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THE VEGETATION OF THE GORGES OF THE FALL CREEK FALLS STATE PARK IN TENNESSEE

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ABSTRACT

Virgin and little-disturbed forests in some gorges on the western margin of the Cumberland Plateau were studied to determine community limits and floristic composition. Six mature community types were distinguished. These were mixed mesophytic, hemlock, hemlock-basswood, hemlock-yellow birch, oak-hickory, and chestnut oak. Two seral communities were studied. The mixed mesophytic community was the most widespread and occupied the more average sites. The chief factor in the determination of community types appeared to be insolation as affected by topography. Seral stands gave indication of rapid development toward mixed mesophytic communities.

INTRODUCTION

The forests of the Cumberland Plateau and the southern Allegheny Mountains were described collectively by Sargent (1884) as ". . . one of the finest bodies of timber now standing in the United States." Since that time the timberlands of the Cumberland Plateau have been logged and burned to such an extent that most of the original forest has been destroyed. Stands of large trees remain only in those places which are relatively inaccessible. Virgin forests of limited extent are found in some of the deep gorges, including those in the Fall Creek region. The forests of these gorges were chosen for the present study because they are probably the least disturbed of those remaining in the southern portion of the Cumberland Plateau, and because they include a wide variety of communities within a relatively small area. The realization that these remnants may be altered or destroyed at any time gave added impetus to the study.

DESCRIPTION OF THE AREA

This study took place in the Fall Creek Falls State Park located in Van Buren and Bledsoe Counties, Tennessee, between 35°40′ and 35°50′ N latitude and 85°20′ and 85°30′ W longitude. It is a game preserve and recreational area of approximately 17,000 acres. The U.S. Government acquired the land within the present boundaries of the park in 1935 and maintained it as a "recreational demonstration area" (Federal Writer's Project 1939) under the supervision of the National Park Service. In 1944 the State of Tennessee obtained the park from the Federal Government for use as a state park and game preserve. Since that time it has been under the supervision of the Division of State Parks of the Tennessee Department of Conservation.

The region of study belongs to a distinct physiographic area called the Cumberland Plateau, which constitutes a part of the oldest unglaciated and uninundated area in the eastern part of the U.S. (Fenneman 1938, Harshberger 1911). The southern extension of the Cumberland Plateau, including all of it that is in Tennessee, is submaturely dissected and includes much even-surfaced tableland, especially in the southern part of the state. It has been eroded almost uniformly to rocks of the Pottsville age (Fenneman 1938). The surface rock of the Cumberland Plateau in Tennessee is Pennsylvanian (Walden) sandstone except in circumscribed areas where the shales have not been completely weathered.

On the western margin of the plateau, streams have cut through the Walden into the Lookout sandstone. The latter is much less resistant to erosion and has allowed the larger streams to reach the still more easily eroded Mississippian (Bangor) limestone in an almost vertical fashion (Braun 1950), thus, deep gorges were cut in certain regions. Some of the deepest and most rugged of these belong to the Cane Creek system of drainage in the Fall Creek Falls State Park. There, within a radius of about one mile, are four deep gorges (Fig. 1 and 2).

Although erosion has cut into limestone within the gorges, this substrate is not often evident because the tali and most of the floor of the gorges are formed of sandstone rubble. Only a few beds of exposed limestone occur.

Four large gorges within the boundaries of Fall Creek

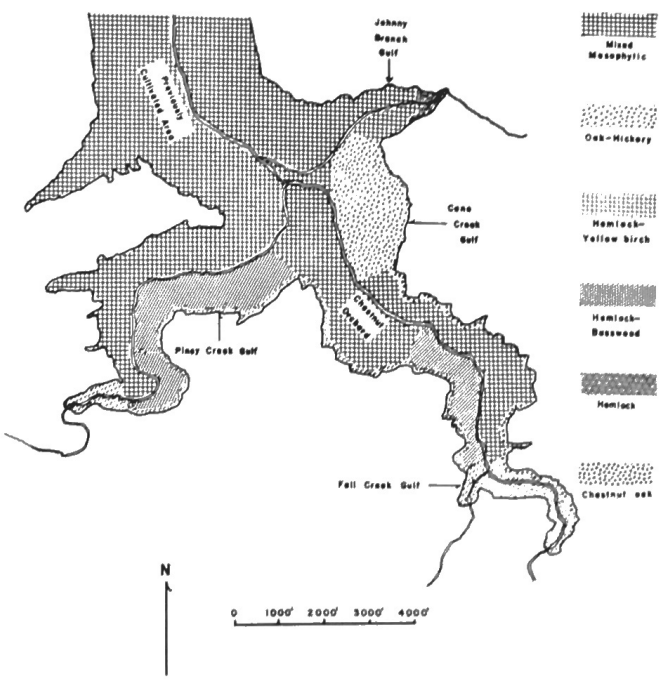

Fig. 1. Outline map of the gorges of the Fall Creek Falls State Park. Positions of the various plant communities are indicated. This map was adapted from one supplied by the Tenn. Dept. of Conservation.

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Falls State Park are the Cane Creek, Fall Creek, Piney Creek, and Johnny Branch Gulfs (Fig. 1 and 2). The largest of these is Cane Creek Gulf to which all others are tributary. Each gorge contains a stream which flows between steep tali and nearly vertical cliffs. The upper portions of the tali are extremely rugged, being strewn with large boulders from overlooking cliffs. The general topographic situation is shown in Fig. 2.

The present study is restricted to the gorges of the park. Inhabitants of the area know them as "gulfs." In this paper they are termed gorges when discussed in a general way. The term "gulf" is employed as a part of the proper name when a specific one is designated. Prior to this study these gorges were relatively inaccessible and were consequently rarely disturbed. The influence of man had been limited largely to one large-scale logging operation in 1921 and 1922. Apparently the long delay and partial nature of the logging operation, as compared with activity in other plateau areas, were caused by the extreme difficulty encountered in transporting the lumber (Killebrew and Safford 1874).

People who were familiar with the gorges before they were logged state that the overstory trees at that time were much larger than those which now replace them and that there was less underbrush. The largest and most abundant trees at the time of logging are reported by local residents to have been yellow poplar (tulip-tree), oak (white, red, and chestnut oak), chestnut, and basswood. These are listed in order of reputed abundance, the oaks comprising a unit. The larger trees of these species were cut, along with some hickory. Hemlock and yellow buckeye were cut only to construct temporary buildings at the sawmills. No maple, beech, birch, or walnut trees were reported to have been cut.

The area which was logged in 1922 includes all of Cane Creek Gulf as far south as the mouth of Fall Creek, approximately the lower half of Piney Creek Gulf, and all of Johnny Branch Gulf except the upper tip (Fig. 2). The following year (1923) the best trees in the upper end of Piney Creek Gulf were cut, and the logs were raised out of the gorge by cables. These were nearly all tuliptree. The remainder of the area of the gorges apparently has not been logged.

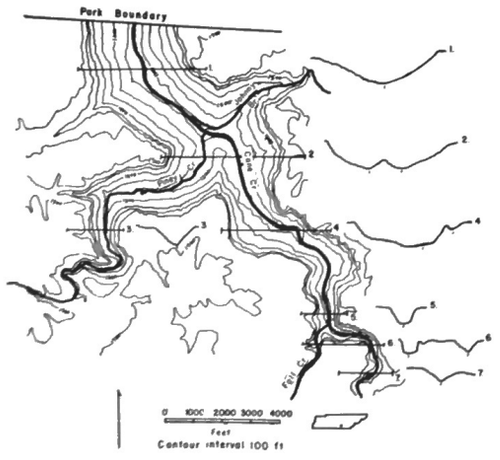

Fig. 2. Relief map of the gorges of the Fall Creek Falls State Park. Relief of seven cross sections are shown at the right corresponding to transect lines on the topographic map to their left.

