence of Tertiary taxa within the region, (2) reinvasion by taxa which were present during the Tertiary but were forced southward during the Quarternary, and (3) invasion by taxa which are becoming established in the region for the first time. Although only two of the genera involved (*Smilax* and *Berchemia*) are primarily tropical, these three possibilities are true for all of the Coastal Plain or Piedmont taxa found in the gorges of the plateau.

The Appalachian-Centered Element

Eleven species, representing both intraneous and extraneous floras, apparently are best represented in the Appalachian region from New York to northern Alabama, although some may be rather common in adjacent provinces (including the Coastal Plain). These include Pinus virginiana, Betula lenta, Castanea dentata, Quercus prinus, Calycanthus floridus, Calycanthus fertilis, Xanthorhiza simplicissima, Aesculus octandra, Rhododendron arborescens, Rhododendron maximum, Rhododendron catawbiense. None of these are known to occur west of the Mississippi River.

Considering that the Appalachians include a land mass that has been suitable for continuous plant habitation longer than any other in North America, it would seem that the eleven species listed above are among those which originated in these highlands and have been centered there since.

Appalachian-Ozarkian Element

Included here are six species of the intraneous flora (Magnolia acuminata, Magnolia tripetala, Philadelphus hirsutus, Robinia pseudeo-acacia, Cladrastis lutea, and Tilia heterophylla) which are essentially Southern Appalachian, but have disjunct distributions in the Ozark or Ouachita highlands west of the Mississippi River. The present distributions and affinities of these species suggest that they were present in the Tertiary forest which apparently extended over much of North America from the present Rocky Mountains eastward and northward (Braun 1950). Subsequent geological and climatic events (especially Eocene marine transgression and period of warm, dry climate) resulted in the present disjunct distributions.

A sixth species of the intraneous flora, Magnolia macrophylla, is included in this category because of its occurrence west of the Mississippi River in Louisiana and on Crowley's Ridge in Arkansas.

The Southern Appalachian Endemics

There seems to be little question that the six species herein considered as Southern Appalachian endemics (*Pyrularia pubera*, *Aristolochia durior*, *Fothergilla major*, *Spiraea virginiana*, *Stewartia ovata*, and *Diervilla rivularis*) originated in the region and have since been restricted to it, except for possible range extensions during the Pleistocene. It is probable that at least some of the species were once more widely distributed in the Southern Appalachians, but became restricted or disjunct as a result of peneplanation of upland areas during the Schooley or later erosion cycles.

All of the genera involved, except *Spiraea*, are either restricted to eastern Asia and eastern North America, or have their closest living relatives in Asia (Li 1952).

VII. SUMMARY

1. The vegetation of five gorges of the Cumberland Plateau is discussed and the major community types occurring in each are described. The five study areas include Buffalo Cove (Fentress County, Tennessee), Fall Creek Falls (VanBuren County, Tennessee), Little Piney Creek (Rhea County, Tennessee), Cloudland Canyon (Dade County, Georgia), and Little River Canyon (DeKalb and Cherokee counties, Alabama).

2. The major community types occurring in all five gorges include (1) the mixed mesophytic stands of the most favorable habitats, (2) the chestnut oak community of the dry, upper slopes, and (3) the oak-hickory community which occupies more or less intermediate habitats. Other distinct communities occurring in Little River Canyon also are discussed.

3. Of the 126 woody species listed as occurring in the five gorges, 105 (83.3 per cent) do not reach a range limit in any direction within the plateau, and are included in the intraneous flora. Twenty-one species (16.7 per cent) do reach a geographical limit within the area, and are included in the extraneous flora.

4. The intraneous flora is divided into the following groups of species, according to distribution:

a. fifty-six species (53.3 per cent) which are widely-distributed over much of the eastern North America from Canada to the Gulf of Mexico;

b. eight species (7.6 per cent) which are widely-distributed over much of eastern North America north of the Gulf states;

c. twenty-one species (20.0 per cent) which are widely-distributed south of the glacial boundary;

d. eight species (8.6 per cent) which are essentially of the southern Coastal Plain or Piedmont;

e. five species (3.8 per cent) which are Appalachian-centered;

f. six species (6.7 per cent) which are Southern Appalachian-centered with disjunct occurrences west of the Mississippi River.

5. The twenty-one species of the extraneous flora are included in the following groups:

a. seven species (33.3 per cent) which are best represented in northern forests from the Great Lakes to New England, with Southern Appalachian extensions;

b. two species (9.5 per cent) which range from Canada and New England southward in the Appalachians;

c. one species (4.8 per cent) which is Canadian trans-continental with a Southern Appalachian extension;

d. five species (23.8 per cent) which are essentially Southern Appalachian with extensions into adjacent regions;

e. six species (28.6 per cent) which are Southern Appalachian endemics.

6. Distribution maps for all but one (Fothergilla major) of the species of the extraneous flora and certain representatives of the intraneous flora were prepared and are included in the Appendix of this paper.

7. The woody flora of the five gorges, excluding wide-ranging species, is divided into the following five distinct floristic elements: (1) northern; (2) Coastal Plain and Piedmont; (3) Appalachian-centered; (4) Appalachian-Ozarkian; and (5) Southern Appalachian endemics.

8. The northern element includes eight species (6.3 per cent of the total flora) which are best represented in Canada and northern states.

The occurrence of these species in the Southern Appalachians may be the result of (1) southward migration due to the climatic changes which produced glaciation, or (2) continuous persistence in the region since before the Pleistocene.

9. The Coastal Plain and Piedmont element includes nine species (7.1 per cent of the total flora) which are best represented in the southern Coastal Plain and, to a lesser extent, the Piedmont. The occurrence of these species in certain gorges of the Cumberland plateau is interpreted as being the result of (1) continuous persistence in the region since Tertiary time, (2) invasion from more southern centers of origin, or (3) reinvasion of the region after southward migration due to climatic stress of the glacial period.

10. The Appalachian-centered element includes eleven species (8.7 per cent of the total flora) which have centers of distribution in the Appalachian highlands from Pennsylvania to Alabama, with range extensions into adjacent regions. These species probably originated in the Appalachians, and have been centered in the region since.

11. The Southern Appalachian-Ozarkian element includes seven species (5.6 per cent of the total flora) which are essentially Southern Appalachian-centered with disjunct populations west of the Mississippi River, especially in the Ozark and Ouachita highlands. These species evidently were present in the wide-spread Tertiary forest but now have disjunct distributions resulting from geologic and climatic events of the Late Tertiary and Early Quarternary periods.

12. The Southern Appalachian endemic element includes six species (4.7 per cent of the total flora) which are restricted to the mountains and plateau of the Southern Appalachian region and, to a lesser degree, the Ridge and Valley Province between. These species undoubtedly originated in the southern highlands and have been restricted to them since, except for possible range extensions during the Pleistocene. Some species probably were once more widely distributed in the region, but now have restricted or disjunct distributions resulting from the reduction of uplands during the Schooley or later erosion cycles. Five of the six species have eastern Asian affinities.

13. The woody flora of the gorges of the Cumberland exhibits a strong southern affinity, as indicated by the Appalachian and Coastal Plain elements and the large number of species of wide distribution south of the glacial boundary.

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APPENDIX

TABLE III

COMPOSITE LIST OF WOODY SPECIES OCCURRING IN FIVE GORGES OF THE CUMBERLAND PLATEAU[a]

Species	Buffalo Cove	Fall Creek[b]	Little Piney[c]	Cloudl. Canyon	Little River
Pinaceae					
Tsuga canadensis	x	x	x	x	
Pinus echinata					x
Pinus strobus			x		
Pinus taeda					x
Pinus virginiana	x	x	x	x	x
Thuja occidentalis		x			
Juniperus virginiana		x			
Liliaceae					
Smilax bona-nox		x			
Smilax ecirrhata		x			
Smilax glauca	x	x		x	x
Smilax laurifolia					x
Smilax rotundifolia	x	x	x	x	x
Salicaceae					
Salix caroliniana		x			
Salix nigra	x			x	
Juglandaceae					
Juglans cinerea	x	x		x	x
Juglans nigra		x			
Carya cordiformis	x	x			
Carya glabra	x	x	x	x	x
Carya ovalis	x	x			
Carya ovata	x	x	x	x	x
Carya pallida					x
Carya tomentosa		x	x		x

TABLE III

COMPOSITE LIST OF WOODY SPECIES OCCURRING IN FIVE GORGES OF THE CUMBERLAND PLATEAU[a] (Continued)

Species	Buffalo Cove	Fall Creek[b]	Little Piney[c]	Cloudl. Canyon	Little River
Corylaceae					
Ostrya virginiana	x	x	x		x
Carpinus caroliniana	x	x	x	x	
Corylus americana		x			
Betula lenta		x		x	x
Betula alleghaniensis (*B. lutea*)		x	x		
Alnus serrulata	x	x	x	x	x
Fagaceae					
Fagus grandifolia	x	x	x	x	x
Castanea dentata	x	x	x		
Quercus alba	x	x	x	x	x
Quercus falcata	x				
Quercus prinus	x	x	x	x	x
Quercus rubra	x	x	x	x	x
Quercus velutina	x	x	x	x	x
Ulmaceae					
Ulmus alata	x	x	x	x	x
Ulmus americana	x	x	x	x	
Ulmus rubra	x				
Celtis occidentalis		x			
Celtis tenuifolia var. *georgiana*	x				x
Moraceae					
Morus rubra	x	x		x	x
Santalaceae					
Pyrularia pubera			x		x

TABLE III

COMPOSITE LIST OF WOODY SPECIES OCCURRING IN FIVE GORGES OF THE CUMBERLAND PLATEAU[a] (Continued)

Species	Buffalo Cove	Fall Creek[b]	Little Piney[c]	Cloudl. Canyon	Little River
Aristolochiaceae					
Aristolochia durior	x	x	x		
Ranunculaceae					
Xanthorhiza simplicissima	x	x	x	x	x
Magnoliaceae					
Magnolia acuminata	x	x	x	x	
Magnolia macrophylla		x	x		
Magnolia tripetala	x	x	x	x	x
Liriodendron tulipifera	x	x	x	x	x
Calycanthaceae					
Calycanthus fertilis				x	x
Calycanthus floridus	x	x	x	x	x
Anonaceae					
Asimina triloba	x		x	x	x
Lauraceae					
Sassafras albidum	x	x	x	x	x
Lindera benzoin	x	x			
Saxifragaceae					
Hydrangea arborescens	x	x	x	x	x
Hydrangea quercifolia					x
Ribes cynosbati		x		x	x
Itea virginica		x			x
Philadelphus hirsutus		x			x

TABLE III

COMPOSITE LIST OF WOODY SPECIES OCCURRING IN FIVE GORGES OF THE CUMBERLAND PLATEAU[a] (Continued)

Species	Buffalo Cove	Fall Creek[b]	Little Piney[c]	Cloudl. Canyon	Little River
Hamamelidaceae					
Hamamelis virginiana	x	x	x	x	x
Fothergilla major					x
Liquidambar styraciflua	x	x	x	x	x
Platanaceae					
Platanus occidentalis	x	x	x	x	
Rosaceae					
Spiraea virginiana		x		x	
Amelanchier arborea		x			x
Amelanchier laevis	x		x		
Rubus occidentalis	x	x			
Rubus pensilvanicus	x				
Prunus serotina		x	x	x	
Leguminosae					
Cercis canadensis	x	x		x	x
Cladrastis lutea	x	x			
Robinia pseudo-acacia	x	x		x	x
Rutaceae					
Ptelea trifoliata				x	
Anacardiaceae					
Rhus copallina	x		x		x
Rhus glabra	x				
Rhus radicans	x	x	x	x	x

TABLE III

COMPOSITE LIST OF WOODY SPECIES OCCURRING IN FIVE GORGES OF THE CUMBERLAND PLATEAU[a] (Continued)

Species	Buffalo Cove	Fall Creek[b]	Little Piney[c]	Cloudl. Canyon	Little River
Aquifoliaceae					
Ilex longipes					x
Ilex opaca	x	x	x	x	x
Ilex verticillata					x
Celastraceae					
Euonymus americanus	x	x	x	x	x
Staphyleaceae					
Staphylea trifolia		x			
Aceraceae					
Acer leucoderme					x
Acer pensylvanicum		x	x		
Acer rubrum	x	x	x	x	x
Acer saccharum	x	x	x	x	x
Hippocastanaceae					
Aesculus octandra	x	x		x	
Rhamnaceae					
Rhamnus caroliniana	x	x			
Berchemia scandens			x		x
Ceanothus americanus			x		x
Vitaceae					
Vitis aestivalis	x	x		x	x
Vitis rotundifolia		x			x
Parthenocissus quinquefolia	x	x	x	x	x

