To the Graduate Council:

I am submitting herewith a thesis written by Ernesto Arends entitled "Vegetation Patterns a Half Century Following the Chestnut Blight in the Great Smoky Mountains National Park." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

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VEGETATION PATTERNS A HALF CENTURY FOLLOWING THE CHESTNUT BLIGHT IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Ernesto Arends

June 1981

ACKNOWLEDGMENTS

I am deeply thankful to the University of Los Andes, Merida, Venezuela, for the scholarship that made my studies possible.

I would like to express my sincere appreciation to my major professor, Dr. J. Frank McCormick, Director, Graduate Program in Ecology, The University of Tennessee, Knoxville, for his guidance and encouragement. Thanks are also extended to Dr. H. R. DeSelm, Botany Department, and to Dr. Frank W. Woods, Forestry Department, for their helpful suggestions and critical reading of the manuscript.

Appreciation is extended to Dr. Peter White and Mr. Mark Harmon, Uplands Field Research Laboratory, who gave of their time to help me with taxonomic determinations.

Sincere thanks to Mrs. Ann Stocum, Graduate Program in Ecology and Uplands Field Research Laboratory, who provided computer programs and generous assistance in the analysis of data. Thanks go also to Mr. Paul Schmalzer for his suggestions in the analysis of data.

For their time and assistance in collecting field data, I wish to thank Mr. Mike Montle, Mr. Ronald Plaza and Wladimir Cañizales. Thanks go also to Sims Crownover who generously read the manuscript.

I am grateful to the Graduate Program in Ecology, The University of Tennessee, Knoxville, and to the Uplands Field Research Laboratory, Gatlinburg, Tennessee, for providing financial assistance and material support.

Special thanks are extended to Mrs. Alice Zimmerman and Mrs. Bernice Stevens for their gracious hospitality at their wonderful "Skylo."

This work could not be realized without the help of my wife, Marlene, and my son, Alejandro. I thank them for their encouragement, help and patience during this project and throughout all my studies.

ABSTRACT

Vegetation patterns approximately 50 years after the chestnut blight were examined in forest stands of the Great Smoky Mountains National Park. Specific objectives of this study were: (1) to determine the present composition of replacement stands following the elimination of chestnut, (2) to examine selected site factors and to relate them to tree species composition, (3) to project future trends in the composition of the replacement stands, and (4) to compare these results with earlier results and predictions of Wood and Shanks (1959) concerning chestnut replacement in the same area.

Data were analyzed from 38 sample plots ranging from 2000 to 4000 feet elevation in the eastern portion of the Great Smoky Mountains National Park.

Species most often involved in chestnut replacement are red maple, northern red oak, sourwood, and chestnut oak. Red maple do not show noticeable differences in importance with respect to moisture conditions. However, mesic species such as northern red oak, hemlock and silverbell are more important under favorable moisture conditions. Chestnut oak and sourwood are more important under relatively xeric conditions.

Species importance values were used to group sample plots into replacement forest types using an agglomerative clustering procedure.

Six replacement forest types were identified: silverbell-red maple, hemlock-hardwood, northern red oak-silverbell, chestnut oak, red maple-oaks, red maple-sourwood.

Discriminant analysis based upon vegetation data indicated that 97% of the samples were correctly identified. Discriminant analysis using environmental variables indicated that environmental conditions in the various replacement forests were not entirely distinct. Elevation and moisture conditions appear to be the most important factors responsible for distinct chestnut replacement forest types.

In the present study, chestnut stump basal area was not an important variable in segregating the chestnut replacement forests. However this may be due to the fact that all sites selected for study had high basal area of chestnut stumps.

Results of this study suggest that chestnut is being replaced in the Smokies by the same species that were its earlier associates, mainly red maple, chestnut oak and northern red oak. Under the most mesic conditions, chestnut is being rapidly replaced by species such as hemlock and silverbell. Under the most xeric conditions, the process of recovery is slow; red maple and sourwood have been most favored by the death of chestnut. Red maple is an important species in several of the replacement forest types.

Chestnut is not being replaced by a single vegetation forest type. Six distinct successional forest types presently occur on sites formerly dominated by chestnut. Subsequent and periodical studies are recommended in order to determine if current trends will continue.