In all of the gorges there are only two places in which all merchantable trees were cut. One was the sawmill site already mentioned which was the only plot in the area of study ever cultivated. It was planted in corn in 1901. The sawmill was set up there in 1921. People who had worked at the sawmill reported that lumber was stacked over the original cornfield during the lumbering, and that all existing vegetation was killed. The plot is said to have been covered with broomsedge (*Andropogon* sp.) prior to the logging operation. The other stand which was almost clear-cut was a chestnut consociation southeast of the mouth of Piney Creek in the Cane Creek Gulf. Comparison of other parts of the lumbered area with the two sites which were almost completely cleared has indicated that many large trees remained in most sections after the logging operation.

Residents of the Fall Creek vicinity who have lived there continuously since 1922 agree that the gorges have not burned since that time. Their impression is corroborated by the fact that chestnut tree tops left on the ground at the logging of 1921-1922 were split in 1938 to prepare rails for the park fence. The history of the incidence of fire in the gorges before 1921 has not been determined. It seems likely from reports of residents that portions burned occasionally. Observation of general conditions indicate that the narrow portions, at least, would not burn readily in February, the time when fires were ordinarily set to clear pastures (Sargent 1884).

It is almost certain that some portions of the gorges are virgin forest. No part of Fall Creek Gulf gives any indication of having been burned or cut. It is also quite likely that the forest in Cane Creek Gulf between the mouth of Fall Creek and Cane Creek Falls, as well as that in upper Johnny Branch Gulf, is virgin. In each of these places there are large, long-standing, dead hemlock trees. There are no burn scars on trees in these places. There are also fallen trees that show no evidence of having been subjected to fire.

The entire park has been fenced since about 1939. It has probably not been subjected to browsing by domestic animals to any extent since that time. Deer have been introduced into the park, but no evidences of them were observed in the gorges during the study, though they were often seen on the plateau itself. Wild turkeys abound in the park and some of them find their way into the gorges. Their effect upon the vegetation is unknown but is probably negligible.

No U.S. Weather Bureau station was ever established in Van Buren County. It has been suggested that data collected at Erasmus, Tennessee, conform more closely to conditions in that county than those from any other station. At that station records had been kept for 20 years prior to 1938. These records indicate an average growing season of 171 days, the average date of the last killing frost being April 23, and the first, October 11. The average temperature for January was 37.2° F. and for July, 72.1° F. The maximum temperature was 97° F. and the minimum, —30° F. For the same period, the average annual rainfall was 59.82 inches. The month with greatest average rainfall was March (6.52 in.), while that with the least was November (3.20 in.).

Wind data from the U.S. Weather Bureau Station at McMinnville, Tennessee, approximately 40 miles west of the park, show that the prevailing winds are from the south during the latter part of March and May, and in June, July, August, September, and October; from the southwest in January, February, April, December, and the first half of March and May; and from the north in November (Yearbook of Agriculture 1941).

Soils of the gorges have been classified by Marbut (1935) as rough and stony land lying between the Muskingum series of the mildly dissected plateau adjacent to and above the gorges, and the Hagerstown series of the bottomlands in the Cane Creek Gulf near the Caney Fork River. Vanderford (1897) considered these gorges to be in an area of sub-carboniferous limestone and to contain red and yellow clay loams. In the upper ends of all the gorges, the only surface soil is a collection of black humus mixed with fine sand and collected between, or in the depressions of, the large sandstone boulders. On the southwest side of Cane Creek, where there are circumscribed areas in which surface stones are absent or rare, the topsoil is dark brownish-gray with a B horizon of pale red clay. On the southwest-facing talus of Cane Creek Gulf near Piney Creek the topsoil itself is a yellowish-red clay. The southwest-facing talus lacks the heavy humus layer which characterizes the northeast-facing one.

Review of Literature

No papers have been found dealing specifically with the ecology or floristics of the Cumberland Plateau in Tennessee. Gattinger (1901) published a flora of Tennessee containing annotations of the distributions of plants known by him to occur in the state. Jennison (1935), in a list of plants of Tennessee with unusual or disjunct ranges, mentioned some as occurring in counties of the Cumberland Plateau. Shaver (1954) has given detailed information regarding the distribution of the ferns and fern allies. Sharp (1939) has done the same for the bryophytes of the eastern half of the state. Two publications have appeared dealing specifically with the grasses of Tennessee, that of Killebrew (1878), and the two-volume work of Lamson-Scribner (1892, 1894). Underwood (1945) dealt with the taxonomy and distribution of *Carex* in the state. Shanks (1952, 1953) annotated the woody species.

Details of the composition of the forests in the Cumberland Plateau in Tennessee may be found in some of the publications to which reference has already been made. Killebrew and Safford (1874) wrote of the tableland of Van Buren County as being thinly wooded, but as containing valuable timber, chiefly oak and chestnut. According to them, the mountainsides, gorges, and ravines were very heavily timbered with chestnut, poplar (tuliptree), maple, walnut, buckeye, cherry, linden (basswood), and beech. The Cumberland Plateau was mentioned by Sargent (1884) as containing chiefly white and chestnut oaks, yellow poplar (tuliptree), black walnut, and cherry. Harshberger (1911) described the Cumberland Plateau of Tennessee as covered with a forest of broad-leaved trees growing on a rolling surface in soil of poor quality. Hall (1910) subdivided the Cumberland Plateau into categories which he called coves, slopes, plateau swales, and plateau ridges and listed the characteristic trees of each subdivision. The difference between the cover (gorge) forest of the Cumberland Plateau and the Appalachian cove type was stated to be in the smaller proportion of hemlock and larger proportion of white oak in the forest of the plateau.

Braun (1950) considered the vegetation of the Cumberland and Allegheny plateaus and made specific reference to the vegetation of the Cumberland Plateau in Tennessee. She included all of this portion in the southern region of the "cliff section." She described the forest of the relatively undissected part of the plateau as being prevailingly oak or oak-hickory. In the ravines and valleys of the dissected portion, she listed the important species as *Liriodendron Tulipifera, Fagus grandifolia, Tilia heterophylla* and other species of *Tilia, Acer saccharum, Aesculus octandra, Magnolia acuminata, Nyssa sylvatica, Quercus alba, Q. borealis* var. *maxima* (*Q. rubra*), *Q. montana* (*Q. Prinus*), *Q. Muhlenbergii, Q. velutina, Carya ovata, C. tomentosa, Carya* spp., *Acer rubrum, Fraxinus americana, Juglans nigra, Ulmus alata,* and *Tsuga canadensis.* She made specific reference to the deep gorges of the Fall Creek area, stating that hemlock is abundant, with tuliptree, basswood, buckeye, red oak, sugar maple, yellowwood, sweet birch, and yellow birch as associates. These species constitute the kind of forest which she has called mixed mesophytic, the type she designated as the climax vegetation of the area.