TABLE III

COMPOSITE LIST OF WOODY SPECIES OCCURRING IN FIVE GORGES OF THE CUMBERLAND PLATEAU[a] (Continued)

Species	Buffalo Cove	Fall Creek[b]	Little Piney[c]	Cloudl. Canyon	Little River
Tiliaceae					
Tilia heterophylla	x	x	x	x	x
Theaceae					
Stewartia ovata	x	x	x	x	x
Guttiferae					
Hypericum frondosum				x	
Nyssaceae					
Nyssa sylvatica	x	x	x	x	x
Araliaceae					
Aralia spinosa	x	x	x	x	x
Cornaceae					
Cornus florida	x	x	x	x	x
Cornus alternifolia		x			
Ericaceae					
Rhododendron arborescens	x	x		x	x
Rhododendron catawbiense				x	x
Rhododendron maximum	x	x	x		
Kalmia latifolia	x	x	x	x	x
Oxydendrum arboreum	x	x	x	x	x
Lyonia ligustrina		x			x
Gaylussacia baccata	x	x			
Vaccinium arboreum	x	x	x	x	x
Vaccinium elliottii					x
Vaccinium stamineum		x	x		x
Vaccinium vacillans	x	x	x	x	x

TABLE III

COMPOSITE LIST OF WOODY SPECIES OCCURRING IN FIVE GORGES OF THE CUMBERLAND PLATEAU[a] (Continued)

Species	Buffalo Cove	Fall Creek[a]	Little Piney[c]	Cloudl. Canyon	Little River
Ebenaceae					
Diospyros virginiana	x	x	x		x
Styracaceae					
Halesia carolina					x
Oleaceae					
Chionanthus virginicus					x
Fraxinus americana	x	x	x	x	x
Loganiaceae					
Gelsemium sempervirens					x
Verbenaceae					
Callicarpa americana					x
Bignoniaceae					
Bignonia capreolata	x	x			x
Campsis radicans	x		x		
Rubiaceae					
Cephalanthus occidentalis		x		x	x

TABLE III

COMPOSITE LIST OF WOODY SPECIES OCCURRING IN FIVE GORGES
OF THE CUMBERLAND PLATEAU[a] (Continued)

Species	Buffalo Cove	Fall Creek[b]	Little Piney[c]	Cloudl. Canyon	Little River
Caprifoliaceae					
Sambucus canadensis	x	x			
Sambucus pubens		x			
Viburnum acerifolium	x	x	x	x	x
Viburnum cassinoides	x	x		x	x
Viburnum dentatum					x
Viburnum rufidulum	x	x	x		x
Diervilla rivularis				x	x

[a]See Maps 2 and 3 for location of these gorges.

[b]Information from Caplenor (1954).

[c]Information provided by Mrs. Lou Woughter, Bryan University, Dayton, Tennessee.

SOURCES OF INFORMATION UTILIZED IN THE PREPARATION

OF SPECIES DISTRIBUTION MAPS

I. Personal communications, mostly with curators of herbaria:

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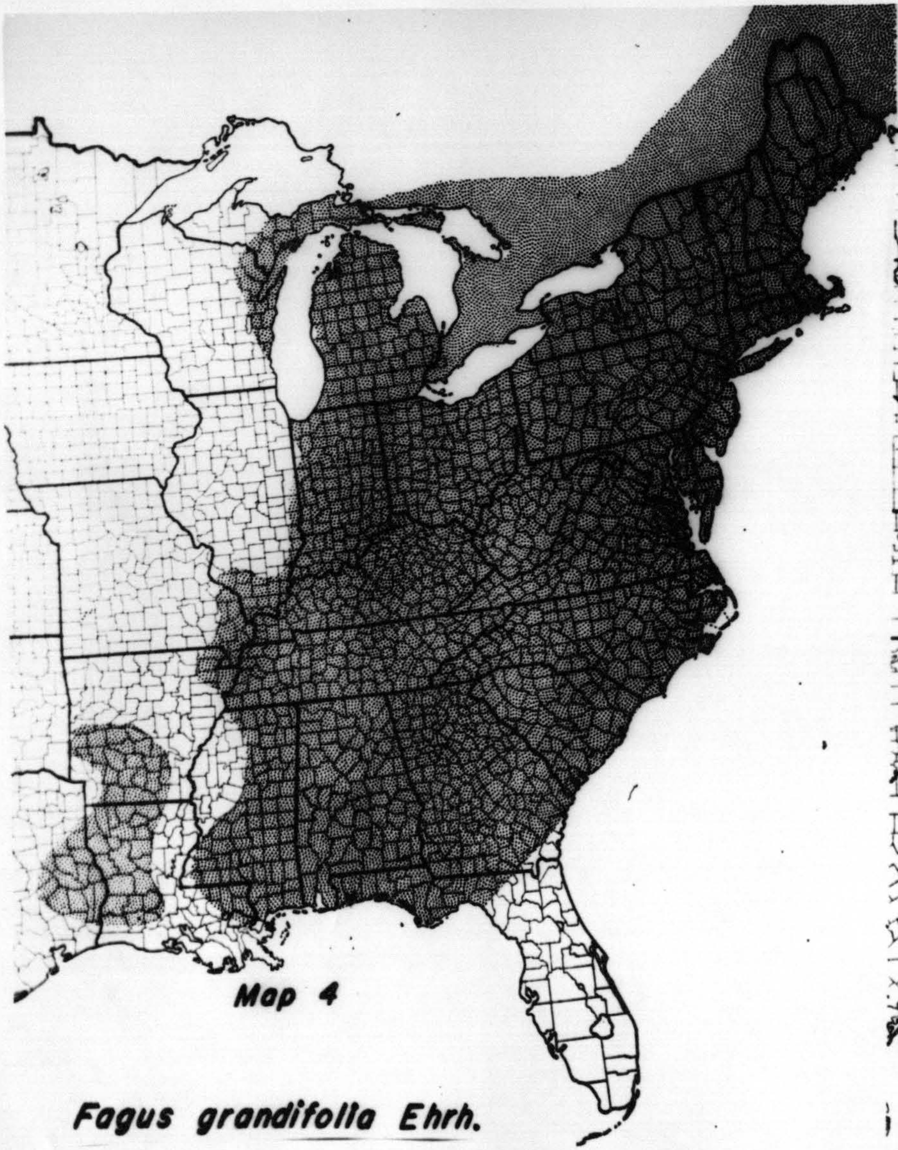
Dr. E. T. Wherry, University of Pennsylvania, Philadelphia.

Mr. Jim Wilson, University of Michigan, Ann Arbor.

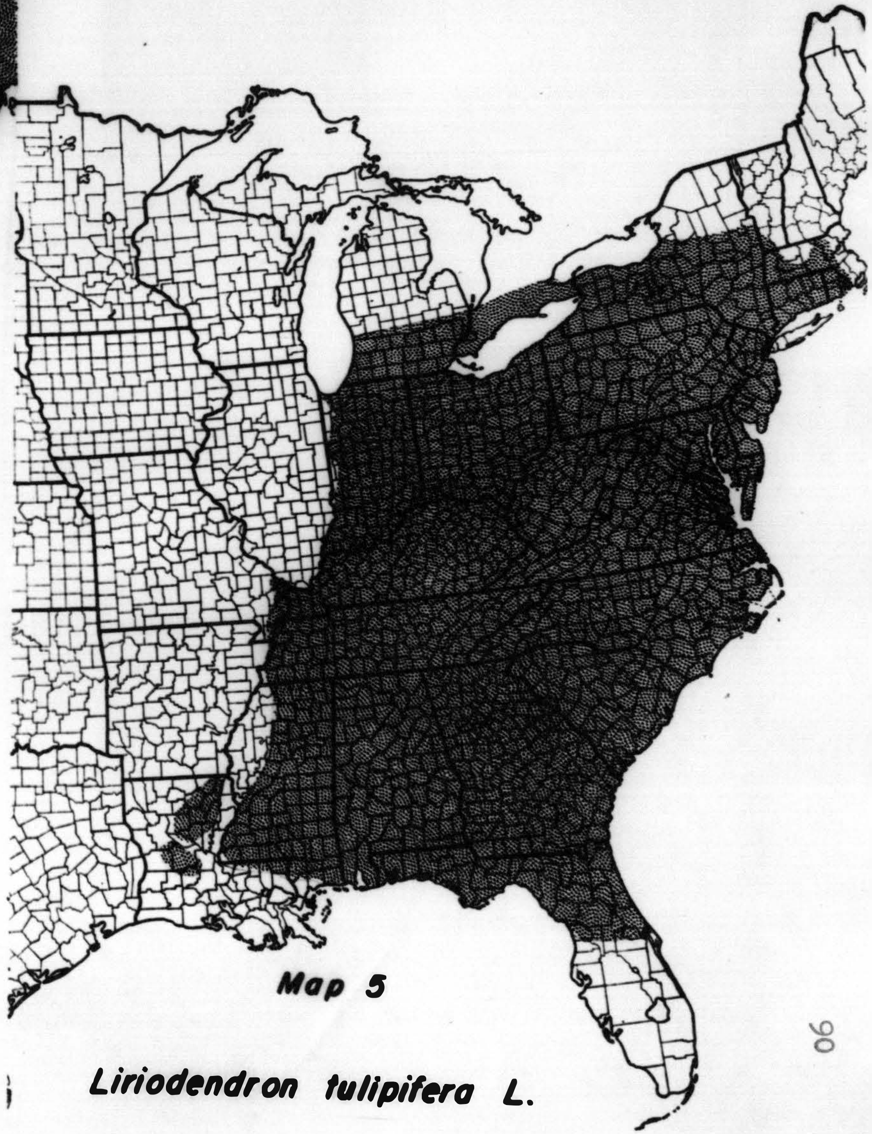
II. Information obtained from publications:

Braun (1943, 1953); Core (1950); Deam (1940); Evans (1942); Harper (1928, 1943); Jones and Fuller (1955); Iltis (1956); Little (1949); Roberts and Cruikshank (1941); Segars *et al.* (1951); Strausbaugh and Core (1952, 1953).



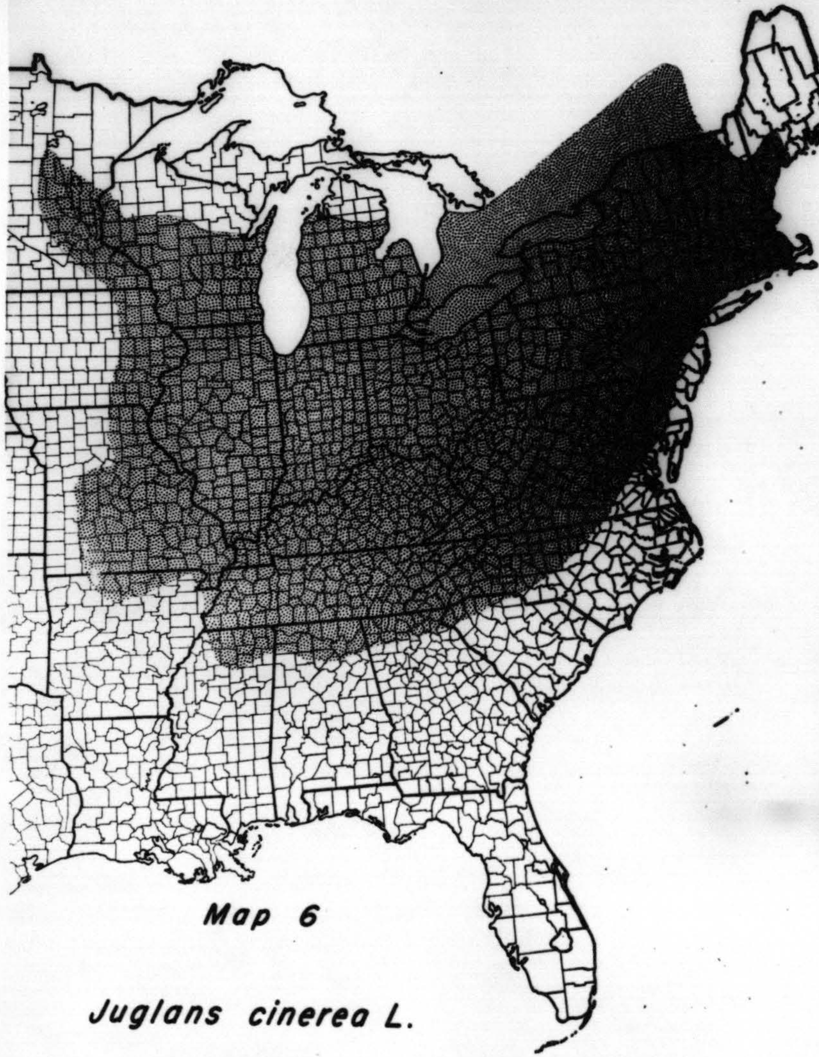
Map 4

Fagus grandifolia Ehrh.