Certain sections of the Allegheny Plateau outside of Tennessee have been discussed in the literature. Shaler and Crandall (1876) listed the percentages of various species (or genera) of canopy trees of some forest stands in northeastern Kentucky. Virgin stands were compared with second growth forest in a total of 15 sample areas. Braun (1937) discussed the relationship of the flora of the same general area to those of other parts of the eastern U.S. She concluded that the vegetation of the Cumberland Plateau displays strong southern affinities and cited as evidence the fact that so large a percentage of the intraneous flora of the Cumberland Plateau consists of species of southern range. She stated that the northern forms are few in the plateau section and interpreted these as survivors from the Tertiary flora.

According to Braun (1950), the forests of the extension of the Cumberland Plateau into Alabama were originally quite similar to those of the same

physiographic region in Tennessee. Mohr (1901) classified them into 2 large groups, the xerophile and mesophile forests. The former occupied the undissected tableland, the latter, the secluded valleys. Additional papers on the flora of the Cumberland Plateau in Alabama are those of Harper (1937), in which he listed and discussed the flora of an outlier of the plateau in that state, and of Segars, Crawford, and Harvill (1951), in which the distribution of hemlock in northern Alabama is given. In the latter paper some of the associates of hemlock in that area are listed.

Griggs (1914) discussed in some detail the vegetation of the Sugar Grove Region of the Allegheny Plateau in Southeastern Ohio. In this region the forests are sharply divided into lowland and upland types. Griggs subdivided the lowland type into hemlock forest and *Liriodendron* forest.

No studies have been made to indicate the trends of secondary succession in the forests of any part of the Cumberland Plateau, although references to secondary forests occur. Shaler and Crandall (1876) pointed out that secondary stands in northeastern Kentucky appear to be improved in value over the primary stands. They cite the greater abundance of white and black walnut in the secondary growth as evidence. Braun (1950) stated that secondary growth following cutting of mixed mesophytic forest may closely resemble the original stand, or may result in *Liriodendron*, oak-hickory, or scrub pine stands. In discussing secondary growth in the plateau region of southeastern Ohio, Griggs (1914) observed that, in ravines following selective logging, west slopes usually maintained lowland-type forest, whereas the east slopes developed an associes resembling the upland forest. He attributed this difference to the greater loss of leaves from the ground of the east slopes due to wind.

Methods

Field sampling was started in the spring of 1952 after a period of general exploration and was continued through the summer of 1953. The method of sampling was modified only slightly from the random pairs method of Cottam and Curtis (1949). Lines were established within selected areas along compass lines or along lines parallel to some natural feature as a cliff or stream bank. The distance between lines in different communities varied so that each could be sampled as widely and as adequately as possible. At each point at a predetermined distance on a given line, a 1 x 1 m. quadrat was established. In this quadrat, all herbaceous plants and woody plants up to 1 ft. tall were counted, and the percentage of the quadrat covered by each species was estimated. The pair of trees to be used as samples was determined exactly by the method of Cottam and Curtis (1949). The tree nearest the quadrat was designated tree no. 1, the other as tree no. 2. The DBH (diameter breast high) of both trees was measured directly with a DBH tape to the nearest 0.1 in. Distances between the pairs of trees were measured with a linear tape to the nearest decimeter. Woody plants exceeding 3.9 in. DBH were considered part of the tree layer. No separation of understory and overstory was attempted. Shrubs and transgressives exceeding 1 ft. in height and less than 3.9 in. DBH were counted in a plot 1 m. wide on the right side of a line extending from tree no. 1 to tree no. 2. These plants were recorded as members of the shrub layer. The number of samples taken in all layers of all stands proved by the method of Cain (1938) to be more than adequate.

Collections were made of the plant species of the gorges. A complete collection of these plants has been deposited in the Herbarium of Vanderbilt University. A limited number of duplicate specimens were sent to the Herbarium of the University of Tennessee.

Names of plants listed without the authority follow the nomenclature of Gray's Manual of Botany, 8th ed. (Fernald 1950). The common names are listed according to Standarized Plant Names (Kelsey and Dayton 1942). When a plant name is given directly from some source in the literature which does not conform to the nomenclature of these manuals, the authority is given or the name assigned in these manuals is appended in parentheses.

With the exception of the term frequency as used with reference to the tree and shrub layers, the phytosociological teminology in this study conforms essentially to that of Braun-Blanquet (1932). In the sense of Braun-Blanquet, frequency is expressed in terms of the rate of occurrence of plant species within plots of uniform size. In the random-pairs method used in this study, no plot was established for the tree layer, and two individuals were measured at a given sample point regardless of density. Frequency data for the shrub layer in this study were determined from plots of various sizes. Thus, in both layers direct comparison with data determined from plots of uniform size is prevented. These data do, however, indicate both homogeneity of the stands and relative frequency of the species. Frequency in the herb layer was determined from sample plots uniformly 1 m. x 1 m. and are comparable to frequency data obtained in studies in which this quadrat size has been employed.

DFD index (Cottam 1949) is the sum of the frequency, the percent of total density and the percent of total dominance. It agrees roughly, when used for canopy species, with the area of the standard phytograph of Lutz (Whitford 1951). This concept is used in this study in describing both tree and herb layers. It does not have the same significance for both layers since dominance in the tree layer is based on a measured factor (basal area), and in the herb layer on an estimated factor (cover).

Results

The vegetation of the gorges was naturally grouped into six rather sharply differentiated stable communities and two areas in secondary succession following different degrees of disturbance. The six stable communities have been named in each case for the major dominant species. These have been termed mixed mesophytic, hemlock, hemlock-yellow birch, hemlock-basswood, oak-hickory, and chestnut oak communities. The general location and boundary of each community is shown in Fig. 1. Data for each community are given in the separate sections below. Then, a general comparative summary of results is presented as the final section of results.

I. Stable Communities

Mixed Mesophytic Community

Five of the stands which were sampled were dominated by species which Braun (1950) considered indicative of mixed mesophytic forest. In terms of area, this was the most important community type within the gorges (Fig. 1). The stands were of two distinct types, one containing significant numbers of hemlock trees, the other few or none. The mixed mesophytic stands without hemlock were widespread, but restricted to those slopes which were rather gentle, received direct sunlight a considerable part of the day, and had a substrate of soil rather than of boulders. Hemlock occurred among the mixed hardwoods along the streams in the narrow portions of the gorges or in areas which were shaded most of the afternoon.

The mixed mesophytic stands were dominated by *Carya glabra, Tilia heterophylla, Tsuga canadensis, Fagus grandifolia, Liriodendron Tulipifera, Betula lutea, Oxydendrum arboreum, Acer saccharum, Quercus rubra,* and *Acer rubrum*. Six of these species were present in all of the stands referable to the mixed mesophytic community. They were *Carya glabra, Liriodendron Tulipifera, Betula lutea, Oxydendrum arboreum,* and *Acer rubrum*. Thirty-seven species occurred in the tree layer of the community. Fourteen species were restricted to single stands. Of the mixed mesophytic stands which were sampled, two were along the side of streams, and three were on tali. Of the latter, one was on a talus facing northeast, one, northwest, and the other, southeast (Fig. 1 and 2).

The only shrub species occurring in all of the stands was *Hamamelis virginiana*. Yet, it was surpassed in density by both *Rhododendron maximum* and *Euonymus americanus*. Both of the latter were distinctly local, *R. maximum* occurring in conjunction with hemlock, and *E. americanus* being prevalent only where hemlock was not abundant. The shrub layers of both the streamside stands were dominated by these two species collectively, even though the two species were rarely in the same quadrat. Neither was important in the stands of the tali where the only important members of the shrub layer were the transgressives. *Xanthorhiza simplicissima* was abundant but was restricted to the edges of the streams.