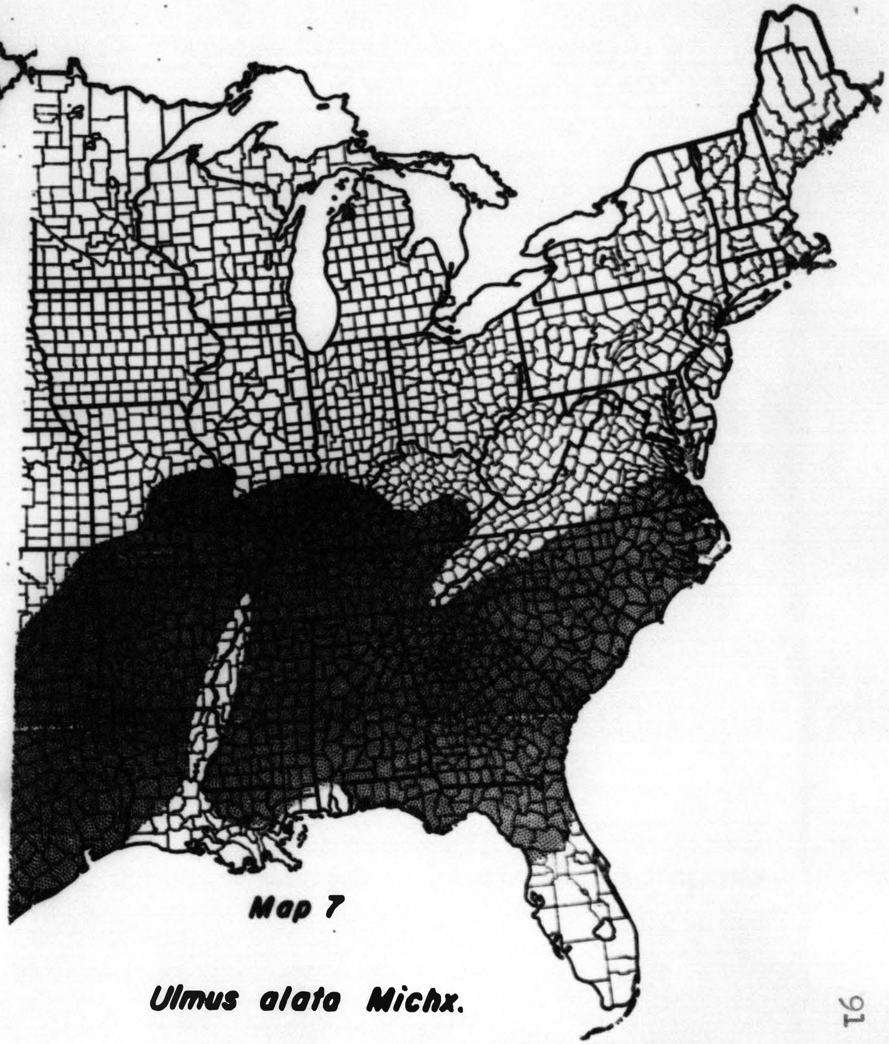
Map 5

Liriodendron tulipifera L.



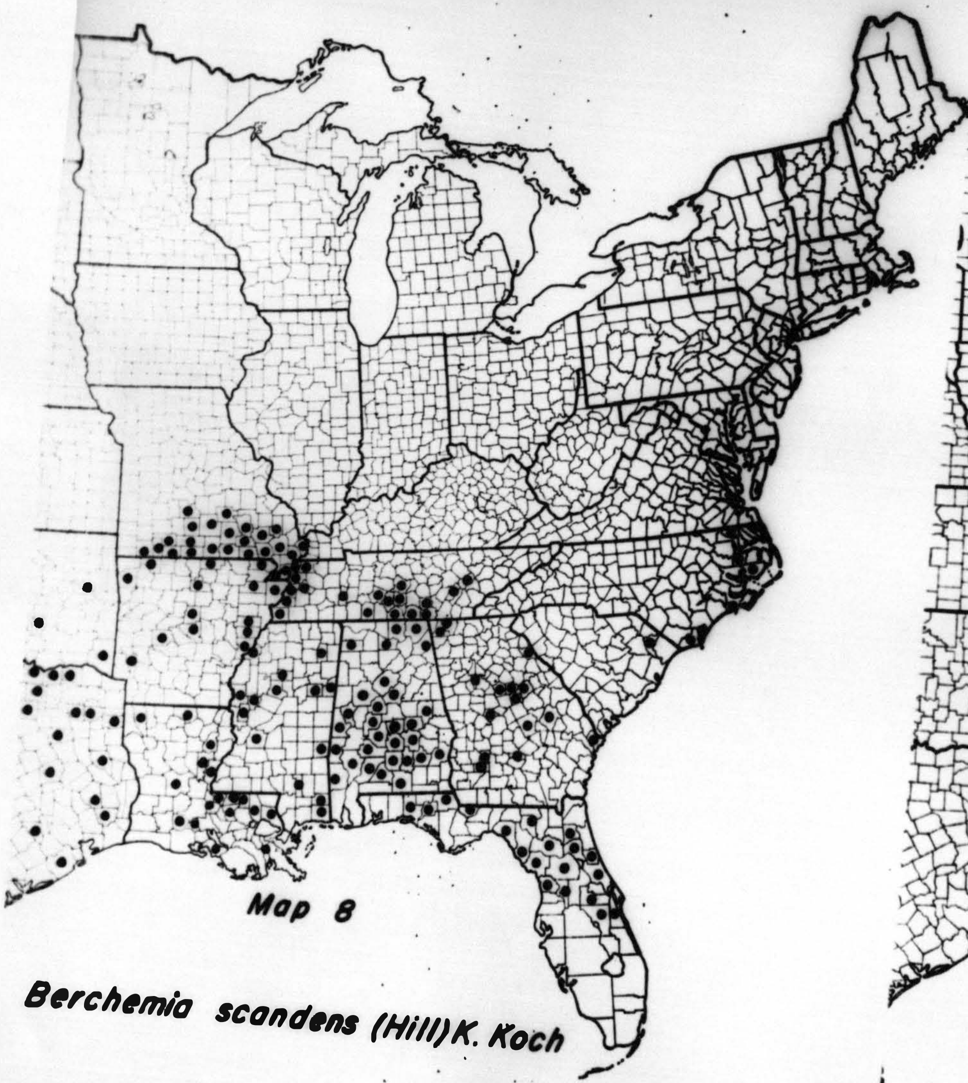
Map 6

Juglans cinerea L.



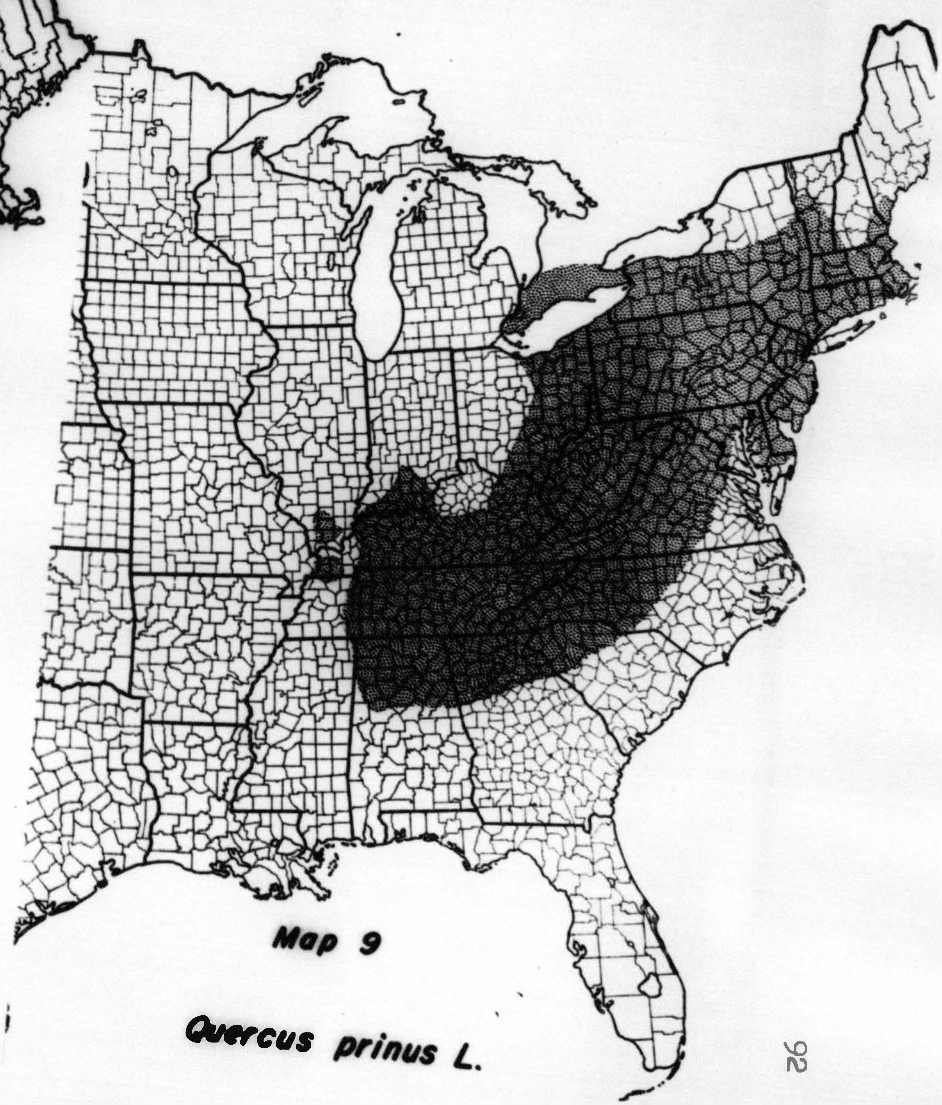
Map 7

Ulmus alata Michx.