The average cover of the herb layer was estimated at 13%. The amount of herbaceous cover where *R. maximum* was the dominant shrub was very slight, amounting to only 5%. The most important herbs in order of their DFD indices were *Polystichum acrostichoides, Sedum ternatum, Tiarella cordifolia, Dryopteris spinulosa* var. *intermedia, Dioscorea quaternata, Viola* spp., *Aster* spp., and *Disporum lanuginosum*. These species were widely scattered throughout the mixed mesophytic community. Each of them, except *S. ternatum* and *D. spinulosa* var. *intermedia*, was in four or five of the five stands sampled.

The most important transgressives in the shrub layer were *Acer saccharum* (440 plants/acre), Cornus florida (212 plants/acre), and *Tilia heterophylla* (203 plants/acre). In the herb layer the most important tree transgressives were *Acer rubrum* (3902 plants/acre), *A. saccharum* (1890 plants/acre), *Tilia heterophylla* (859 plants/acre), and *Fraxinus americana* (451 plants/acre). Thus, the most important transgressive species in both the herb and shrub layers were species typical of the mixed mesophytic community.

Hemlock Community

There were several communities which were floristically related to the mixed mesophytic community which differed from it since they were dominated by one or two species of trees. Thus communities were found which contained many mesophytic species, but were dominated by hemlock, hemlock and yellow birch, or hemlock and basswood.

The hemlock community was a virgin stand dominated solely by hemlock and confined to the narrow upper portion of Johnny Branch Gulf (Fig. 1). The habitat was a deep, rugged gorge whose floor was littered with large, loose sandstone boulders with very little obvious soil. The cliff bordering the south side was tall and abrupt so that the floor of the gorge was shaded much of the day. Direct sunlight rarely reached the bottom.

Tsuga canadensis was, by far, the most important species in the tree layer where it formed an almost complete canopy cover. Its importance was indicated by the fact that it had a frequency of 85% and constituted 88% of the total basal area. There were only eight species of trees associated with the hemlock. These were *Magnolia tripetala, Oxydendrum arboreum, Liriodendron Tulipifera, Betula lutea, Carya glabra, Cladrastis lutea, Sassafras albidum,* and *Acer pensylvanicum*. These were of slight numerical importance. Their DFD indices ranged from 8 to 28 as compared with 233 for hemlock. The stand was unique in having a conspicuous number of trees of *Magnolia tripetala* in the understory.

The most important member of the shrub layer was *Rhododendron maximum*. It accounted for 39% of the total density in this layer, and was widely distributed, as indicated by a frequency of 55%. Other shrubs and lianas present were *Kalmia latifolia, Parthenocissus quinquefolia, Rhus radicans, Vitis rotundifolia, Stewartia ovata, Smilax rotundifolia,* and *Cornus alternifolia*.

Twenty-six species occurred in the herb layer. The most important of these were *Polypodium virginianum, Aster* spp., *Dryopteris marginalis, Laportea canadensis,* and *Polystichum acrostichoides*. A small colony of *Lycopodium lucidulum* was in the stand but did not appear within the quadrats.

The most important transgressives in the shrub layer

were *Betula lutea* (321 plants/acre), *Tsuga canadensis* (240 plants/acre). *Acer rubrum* (225 plants/acre), and *Magnolia tripetala* (195 plants/acre). The only three transgressives in the herb layer were *T. canadensis* (1416 plants/acre), *A. rubrum* (1214 plants/acre), and *A. saccharum* (202 plants/acre). All of these species were present in the tree layer except *A. saccharum*, which was relatively unimportant in both lower layers. *T. canadensis* was the only tree species sampled in all three layers.

Hemlock-yellow birch Community

This community was composed entirely of virgin stands. The habitats of the two stands of the community were very similar to the habitat of the hemlock community in that these stands occurred between the cliffs of deep, narrow, rugged gorges (Fig. 1). The hemlock-yellow birch stands were not confined to the narrow gorges or streamsides, for one was found along the base of a northeast-facing cliff in the wide part of Cane Creek Gulf. This habitat had the following in common with the habitat of the narrow gorges: (1) the substrate in both was composed mostly of large boulders of sandstone rubble from adjacent cliffs, (2) the soil which was present among the boulders was black, and very loose and porous, and (3) the area was shaded by cliffs for a considerable part of the day, particularly in the afternoon.

The overwhelming importance of hemlock and yellow birch in this community was indicated by the fact that together they comprised 81% of the total basal area of the tree layer. Their major associates in the tree layer were *Oxydendrum arboreum* and *Tilia heterophylla*, which were present in all stands sampled.

The only important shrub in the shrub layer of the community was *Rhododendron maximum*. The only consistently important tree species in the shrub layer were transgressive hemlocks and yellow birches. These three species were unique by being present in all stands of the community. In the shrub layer the streamside stands were quite similar to each other, but they were distinctly different from the cliffside stands.

There were distinct differences between the species in the herb layer in the cliffside stand and those in the other stands. In the community as a whole the characteristic members of the herb layer were *Polypodium virginianum* and *Dryopteris spinulosa* var. *intermedia*. In many places in the community a mosaic of the two completely covered the substrate in large areas. These species were important in the cliffside stand but were exceeded there by *Mitchella repens, Galium circaezans, Dryopteris marginalis*, and *Arisaema* species. One of the streamside stands was unique in having only five species in the herb layer. The average herbaceous cover in the whole community was 19%.

Hemlock and yellow birch were the most important species in both the tree and shrub layers. Red maple exceeded both in the herb layer. The only species present in all three layers were hemlock, yellow birch, basswood, red maple, chestnut oak, sassafras, and striped maple (*A. pensylvanicum*). Thus, there was no indication of change of relative status of members of the community.

Hemlock-basswood Community

The hemlock-basswood community was intermediate in composition between the hemlock-yellow birch and the mixed mesophytic communities. It was distinct from the mixed mesophytic community, with which it shared most species, in the overwhelming importance of only two species. In each stand hemlock was more than three times, and basswood approximately twice as important as the third most important species. The hemlock-basswood community was distinct from the hemlock-yellow birch community in having both basswood and sugar maple more important in the tree layer than yellow birch, and in having certain of the more typical mixed mesophytic species (*Tilia heterophylla, Acer saccharum, Liriodendron Tulipifera, Carya cordiformis*, and *Aesculus octandra*) relatively more common.

Species common to the two stands sampled were *Tsuga Canadensis, Tilia heterophylla, Acer saccharum, Betula lutea, Liriodendron Tulipifera, Carya cordiformis, Aesculus octandra, Quercus rubra*, and *Fagus grandifolia*. Of these, the first two were of outstanding importance, hemlock having approximately four times, and basswood twice the DFD index of the next most important species. *Aesculus octandra* occurred only in this community and in the mixed mesophytic community. Even in these it was restricted to the most favorable sites where the soil was deep and free of boulders. Individuals of this species were the largest trees in the gorges, some of them exceeding 4 ft. DBH.

Although *Rhododendron maximum* occurred in the hemlock-basswood community, it was exceeded in importance by *Ribes Cynosbati*. Other important shrubs and lianas were *Smilax rotundifolia, Asimina triloba*, and *Viburnum acerifolium*. The liana, *Aristolochia durior*, was abundant in this community though it did not occur elsewhere in the gorges.

Fifty-eight species occurred in the herb layer. The total herbaceous cover was 14%. The outstanding herbs were *Laportea canadensis, Sedum ternatum, Polystichum acrostichoides, Phacelia bipinnatifida, Tiarella cordifolia, Hepatica acutiloba, Camptosorus rhizophyllus, Impatiens capensis*, and *Dryopteris spinulosa* var. *intermedia*. The fern, *C. rhizophyllus*, was restricted almost entirely to the hemlock-basswood community. *Carex plantaginea* was locally abundant.

The hemlock-basswood community was selectively cut in 1921-1922. Of the communities from which trees were removed, it appeared to have been least affected. This generalization is supported by the following observations: (1) very little hemlock was cut, (2) basswood was cut less frequently than oak and chestnut, and (3) basswood appeared to have reproduced itself by stump-shoots which grew very rapidly. Basswood trees were frequently observed growing in clumps or circles, obviously as a result of having been produced in this manner around a large stump.

The most important transgressives in the shrub layer were *Acer saccharum* (527 plants/acre), *Carya cordiformis* (159 plants/acre), *Acer pensylvanicum* (150 plants/acre), *Tilia heterophylla* (110 plants/acre), and *Tsuga canadensis* (106 plants/acre). In the herb layer the most important transgressives were *Acer saccharum* (3320 plants/acre), *Tilia heterophylla* (1103 plants/acre), and *Carya cordiformis* (324 plants/acre).

Oak-Hickory Community

The oak-hickory community occupied the central portion of the southwest-facing and west-facing slopes of Cane Creek Gulf (Fig. 1). There were differences between the habitats of the oak-hickory community and those communities previously discussed which were immediately evident. They were as follows: (1) the oak-hickory community received the full effect of the midday and afternoon sunlight while the other communities did not, (2) the topsoil of the oak-hickory community was a yellowish-red clay with a poorly developed humus layer, while that of the other communities was either black or brownish-gray, and (3) the boulders in the oak-hickory community did not generally support a cover of herbs and bryophytes like those in other communities.

Sixteen species of trees were present in the community. The most important was white oak, with a DFD index more than twice that of the next most important species. It comprised 43% of the total basal area of the community. Major associates were *Carya glabra, Quercus rubra, Liriodendron Tulipifera, Carya ovalis*, and *Oxydendrum arboreum*. In the community oaks comprised 36% of the total density and 57% of the total basal area. Hickories comprised 25% of the total density and 24% of the total basal area. Thus, oaks and hickories accounted for 61% of the density and 81% of the basal area. Tuliptree, dogwood, black gum, red maple, and sourwood were the only numerically important species not belonging to the genera *Quercus* or *Carya*.

Sixteen shrub species occurred in the shrub layer. In density the most important of these were *Kalmia latifolia, Calycanthus fertilis, Stewartia ovata*, and *Hamamelis virginiana*.

A comparatively large number of species (66) occurred in the herb layer. Of these, 36 were herbaceous species. The most important were *Desmodium nudiflorum, Solidago* spp., *Polystichum acrostichoides*, and *Hepatica americana*. Although a great number of species was present, growth was not dense, so the herbaceous cover averaged only 19%. The highest frequency of any herbaceous species was 20%.

Since this community was surrounded by communities of other types, it was deemed important to determine whether it was stable or in a transient stage tending toward a climax of another type. All of the species of the tree layer were present in the shrub layer with the exception of yellow birch. Fifteen species genetically capable of reaching the tree layer, but not present there, were in the shrub layer. The most important of these were *Sassafras albidum, Quercus Prinus, Magnolia macrophylla, Acer saccharum, Ulmus alata, Liquidambar Styraciflua, Diospyros virginiana, Fagus grandifolia*, and *Prunus serotina*. In no other community was there such definite indication of change of composition. However, it was also evident that species of oak and hickory were also actively reproducing.

Chestnut Oak Community

The chestnut oak community was restricted to the upper part of the southwest-facing talus of the Cane Creek Gulf (Fig. 1). It was thus parallel to the cliff-side stand in the hemlock-yellow birch community but on the opposite talus. The differences in composition were remarkable. The northeast-facing slope was dominated by hemlock and yellow birch while the exactly corresponding southwest-facing slope was dominated solely by chestnut oak (*Q. Prinus*). Furthermore, of the 69 species in the herb layers of both stands, only nine were common to both. The two communities were very similar topographically. The only great difference was in exposure. The habitat of this community was generally similar to that of the oak-hickory community contiguous with it except that the latter contained a smaller proportion of large boulders and was lower on the talus. The general aspect was that of a sparse stand of large chestnut oak trees with little cover in the shrub and herb layers except where there were dense clumps of *Kalmia latifolia* and *Vaccinium* species.

The dominant species of the tree layer was *Quercus Prinus* with a DFD index more than 5½ times that of any other species. It was well dispersed as shown by the frequency, 69%. Other important trees were *Acer rubrum, Robinia Pseudo-Acacia, Liriodendron Tulipifera*, and *Nyssa sylvatica*.

In terms of density, the most important shrubs were *Kalmia latifolia, Vaccinium arboreum, Polycodium candicans* Small, and *Viburnum acerifolium*.

Twenty-eight species were present in the herb layer. Of these, only seven were tree species, and 12 were herbs. The important herbs were *Antennaria plantaginifolia, Dryopteris marginalis, Eupatorium dubium*, and species of *Desmodium*.

Chestnut oak was the most important tree species in each of the three layers. In the shrub layer it occurred at a density of 616 plants/acre. The only other important transgressive was red maple with 405 plants/acre. No other transgressive had a density greater than 97 plants/acre.

II. Secondary Successional Stands

Two stands occurred in obvious stages of secondary succession following profound disturbances. These are presented separately because of their general distinctiveness.

Stand Following Clear-cutting

This stand occupied a portion of the lower slope of the northeast-facing talus of Cane Creek Gulf. The site was a gentle slope with a few surface boulders. It was far enough from the cliff to be exposed to direct sun-

light almost all day. The general aspect of the stand was that of young even-aged trees in an area of luxuriant herbs. A very few large trees were scattered among the smaller ones. Large, partly decayed stumps were conspicuous. These apparently remained from a logging operation of 1921-1922. The results of an actual count of the remaining stumps are presented in Table I. Since the stumps are relatively well preserved, these data are presumed to represent the approximate composition of the stand prior to logging. Approximately 71% of the trees were chestnut, 14% tuliptree, and 9% oak. Also present were *Carya ovata, Tilia heterophylla, Juglans nigra, Aesculus octandra, Tsuga canadensis,* and *Liquidambar Styraciflua*. Some of the latter were represented by large living trees rather than by stumps. Apparently no species were cut except chestnut, tuliptree, oaks, black walnut, basswood, and a single hemlock. No stumps of basswood remained, but there were clumps of medium-size trees assumed to have been derived from stump sprouts. Increment borings showed these to be approximately 30 years old.

The most important members of the tree layer of this stand were *Liriodendron Tulipifera, Tilia heterophylla, Juglans cinerea, Carya ovata, Cornus florida, Carya cordiformis, Juglans nigra,* and *Aesculus octandra*. Seventeen species occurred in the tree layer. In general they were small, averaging 9.5 inches DBH.