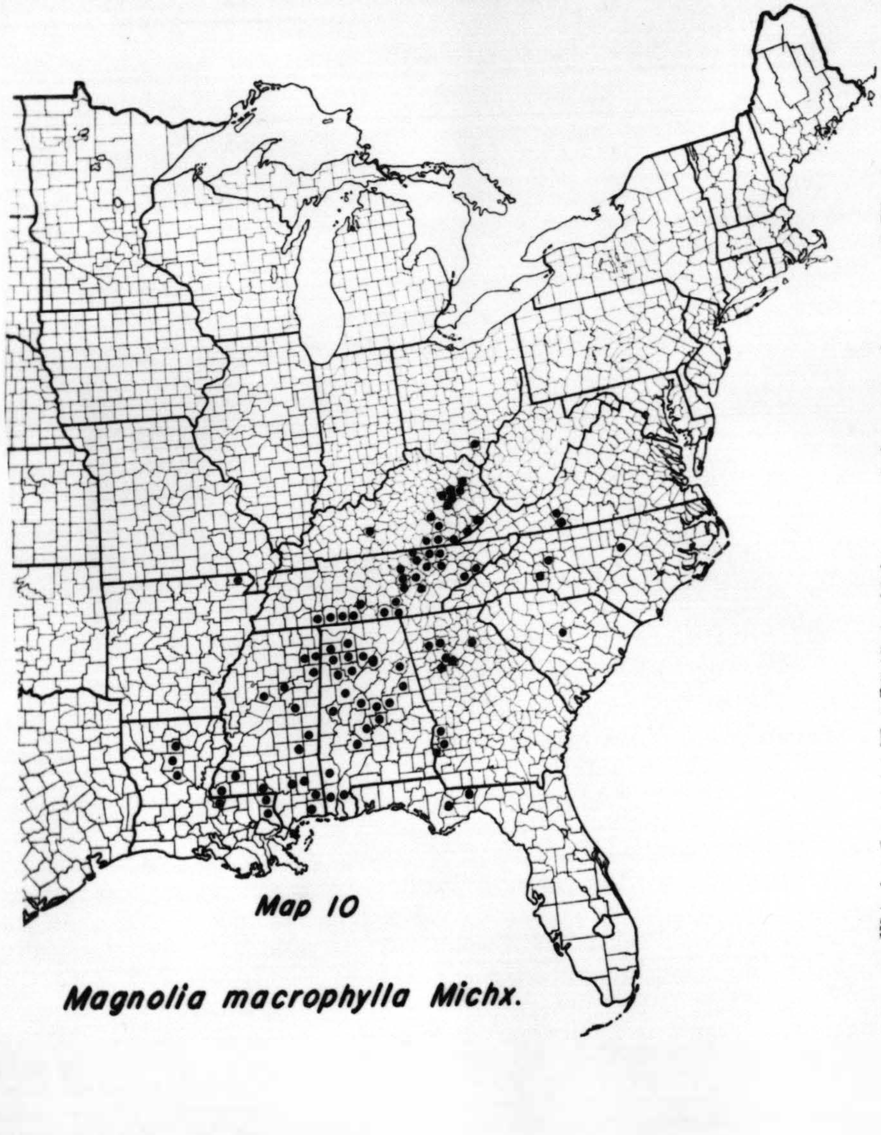
Map 8

Berchemia scandens (Hill) K. Koch



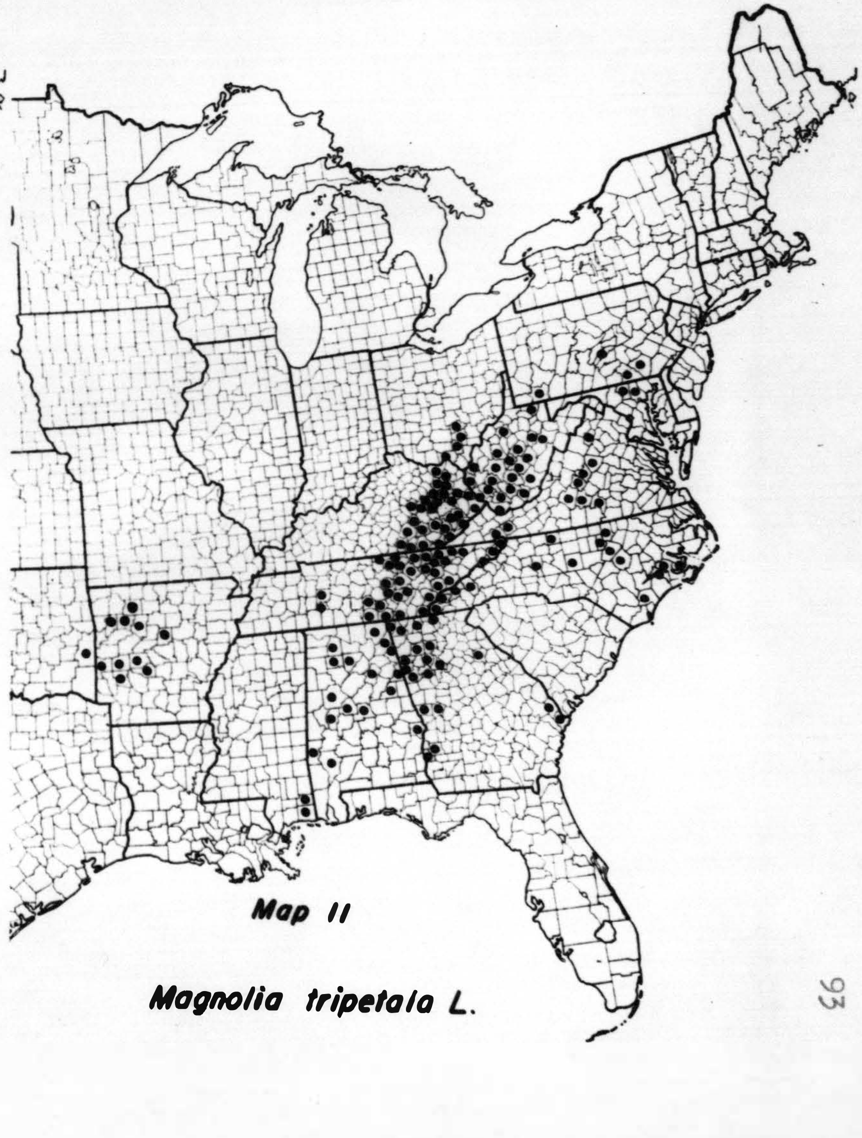
Map 9

Quercus prinus L.



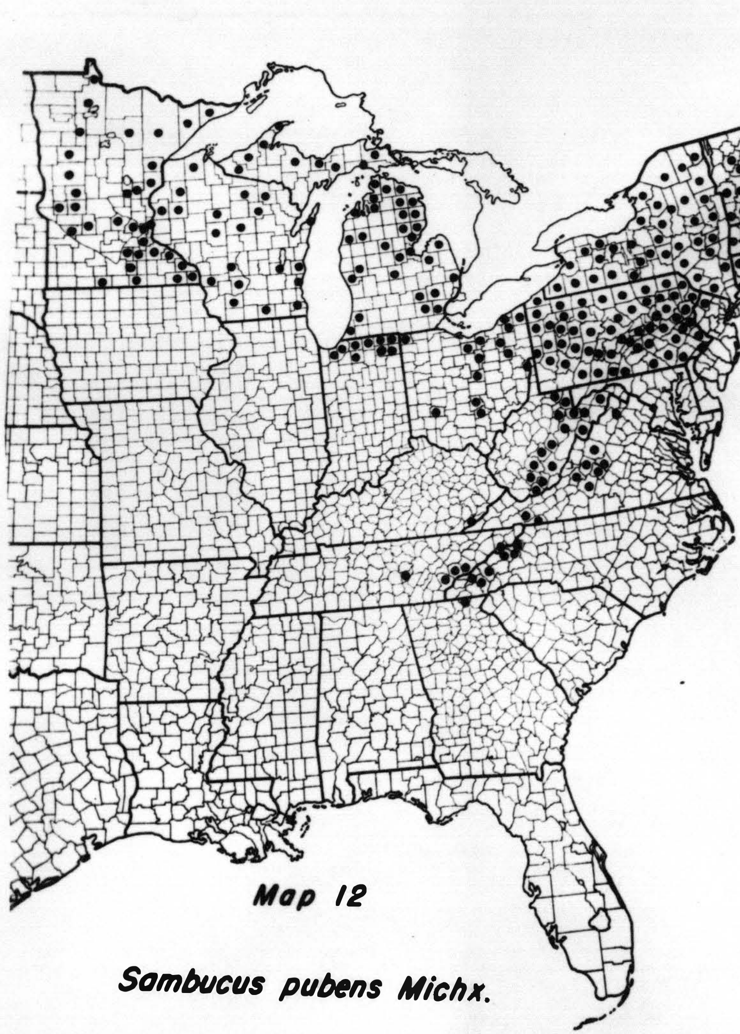
Map 10

Magnolia macrophylla Michx.



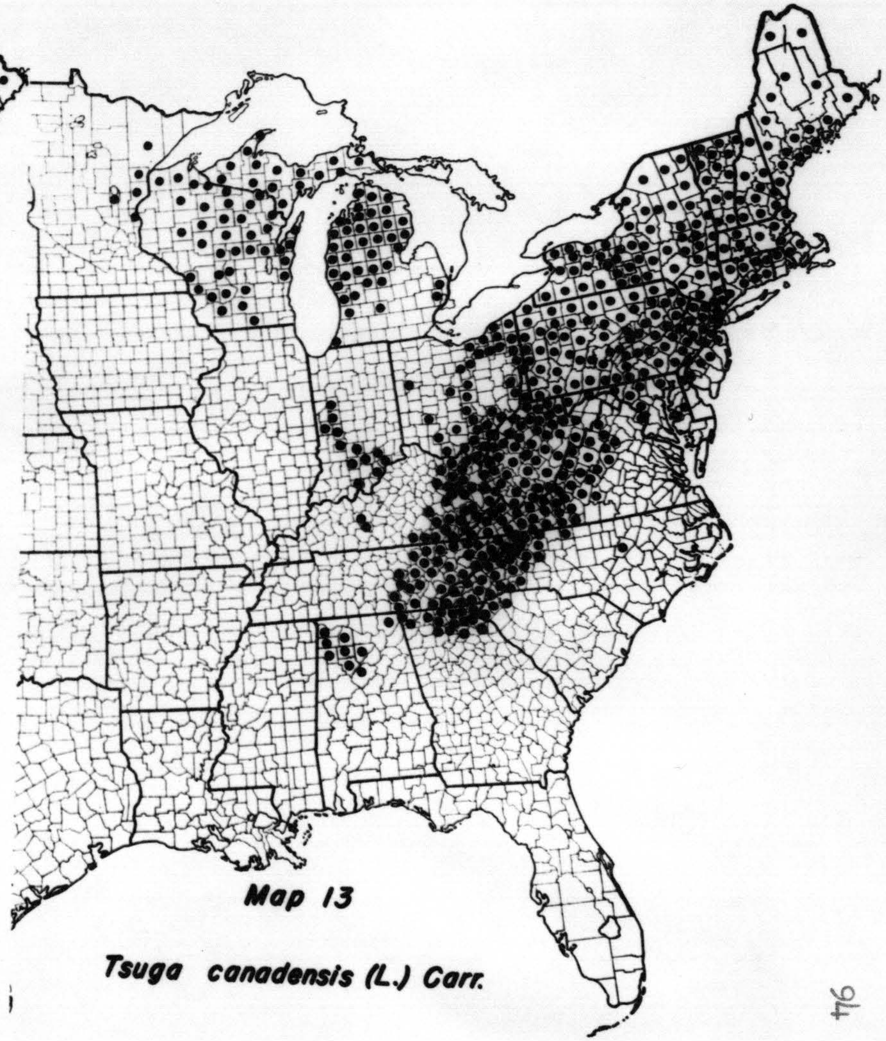
Map 11

Magnolia tripetala L.



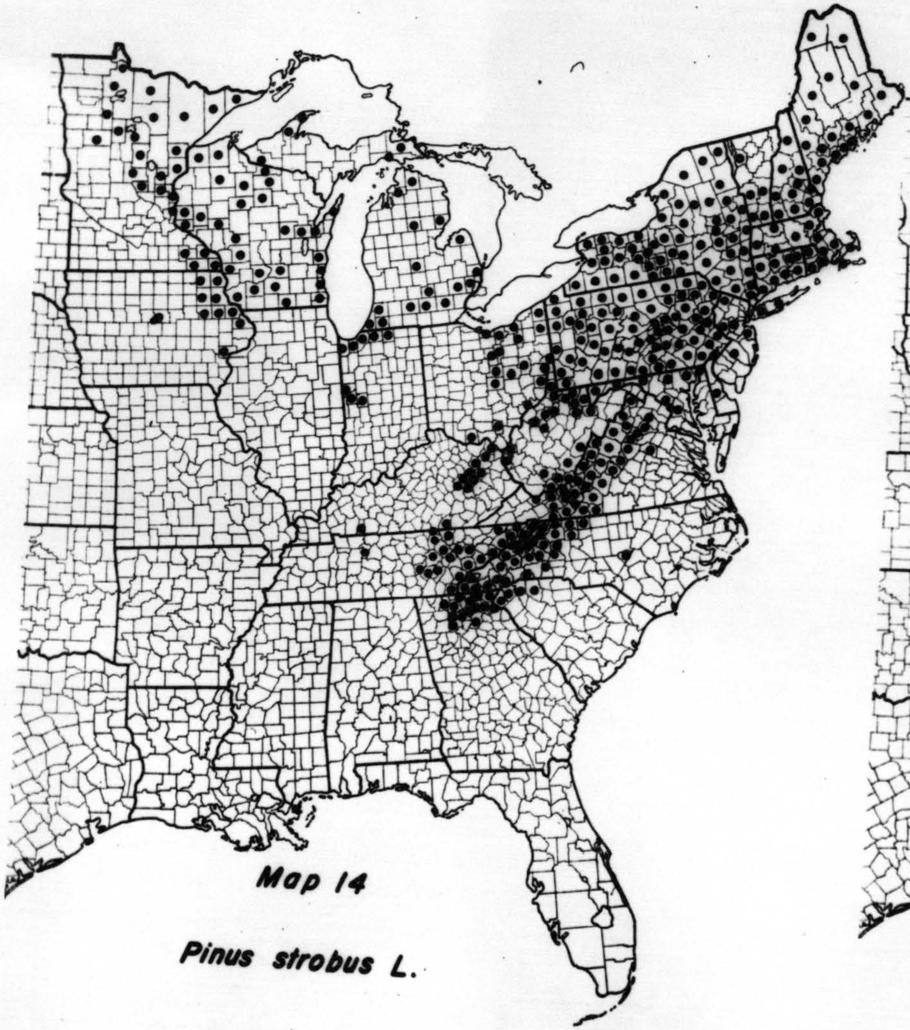
Map 12

Sambucus pubens Michx.