Although the eight most important members of the shrub layer were transgressives, 13 shrubs occurred in the community. None of the latter accounted for more than 4% of the total density. Thus, the shrub layer was conspicuously dominated by tree species. The most important of the shrubs were *Lindera Benzoin, Smilax rotundifolia,* and *Euonymus americanus*. No other shrub accounted for more than 2% of the total density. Neither *Rhododendron maximum* nor *Kalmia latifolia* was present.

Sixty-seven species were growing in the herb layer, accounting for a total herbaceous cover of 28%. The most important species were *Smilacina racemosa, Polystichum acrostichoides, Phlox divaricata, Tiarella cordifolia, Anemonella thalictroides, Viola,* sp. and *Disporum maculatum*.

The most important transgressives in the shrub layer were basswood, sugar maple, american ash, and butternut hickory. In the herb layer, the most important tree seedlings were *Tilia heterophylla, Acer saccharum, Acer rubrum, Carya cordiformis,* and *Carya glabra* and/or *Carya ovalis*. Thus, sugar maple, which was absent from the tree layer, was the second most important species in both the shrub and herb layers. Apparently butternut was not reproducing, for no seedlings were present.

Forest Following Cultivation

Within the gorges of the park, the only area ever cultivated was a small area of about 10 acres at the base of the northeast-facing talus on the west side of Cane Creek near the north boundary (Fig. 1). The plot was level and contained poorly drained depressions. The general aspect of this area was that of a former grassy meadow in the process of being overgrown with mixed mesophytic forest. This plot was cleared about 1900 and was cultivated in 1901. It then lay fallow. It is reported to have been covered with broomsedge (*Andropogon* sp.) in 1921. It was then used as a lumberyard for a temporary sawmill. For two years it was almost completely covered with stacked lumber and was thoroughly trampled.

This community contained a larger number of trees per acre (212) than any other sampled. The most important were *Liriodendron Tulipifera* and *Liquidambar Styraciflua*. Chief associates were *Platanus occidentalis, Carya cordiformis, Ulmus rubra,* and *Juglans cinerea*.

Thirty-eight species occurred in the shrub layer, only 15 of which were shrubs. The most important of these were *Rubus phoenicolasius, Parthenocissus quinquefolia, Rhamnus caroliniana, Smilax glauca, Lindera Benzoin,* and *Calycanthus fertilis*.

Seventy species were in the herb layer. The most important were *Desmodium* spp., *Viola,* sp., *Geum* sp., *Panicum polyanthes, Houstonia purpurea, Lysimachia tonsa, Sanicula canadensis,* and *Galium triflorum*. This stand was distinctive in containing pasture weeds such as dandelion, burdock, and ironweed (*Vernonia* sp.). The total herbaceous cover was 33%.

This stand showed greater evidence of disturbance than the secondary stand previously discussed. As evidence of this fact, it contained species in all layers

Table 1

Probable composition of the tree layer of the former chestnut consociation prior to logging in 1921-1922.

Species	Total number of stumps	Total number of large living trees	% total tree density	Species	Total number of stumps	Total number of large living trees	% total tree density
Castanea dentata	284		71.2	*Juglans nigra*	3		0.8
Liriodendron Tulipifera	54		13.5	*Aesculus octandra*		2	0.5
Quercus spp.	35		8.8	*Tsuga canadensis*	1		0.3
Carya ovata		11	2.8	*Liquidambar Styraciflua*		1	0.3
Tilia heterophylla	8		2.0	Totals	385	14	100.2

which were not typical of the mature communities of the gorges. Notable among these were sycamore, scrub pine, black oak, black locust, red mulberry, sugarberry, red raspberry, ironweed, nightshade, dandelion, and certain species of sedges and grasses. These were probably remnants of earlier stages of secondary succession. Those species in the tree layer not typical of mixed mesophytic forest were not successfully reproducing, with the possible exception of *Pinus virginiana*. It was present in isolated groups and was not part of the general community. Species present in the tree layer which were reproducing most successfully were *Ulmus rubra, Liquidambar Styraciflua, Tilia heterophylla, Carya cordiformis,* and *Liriodendron Tulipifera*. Those which appeared to be invading the plot were *Fraxinus americana, Acer rubrum, Acer saccharum, Ulmus americana,* and *Tsuga canadensis*. *Juglans cinerea* was not successfully reproducing.

Summary of Results

Tables 2, 3, and 4 summarize the relative importance of the major species of the various communities. Only the numerically most important species have been included in the tables. A complete list of the species collected in the gorges in connection with this project has been published (Caplenor 1955).

In the tree layer, *Liriodendron Tulipifera* was the most widespread species. It was the only one occurring in the canopy of all the communities in the gorges. The next most widespread species were *Betula lutea, Oxydendrum arboreum,* and *Quercus rubra,* each of which was present in six of the seven communities. Of the more important trees, the most restricted were *Fagus grandifolia,* present only in the mixed mesophytic and hemlock-basswood communities, and *Quercus alba,* in the mixed mesophytic and oak-hickory communities. More (15) of the generally important tree species were present in the mixed mesophytic community than in any other. The hemlock community had a smaller number than any other.

The distribution of shrubs was rather sharply delineated (Table 3). In those communities in which hemlock was a co-dominant, *Rhododendron maximum* was conspicuous. It wholly dominated the shrub layer of the hemlock and hemlock-yellow birch communities, and shared dominance with *Euonymus americanus* in the mixed mesophytic community and with *Ribes Cynosbati* in the hemlock-basswood community. *Kalmia latifolia* was the outstanding shrub of the more xerophytic communities. The secondary associes did not have a characteristic shrub or group of shrubs. The shrub layer there was dominated by transgressives.

Only three herbaceous species were included in the samples of all seven communities. These were *Polystichum acrostichoides, Dryopteris marginalis,* and a species of *Arisaema. Hepatica americana, Desmodium cuspidatum, Euphorbia mercurialina,* and *Spigelia marilandica* were restricted to the oak-hickory community. *Antennaria plantaginifolia* and *Asplenium platyneuron* were restricted to the chestnut oak community. Generally, no single species was restricted to one community type. This was especially true of the more mesophytic communities. The more highly restricted of the most mesophytic species were *Sedum ternatum* and *Asarum canadense* (mixed mesophytic and hemlock-basswood communities), *Camptosorus rhizophyllus* (mixed mesophytic and hemlock, and hemlock-basswood communities), and *Hydrophyllum canadense* and *Phlox divaricata* (mixed mesophytic, hemlock-basswood, and secondary communities). Although highly restricted and of minor numerical importance, of especial importance because of their recognition as major indicators (Braun 1950), were *Pachysandra procumbens* (mixed mesophytic community) and *Trillium recurvatum* (hemlock-basswood community). The distribution of all species with a DFD index greater than 10, and/or occurrence in more than one community is given in Table 4. Noteworthy was the wide variety of species in the herb layer of the secondary associes.

Discussion

Plant Associations and Relationships

The primary purpose of this study was the careful description of a relatively slightly disturbed forest in a

Table 2

A comparison of the relative importance (by DFD index) of the major trees in the separate communities. (Key to the headings: M.M.=Mixed mesophytic; H=Hemlock; H-B.=Hemlock-basswood; H-Y.=Hemlock-yellow birch; O-H.=Oak-hickory; C.O.=Chestnut oak; S.A.=Secondary associes.)