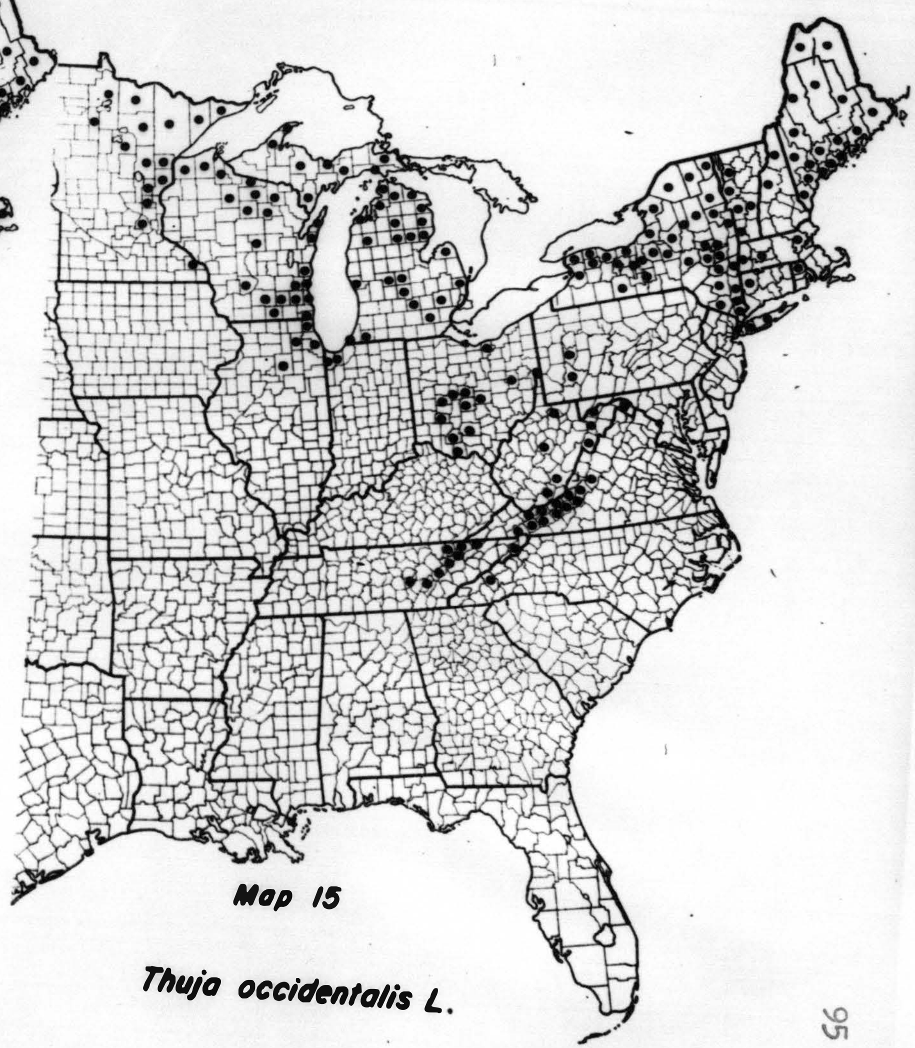
Map 13

Tsuga canadensis (L.) Carr.



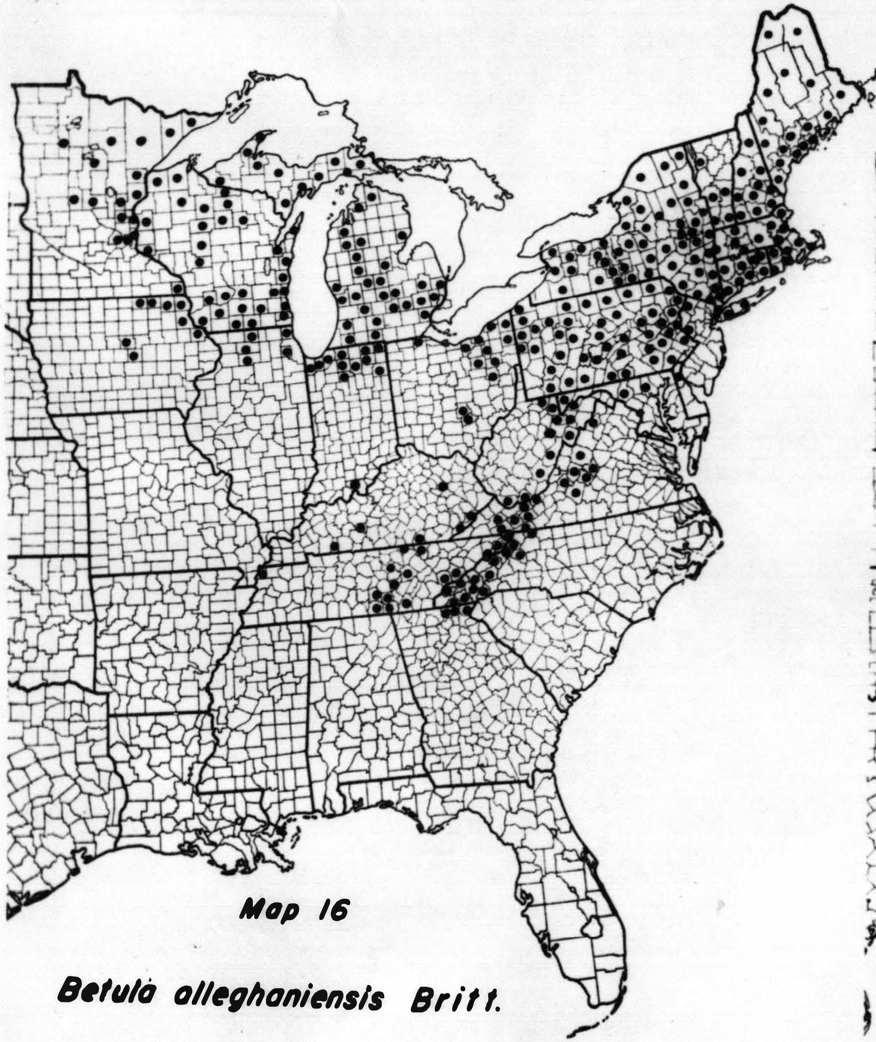
Map 14

Pinus strobus L.



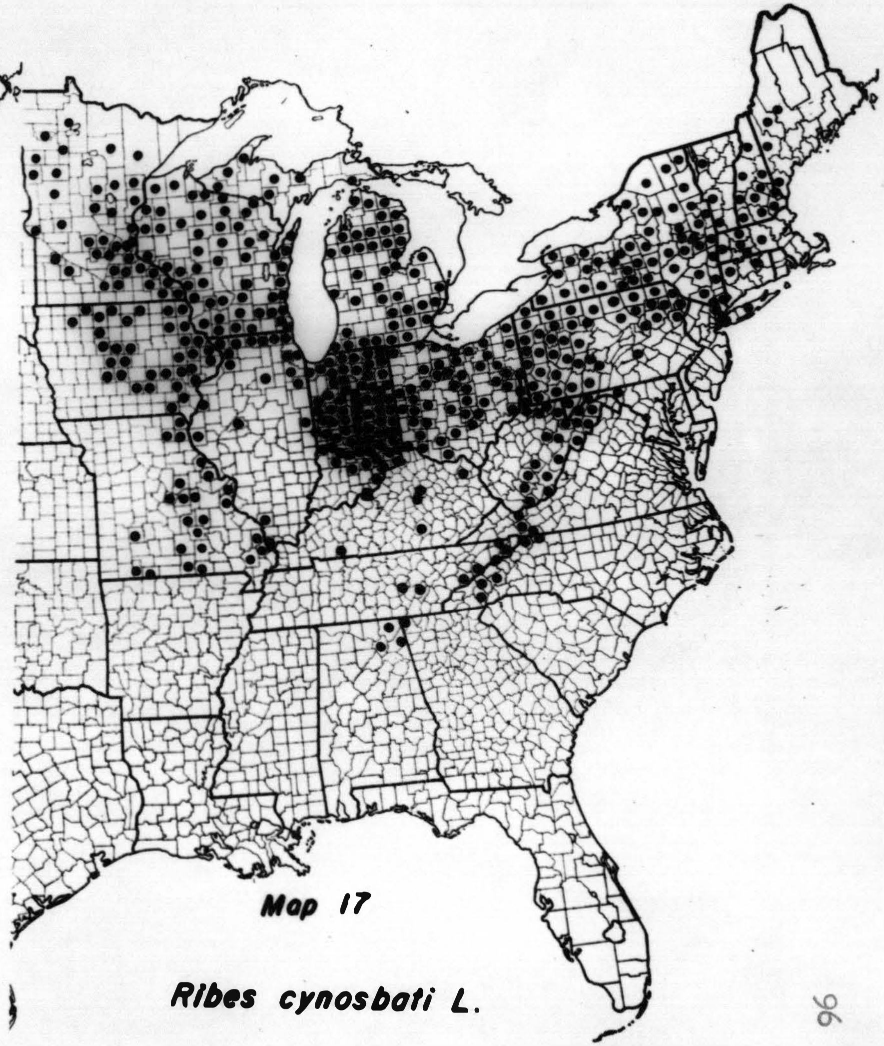
Map 15

Thuja occidentalis L.



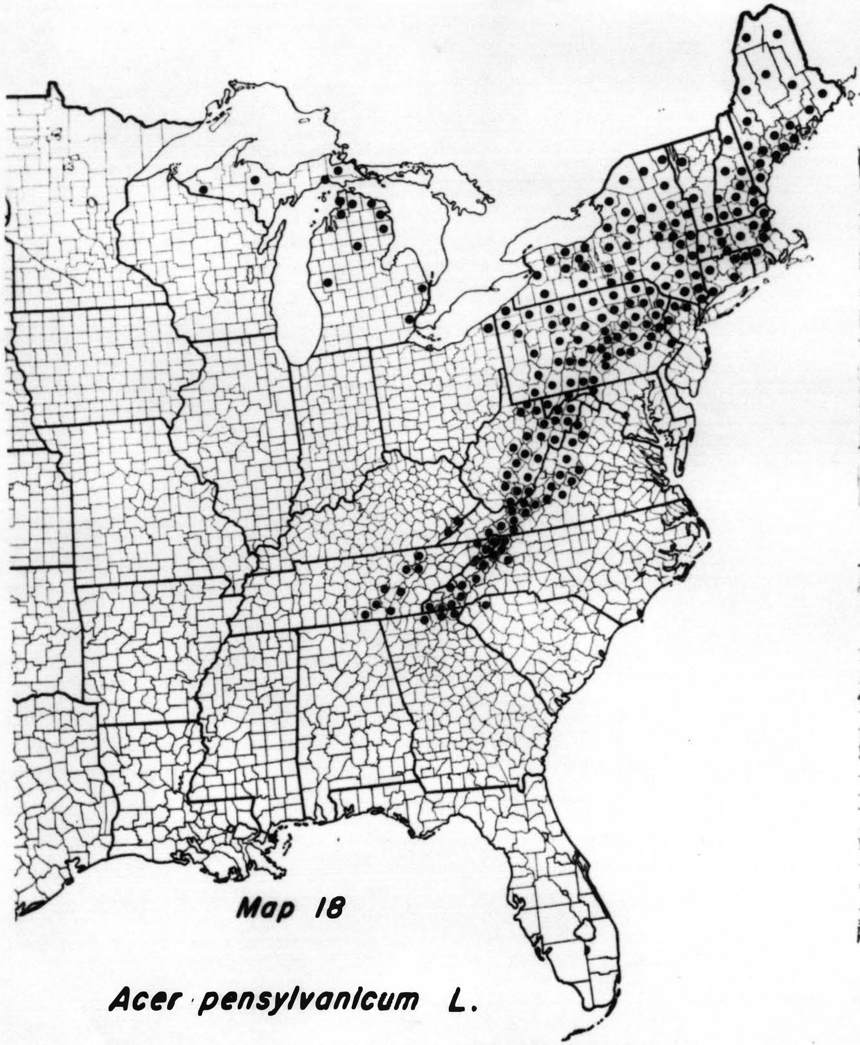
Map 16

Betula alleghaniensis Britt.



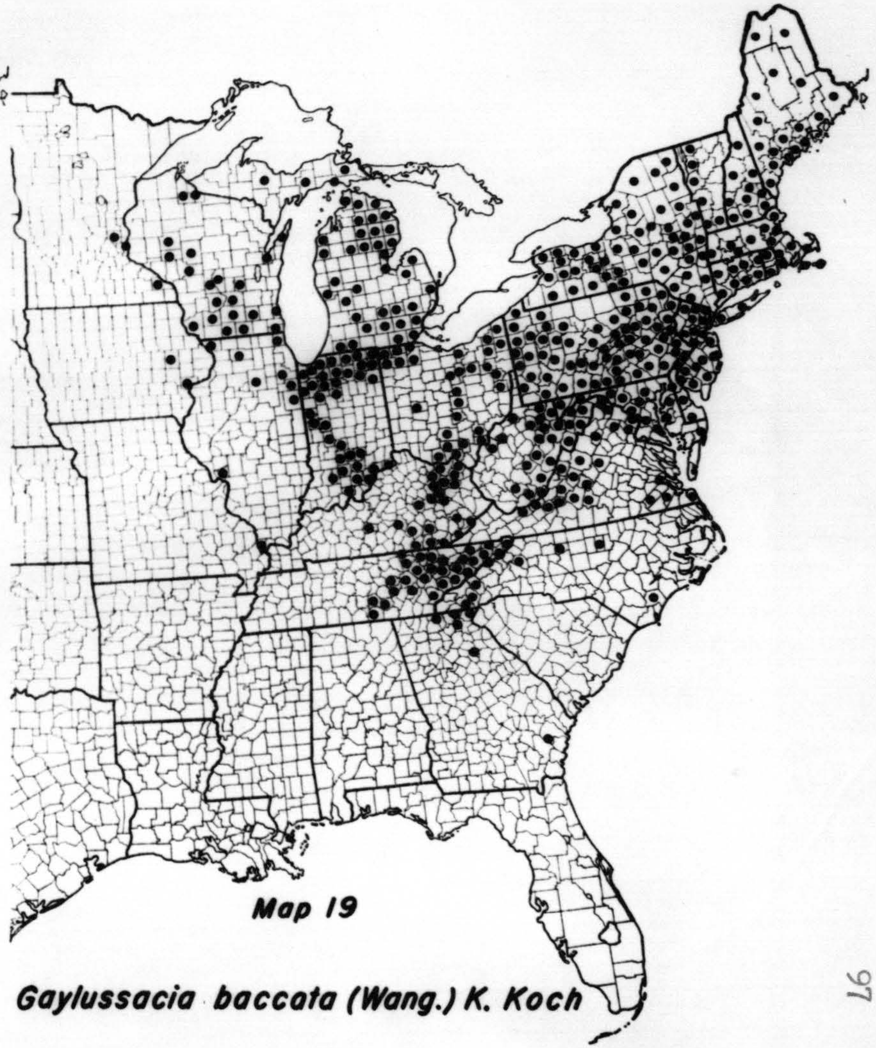
Map 17

Ribes cynosbati L.



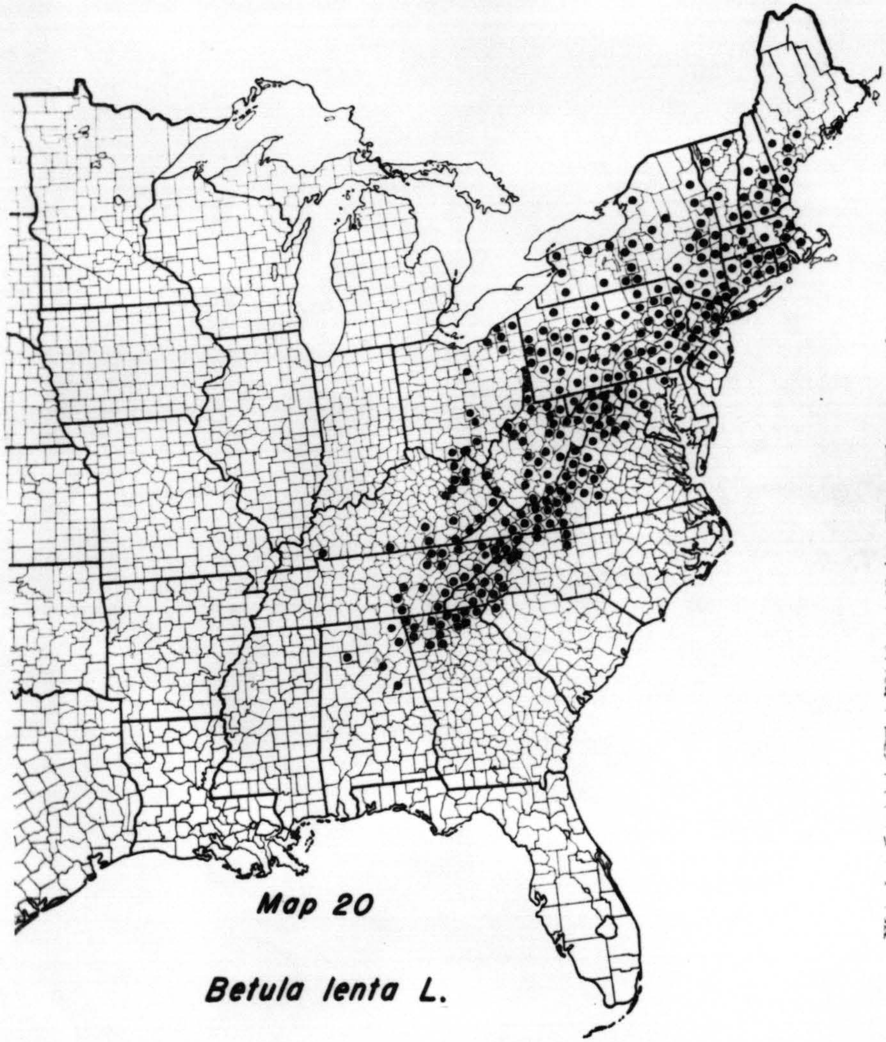
Map 18

Acer pensylvanicum L.



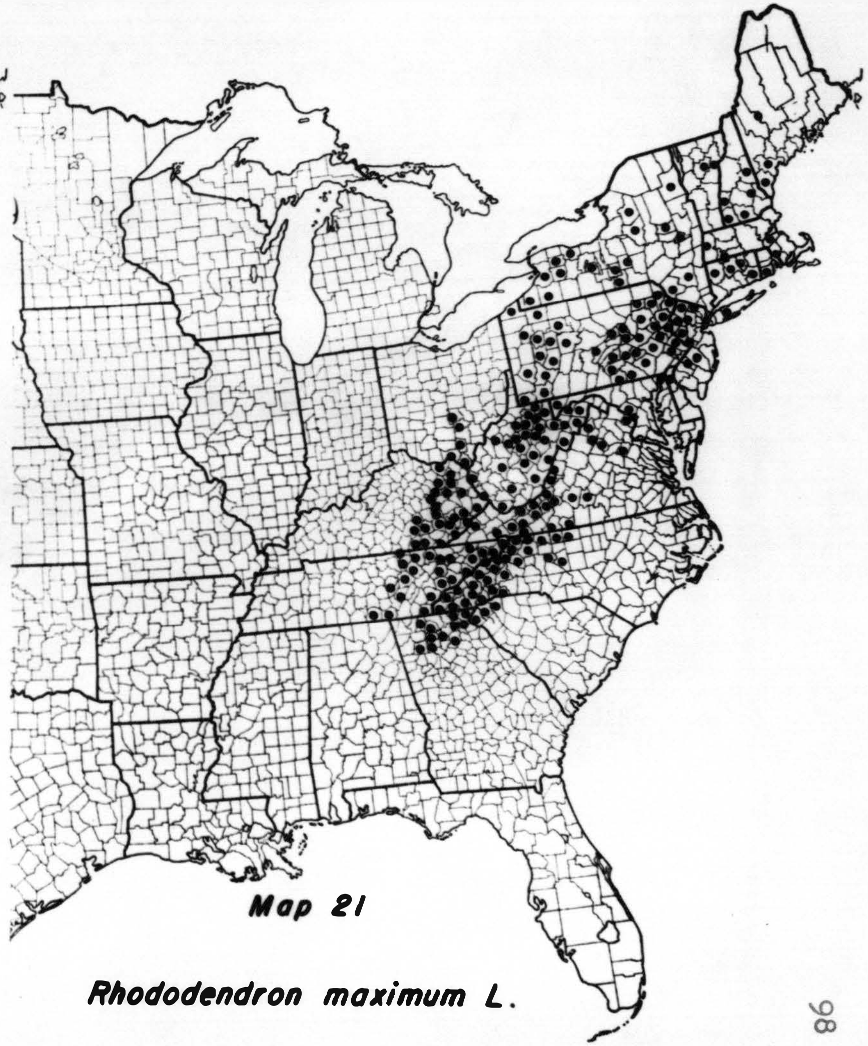
Map 19

Gaylussacia baccata (Wang.) K. Koch



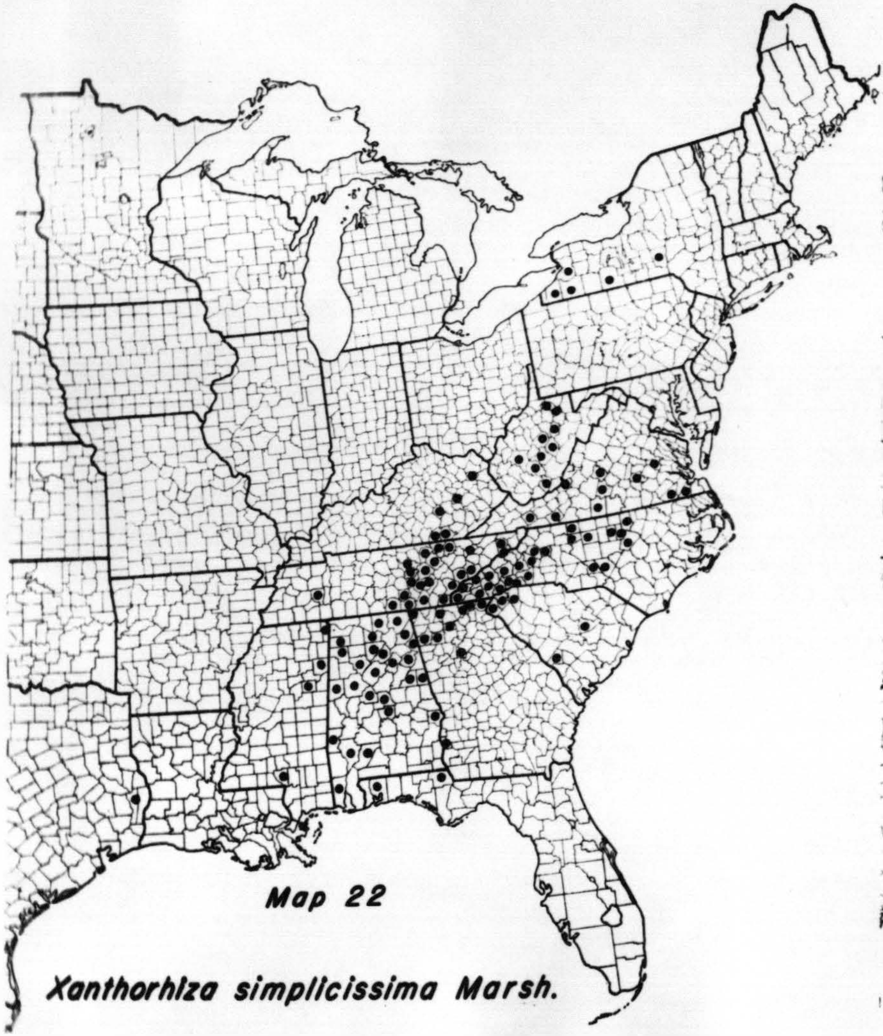
Map 20

Betula lenta L.