Species	Communities							Species	Communities						
	M.M.	H.	H-B.	H-Y.	O-H.	C.O.	S.A.		M.M.	H.	H-B.	H-Y.	O-H.	C.O.	S.A.
Carya glabra	33	11			46	10		*Quercus rubra*	23		7		36	10	5
Tilia heterophylla	33		67	21	8		39	*Acer rubrum*	22		7	14		34	8
Tsuga canadensis	31	233	131	182		10		*Quercus alba*	10				111		
Fagus grandifolia	31		4					*Carya cordiformis*	10		17		15		25
Liriodendron Tulipifera	28		24	23	8	34	19	*Carya ovata*	9		4		6	5	17
Betula lutea	27	16	29	73	5		4	*Quercus Prinus*	9		11	6		198	
Oxydendrum arboreum	25	24	2	28	30	9		*Aesculus octandra*	3		10				9
Acer saccharum	23		32	3											

Table 3

A comparison of the relative importancve (by % of total shrub layer density) of the major shrubs in the separate communities. (Key to table headings as in Table 2.)

Species	Communities						
	M.M.	H.	H-B.	H-Y.	O-H.	C.O.	S.A.
Rhododendron maximum	17	39	15	50		3	
Euonymus americanus	10		2				2
Rhus radicans	7	4	2			1	2
Smilax rotundifolia	5	1	8	2	1	5	2
Hamamelis virginiana	3		2	2	6	1	1
Ribes Cynosbati	3	29				1	
Lindera Benzoin	2		1				4
Hydrangea arborescens	2		1				2
Viburnum acerifolium	1		3	1		7	
Parthenocissus quinquefolia	1	4	1	1		3	3
Kalmia latifolia		6	1	1	21	40	
Stewartia ovata	1	3			7		1
Calycanthus fertilis	1				9		1
Vitis rotundifolia		3		1	3	3	1
Cornus alternifolia		1	2		1		
Vaccinium arboreum				2	1	8	
Asimina triloba			3	1	1		1

physiographic region which previously had been neglected in phytosociological research. Little attempt was made to determine those factors controlling the development of the various associations. It became evident in the course of the study that these gorges contained many sharply delimited communities within a relatively small area. Although tentative conclusions can be drawn, most of them indicate the necessity for detailed investigation of the microenvironmental factors which control the development of such diverse communities within a single macroclimatic area.

Six communities were distinguished in the gorges of the Fall Creek Falls State Park. These are as follows: mixed mesophytic, hemlock, hemlock-yellow birch, hemlock-basswood, oak-hickory, and chestnut oak communities. In addition, two stands are in the late stages of secondary succession following disturbances. The variations in vegetation resulting in distinct communities in such a small area are undoubtedly the result of the extreme variations in soil, microclimate, and exposure which occur in this region of very rugged topography. The general vegetational matrix of these gorges is a mixed mesophytic community from which the other communities are extended. The mixed mesophytic community occupies every habitat in which there is a combination of (1) a deep, boulder-free soil, (2) a level area or a slope facing the north or east, and (3) direct insolation for most of the day which is not excessive (due to slope) in the afternoon. If any of these factors is absent, a community has developed which is not typically mixed mesophytic. If the substrate is similar to that which supports typical mixed mesophytic vegetation, but the area is exposed to the full effect of the afternoon sunlight, an oak-hickory or chestnut oak community is supported. These communities differ topographically only in that the latter is higher on the talus than the former. If the subtrate is composed largely of boulders and is in a position to be shielded from direct sunlight in the afternoon, a hemlock or hemlock-yellow birch community occurs. The hemlock-basswood community occupies a habitat intermediate to that supporting a mixed mesophytic community and supporting a hemlock-yellow birch community.

The relative mesophytism of hemlock communities is a disputed matter. They have been considered post-climax to deciduous forest communities (Clements 1934), ecologically equivalent to mixed mesophytic communities (Braun 1950), more mesophytic than beech-maple communities (Moore, *et. al.* 1924) and approximately as mesophytic as beech-maple communities (Daubenmire 1930). Daubenmire (1931) indicated that dry soil inhibited invasion of hemlock communities by beech-maple forest in Indiana. The confusion may exist because the species does not fit the scheme into which it has been thrust. It is quite possible that relative mesophytism is not even the chief controlling factor. The relative position of the hemlock-dominated communities in the gorges of the Fall Creek area was definitely related to the dominance of the substrate by large boulders, the corresponding absence of a conspicuous soil, and the occurrence of shade for a considerable part of the day, particularly in the afternoon. The more mesic condition created by shade may be counter-balanced by less favorable soil conditions. The situation in these gorges indicated that the most critical controlling factor is the absence of sufficient sunlight to support other species in competition with hemlock. This has been suggested by Martin (1959) in reference to hemlock succession in Ontario. Hemlock, then, seems tolerant of a wide range of conditions regarding water supply and is successful in relatively dense shade.

The major tree species (Table 2) which are restricted to the mixed mesophytic community and its association segregates and are, presumably, most representative of the mixed mesophytic forest in the area are *Fagus grandifolia, Acer saccharum,* and *Aesculus octandra. Tilia heterophylla,* which, with *A. octandra,* is one of the most characteristic trees of the Mixed Mesophytic Forest Association (Braun 1950), is found in these communities in the secondary associes and in the oak-hickory community where it is rare.

Liriodendron Tulipifera is a widespread species in the gorges, appearing in all of the communities. It is most important in those communities which have been most severely disturbed in the relatively recent history of the gorges. It is only in secondary successional stands

Table 4

A comparison of the relative importance (by DFD index) of the major herbs in the various communities. (Key to the table headings as in Table 2.)

Species	Communities						
	M.M.	H.	H-B.	H-Y.	O-H.	C.O.	S.A.
Polystichum acrostichoides	34	28	22	1	28	6	37
Sedum ternatum	30		24				
Tiarella cordifolia	23	26	22		4		25
Dryopteris spinulosa var. *intermedia*	19	16	17	63			
Dioscorea quaternata	19		5		29		6
Viola spp.	17	28	17	7	19		42
Aster spp.	14	51		5	23	13	10
Disporum lanuginosum and *D. maculatum*	12		6		3		17
Arisaema sp.	11	22	12	18	4	6	5
Solidago spp.	8					39	13
Medeola virginiana	8	25	2		3		12
Uvularia perfoliata	8				3		1
Desmodium glutinosum	8					6	3
Viola blanda	7		6	36			
Dryopteris marginalis	6	34	8	23	6	21	2
Smilacina racemosa	6		11	1	3		33
Desmodium nudiflorum	5		6		44		
Geranium maculatum	5				6		
Anemonella thalictroides	5		8				19
Prenanthes alba	5						8
Desmodium spp.	4				28	15	52
Laportea canadensis	4	28	42	2			8
Carex Jamesii	4		3				6
Viola conspersa	4	7	9	1	3		2
Hydrophyllum canadense	4		2				3
Hepatica acutiloba	4	10	20		3		14
Phlox divaricata	4		3				31
Phacelia bipinnatifida	3		22	3			7
Impatiens capensis	3		19	7			6
Carex plantaginea	2	7	13	1			13
Camptosorus rhizophyllus	1	7	20				
Polymnia canadensis	2		6	4			2
Asarum canadense	1		8				
Polypodium virginianum	1	52	7	78			
Danthonia spicata		13	6		7	9	
Galium circaezans		6		27	7		
Cystopteris bulbifera		6		4			
Eupatorium dubium		6			9	16	3
Hepatica americana					27		
Desmodium cuspidatum					23		
Euphorbia mercurialina					21		
Spigelia marilandica					12		
Athyrium thelypterioides					11		4
Agrimonia rostellata					6		10
Antennaria plantaginifolia					73		
Asplenium platyneuron					10		
Galium latifolium							24
Lysimachia tonsa							15
Panicum polyanthes							14
Carex digitalis							14
Houstonia purpurea							13
Trillium erectum							12
Sanicula canadensis							12
Galium triflorum							12
Carex amphibola var. *globosa*							10
Osmorhiza Claytonia							10

that it is the most important species. This suggests that open canopy favors reproduction of the species. The reason for this is unknown. Since it is a component of the hemlock-dominated stands, it would not appear to have an exceptionally great light requirement as a seedling. Braun (1950) noted that it is reproducing abundantly on some of the cutover mesic slopes in other parts of the Mixed Mesophytic Forest Association.

Juglans cinerea is the most definite indicator of secondary succession in the gorges. It is present only in places where major disturbances have occurred. This may be a phenomenon peculiar to the gorges, since it has not been noted by those investigators most familiar with mixed mesophytic forests.

Pinus virginiana is frequent only in the area which was formerly cultivated. Even though it is the most common tree of the thin soil at the tops of the cliffs bordering the gorges and must shed many seeds into the gorges below, it is practically absent from undisturbed stands. Its relative importance in the formerly cultivated plot suggests that it is a normal component of associes following cultivation of land originally covered with mixed mesophytic forest.

Where hemlock is the most important member of the tree layer, rhododendron is the most important member of the shrub layer. The latter is rarely found in the gorges except in association with the former. The affinity of the two species is a well-recognized phenomenon (Braun 1950, Shaler and Crandall 1876). Yet, neither Griggs (1914) in Ohio nor Segars, *et. al.* (1951)

in Alabama mention rhododendron as important in the hemlock stands they described. Oosting and Billings (1939) found hemlock stands with and without rhododendron in southwestern North Carolina. Rhododendron distribution in the gorges indicates that it is exceptionally tolerant of shade. It is quite possible that it exists only in habitats which are so shaded as to exclude competition. Herbaceous species are almost absent from areas whose shrub layers are dominated by rhododendron.

The herb layer of the communities of the gorges is characterized by low frequency and little cover. This is probably due to unfavorable edaphic conditions and excessive shading. In the mixed mesophytic community where the soil is deep and the upper layers fairly open the herb layer is well developed, but it is best developed in those stands in secondary succession. Some parts of the hemlock and hemlock-yellow birch communities have a well-developed herbaceous layer because the sandstone boulders which form the substrate are completely covered with *Polypodium virginianum* and *Dryopteris spinulosa* var. *intermedia*.

Pachysandra procumbens and *Trillium recurvatum* are notable species in the herb layer because they might not ordinarily be expected to occur in the region. Braun (1950) listed these species as characteristic of the Western Mesophytic Forest region, but considered the gorges of the Fall Creek area to be part of the Mixed Mesophytic Forest region. She stated that *P. procumbens* rarely extends into the Mixed Mesophytic Forest region, and *T. recurvatum* is unknown there. Their presence in the gorges does not invalidate the regional classification of the area. It only illustrates the danger of proposing inclusive schemes for the distribution of plants and plant associations. Since these gorges occur at the margin of the Cumberland Plateau and since the Highland Rim below the Cumberland Plateau is within the Western Mesophytic Forest region, it is normal for some overlapping of characteristic species to occur.

Succession

Four conditions occur in the gorges with respect to relative severity of disturbance. These are (1) cultivation, (2) clear-cutting, (3) selective cutting, and (4) absence of major disturbance.

The plot which was cultivated has undergone the most complex pattern of secondary succession. It had a herbaceous stage dominated by *Andropogon*, but apparently contained a great many other pasture weeds since some of these species still remain. During the next stage local areas were dominated by *Pinus virginiana* and *Celtis occidentalis*, but most of the plot was reinvaded directly by mixed mesophytic species, particularly *Liriodendron Tulipifera, Liquidambar Styraciflua, Platanus occidentalis*, and *Carya cordiformis*. Invasion by *Tsuga canadensis, Acer saccharum*, and *Tilia heterophylla* strongly indicates development into a typical mixed mesophytic stand. According to Braun (1950) there is a variety of types of secondary succession in the Mixed Mesophytic Forest region, depending upon the original vegetation, the topography, and the degree of disturbance. Evidence from this study indicates that even cultivated land undergoes secondary succession leading rather directly to mixed mesophytic stands.

The former chestnut consociation from which nearly all of the large trees had been removed approximately 30 years before the initiation of this study is in the process of natural reforestation. It is apparent that mixed mesophytic species began to replace the chestnut stand immediately after the mature trees were taken out. Since these chestnut trees were removed at a time close to the time of their natural death by blight, the present study gives an indication of the natural replacement of chestnut in the area. Results in this study definitely indicate replacement with mixed mesophytic forest. Most reports of forests replacing oak-chestnut stands after the death or final removal of the chestnut trees indicate replacement by oak-hickory forest (Korstian and Stickel 1927, Aughanbaugh 1935, Oosting 1942, and Keever 1953). Apparently chestnut has been replaced in relatively undisturbed forests by species typical of the forest region, the replacing species being slightly less mesophytic than chestnut. In the former chestnut consociation of the Cane Creek Gulf this was not the case. The replacing forest is more mesophytic than the original. Similar results have been obtained by Woods and Shanks (1959) in the Great Smoky Mountains National Park. There the general development was toward an oak association complex, but in mesic coves there was often a tendency toward the development of more mesophytic forest types. Species included in the replacing forest there included *Tsuga canadensis, Liriodendron Tulipifera, Tilia heterophylla*, and *Acer saccharum*.

The parts of the gorges which were selectively logged approximately 30 years prior to the initiation of this study have regained their status as mature stands. The communities in this category are the mixed mesophytic, hemlock-basswood, oak-hickory, and chestnut oak communities. With the possible exception of the oak-hickory community, these are definitely stable communities without any indication of change of dominant species. The situation in the oak-hickory community is complex. Braun (1950) interprets oak-hickory communities in the Mixed Mesophytic Forest region as subclimax or physiographic climax to mixed mesophytic forest rather than a seral stage in its development. She believes that oak-hickory communities as segregated groups result from the dropping out of the more mesophytic species. There is insufficient evidence from the forests of the gorges to warrant definite conclusions regarding this matter. The presence of relatively larger numbers of mixed mesophytic species in the lower layers than in the tree layer indicates that the oak-hickory community there is being replaced slowly by a mixed mesophytic community. It is possible, however, that the present forest is the result of logging to an unsuspected degree. This problem can best be solved by further work in the same area in the future.

The virgin communities of the gorges (hemlock and yellow-birch communities) are fully as stable as the mixed mesophytic communities. There is no evidence of stress between these communities even where they are contiguous. Apparently each is well established and strictly delimited under present climatic and edaphic conditions.

One of the most striking aspects of the communities of the gorges is the remarkable stability of most of them. The mixed mesophytic, hemlock, hemlock-yellow birch, hemlock-basswood, and chestnut oak communities give definite indication of remaining as they are. The existence of these stable, mature communities in a small area within a given climate appear to defy the general concept of "climatic climax." It is clear that the chief causes of differentiation of the communities are topographic in nature. This does not, however, offer a simple answer to the problem of environmental control of plant communities. In such severely dissected areas as those included in this study, topographic differences result in differences in temperatures, water relations, soil composition, and insolation.

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