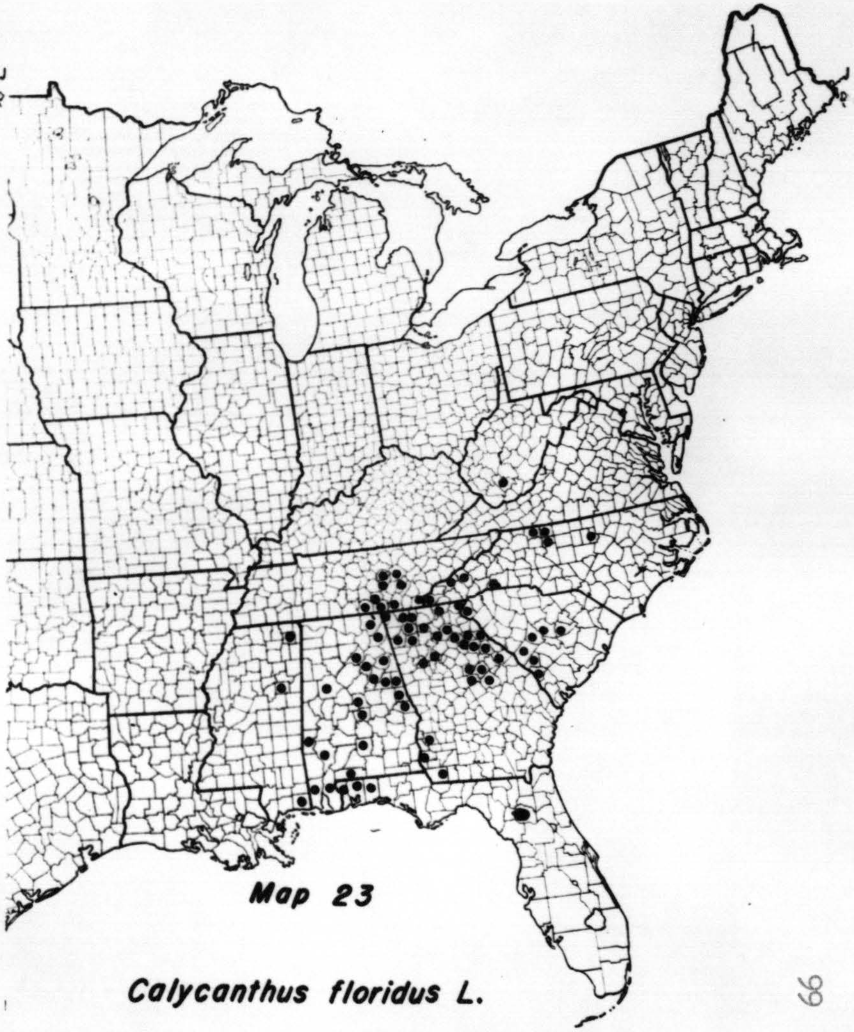
Map 21

Rhododendron maximum L.



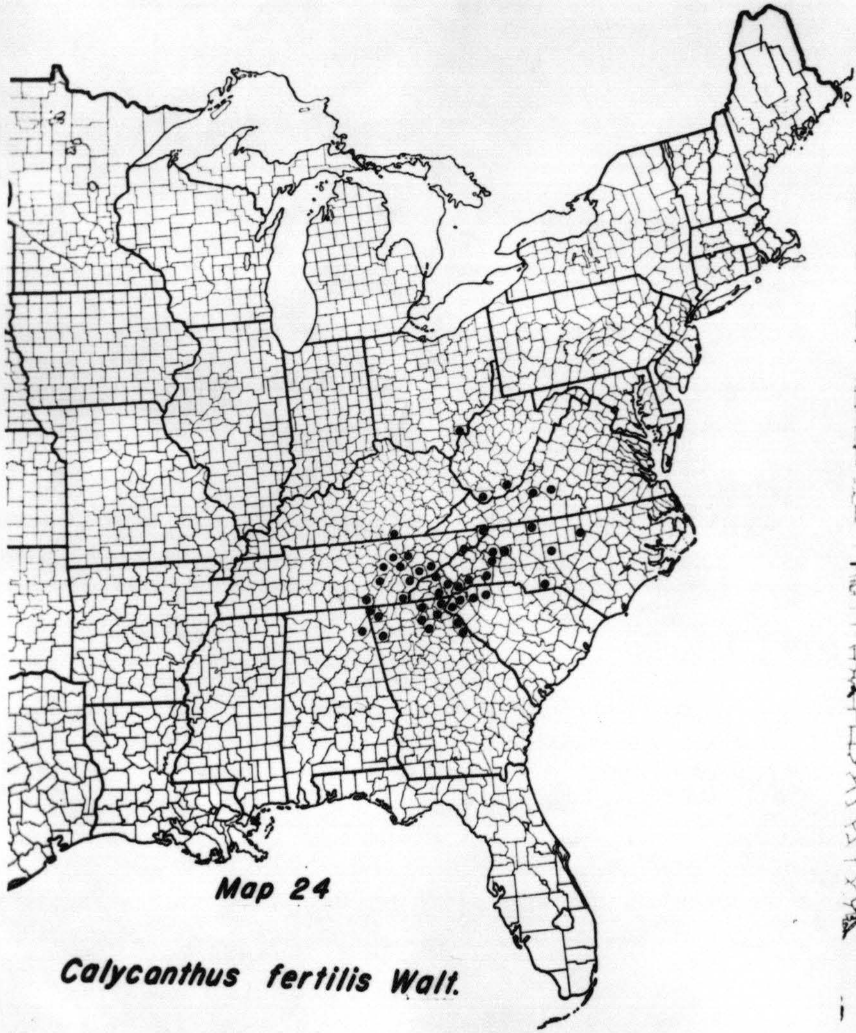
Map 22

Xanthorhiza simplicissima Marsh.



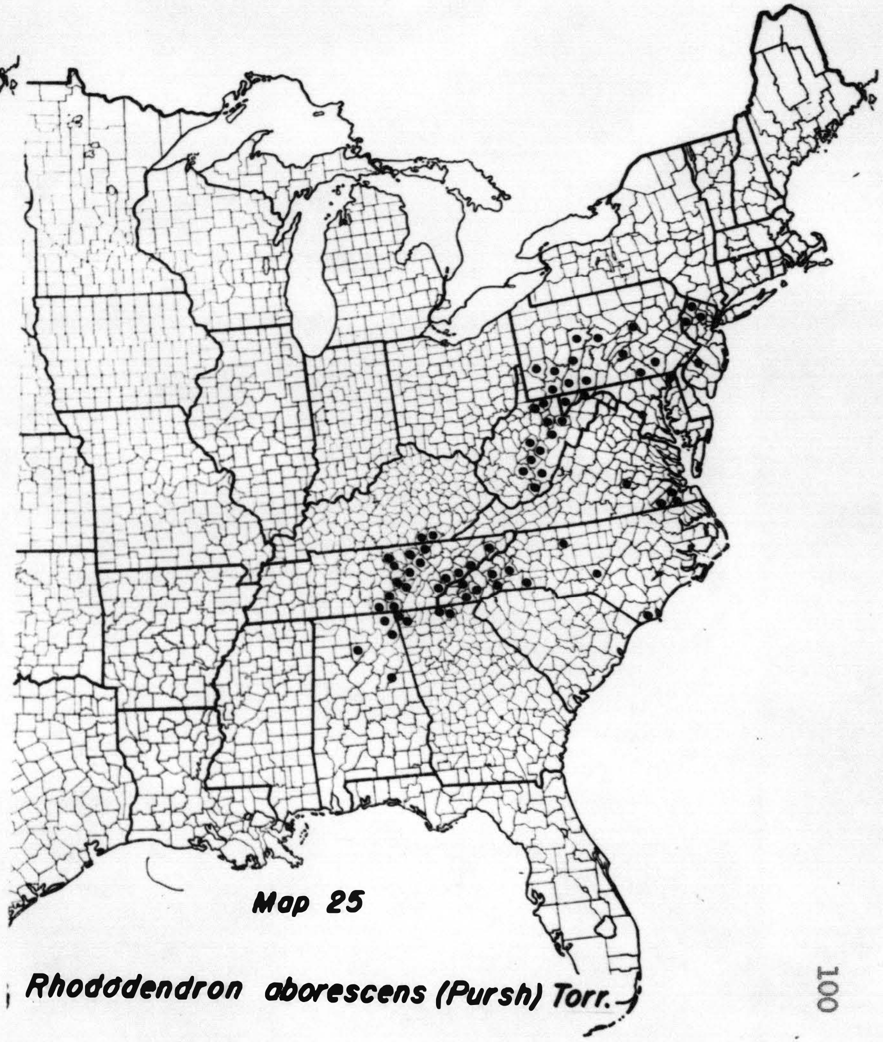
Map 23

Calycanthus floridus L.



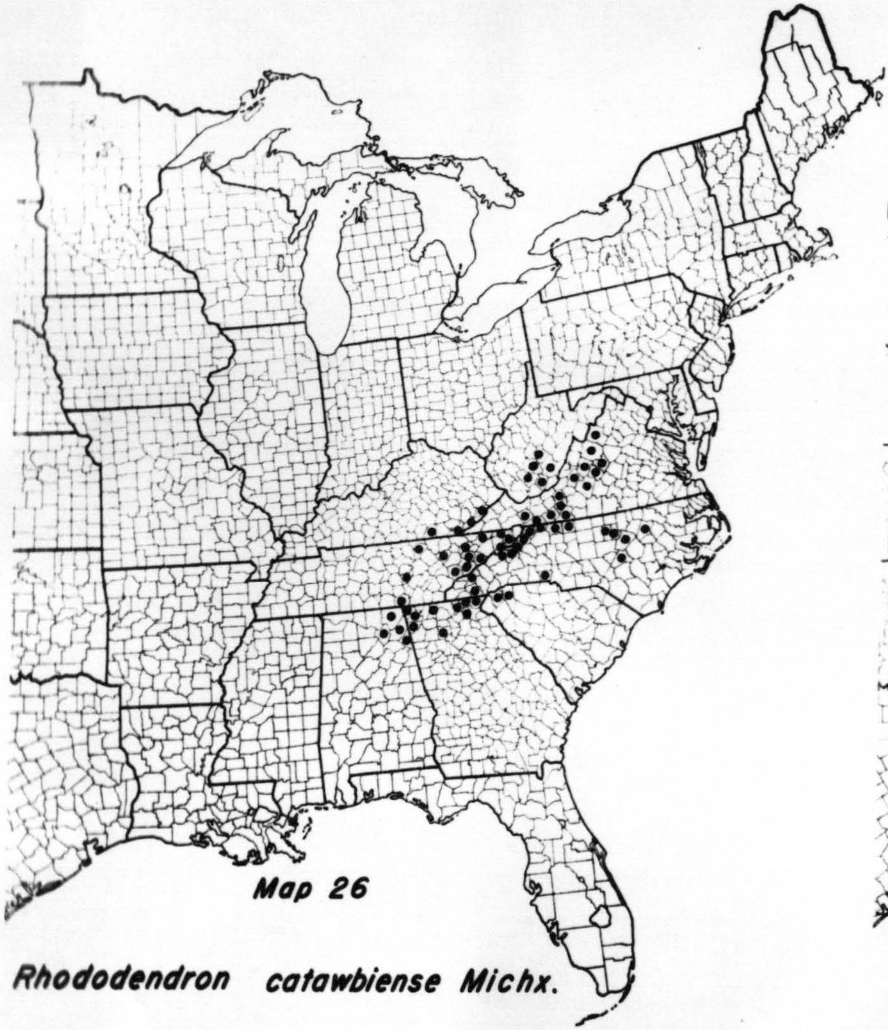
Map 24

Calycanthus fertilis Walt.



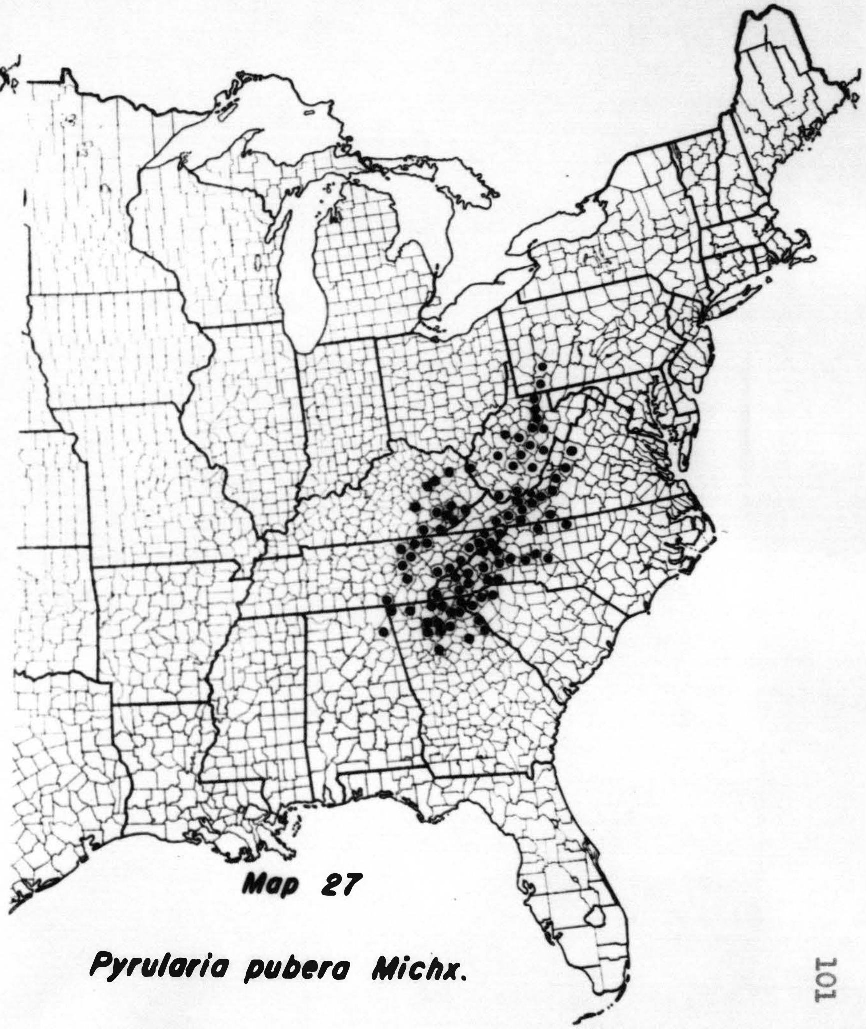
Map 25

Rhododendron aborescens (Pursh) Torr.



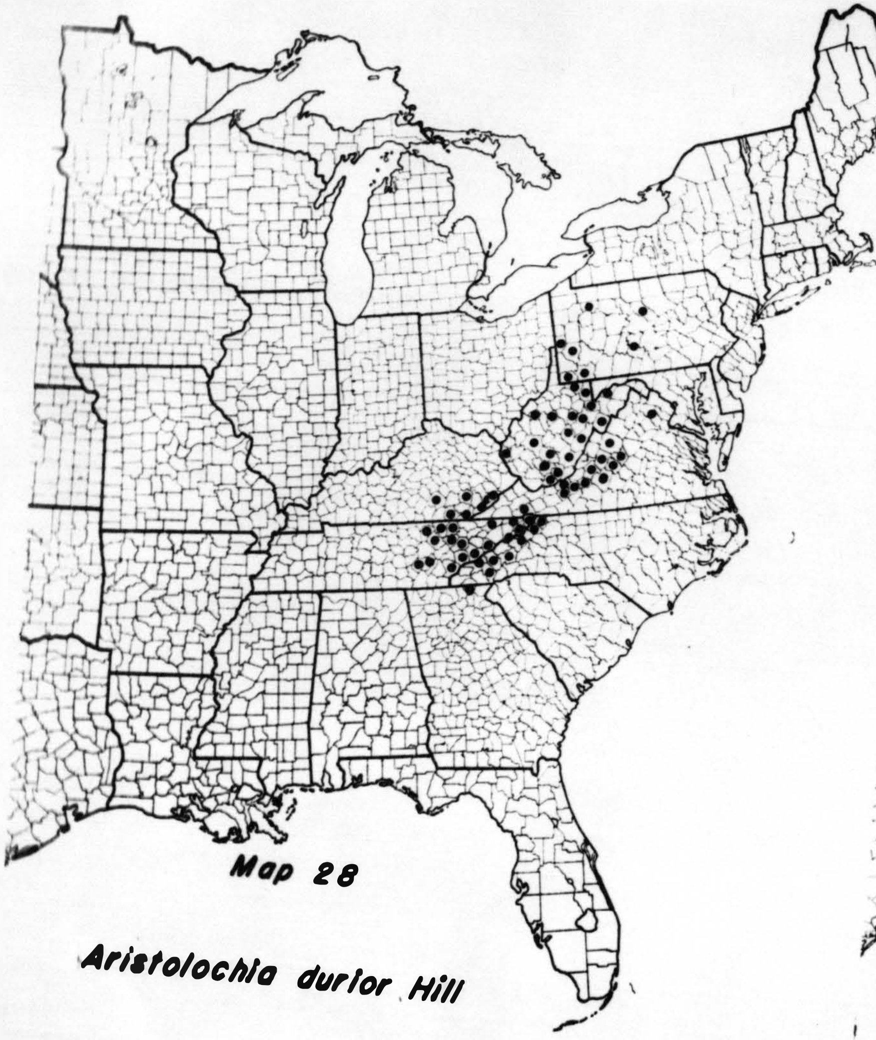
Map 26

Rhododendron catawbiense Michx.



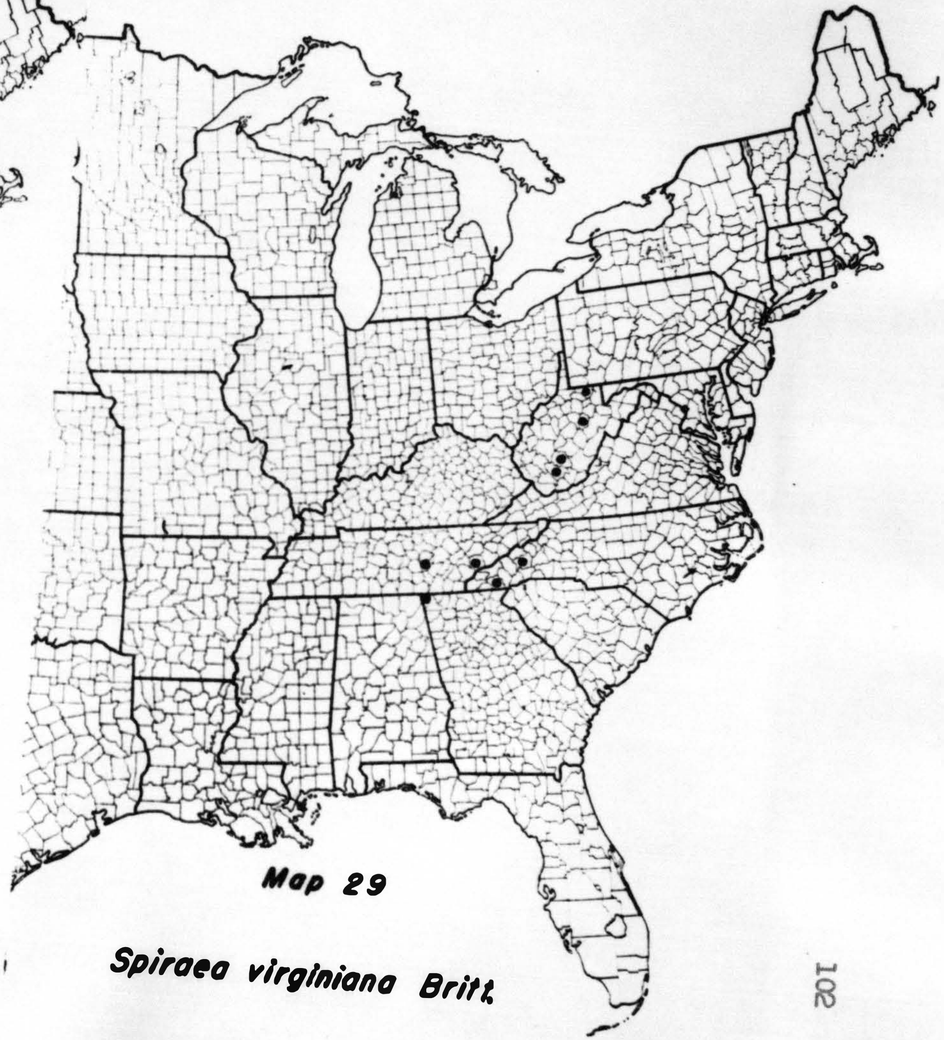
Map 27

Pyrularia pubera Michx.



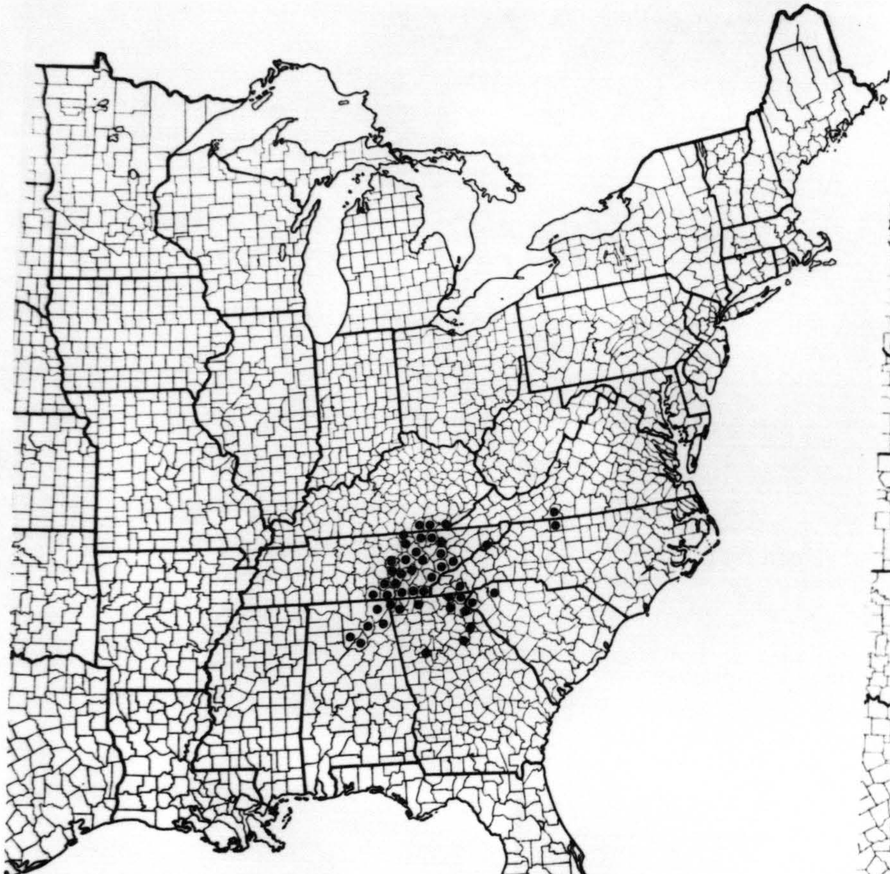
Map 28

Aristolochia durior Hill



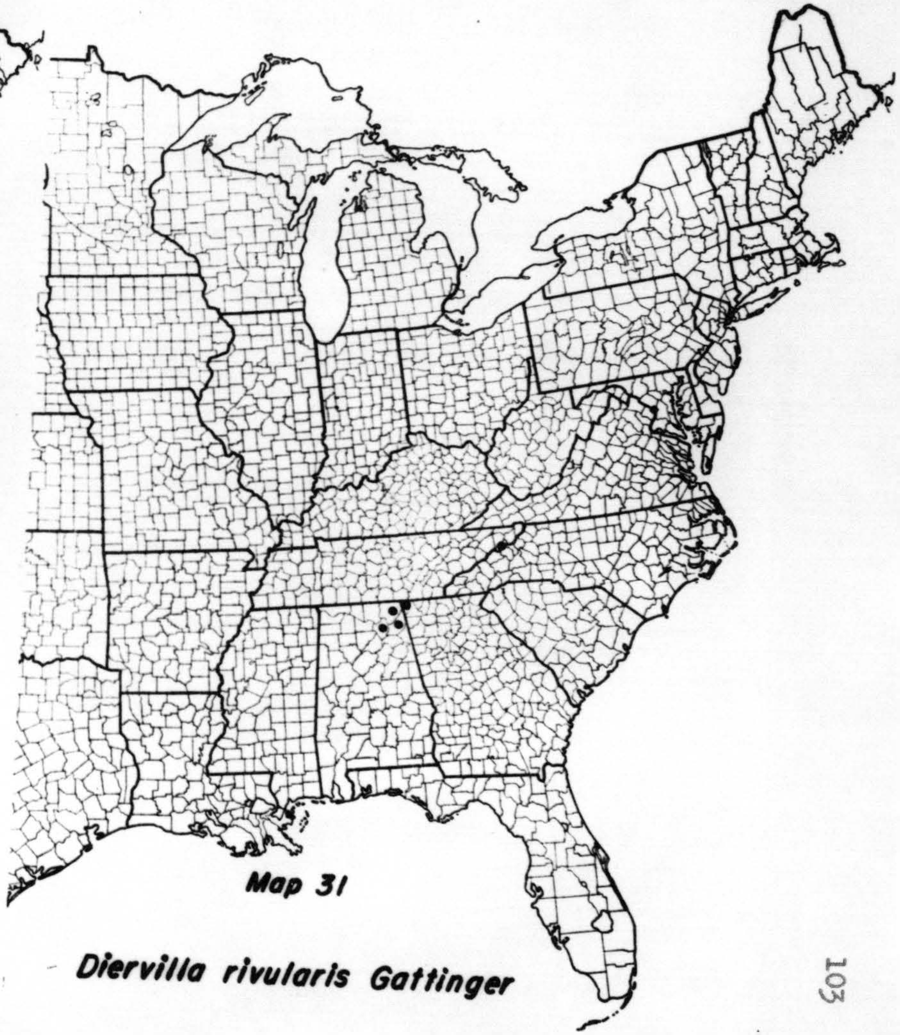
Map 29

Spiraea virginiana Britt.



Map 30

Stewartia ovata (Cav.) Weatherby



Map 31

Diervilla rivularis Gattinger