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CHAPTER I

INTRODUCTION

At the beginning of this century the chestnut, Castanea dentata (Marsh), was an important component of many forests in the eastern United States. By 1930 the chestnut blight, Endothia parasitica (Murr.) Anderson, had heavily infected the forests of southern Appalachia and eliminated chestnut as a dominant or codominant of the former oak-chestnut forests, and as an important member of the deciduous forest formation. Removal of the chestnuts provides us with an opportunity to observe and analyze recovery following a major perturbation of the vegetation.

The former presence of chestnut in Eastern Tennessee has been documented in several studies (Ayres and Ashe, 1902; Hall, 1910: cited by West, 1970). According to these studies the proportion of canopy composition occupied by chestnut was approximately 30%. In the oak-chestnut forests of the Great Smoky Mountains, chestnut probably formed 30 to 70% of canopy stems (Whittaker, 1956). Presently, the former abundance of chestnut in a stand is indicated by the presence of stumps, logs, and living sprouts.

The present study examined vegetation patterns developed approximately 50 years after the elimination of chestnut in forest stands of the Great Smoky Mountains National Park. Study sites were located in the same areas as those examined by Woods and Shanks (1954) a quarter century ago.

Specific objectives of the present study were: (1) To determine the present composition of replacement stands following the elimination of chestnut, (2) to examine selected site factors and to relate them to tree species composition, (3) to project future trends in the composition of replacement stands, and (4) to compare these results with earlier predictions of Woods and Shanks (1959) concerning chestnut replacement in the same area.

CHAPTER II

REVIEW OF SELECTED LITERATURE

Several studies have described the composition of pre-chestnut blight vegetation, although accurate site specific records are rare. Braun (1950) reported chestnut to be one of the eight most abundant species of the mixed mesophytic forest, and a dominant in certain of its segregates. In the Western Mesophytic Forest region it was a codominant with beech (Fagus grandifolia), and in the Oak-Chestnut Region it was often codominant with oaks on mesic slope forests.

According to Woods and Shanks (1959), the oak-chestnut forest association was characterized by chestnut, chestnut oak (Quercus prinus), red oak (Q. rubra), white oak (Q. alba), scarlet oak (Q. coccinea), red maple (Acer rubrum), and hickories (Carya spp.). Two other species, black oak (Quercus velutina) and sweet birch (Betula lenta) were also abundant in the oak forests of the Oak-Chestnut Forest region.

In the Southern Appalachians (Southern Blue Ridge), oak-chestnut communities occurred at elevations from about 1300 feet to about 4500 feet, or even higher on southern exposures. In some sites, chestnut occurred in almost pure stands. At lower elevations the oak-chestnut forest on mesic sites was a dense forest mainly of chestnut and yellow poplar (Liriodendron tulipifera); a mixture of oaks was the principal associates of chestnut on drier sites. At higher elevations northern red oak was often dominant with chestnut; chestnut oak also was abundant; white oak shared dominance with chestnut on some exposed southerly slopes (Braun, 1950).

At moderate elevations in the Smoky Mountains chestnut forests were widespread, almost regardless of slope exposure and steepness (Braun, 1950). In submesic and subxeric stands analyzed by Whittaker (1956), chestnut formed 30-60 percent of the canopy stems. He described four vegetation types which were co-dominated by oaks and chestnut. At elevations below 3500-4000 feet chestnut oak-chestnut heath and chestnut oak-chestnut forests occurred on almost all slopes except those facing south and southwest. Above these elvations northern red oak-chestnut forests occupied sub-mesic sites while white oak-chestnut forests were on the more xeric sites.

The death of chestnut trees infected by the blight was a slow process (Aughanbaugh, 1935; Wood and Shanks, 1959). Openings of the canopy increased light penetration and concomitant changes in environmental conditions were brought about at or near the forest floor. Available spaces were gradually filled by the extension of the crowns of co-dominant species, growth of suppressed seedlings and saplings, and/or invasion of new species (Korstian and Stickel, 1927a; Nelson, 1955; Woods and Shanks, 1959).

Species composition in post-chestnut forests has been studied in several regions of the deciduous forest. In southern New England, Korstian and Stickel (1927a, 1927b) reported that chestnut had been largely replaced by northern red oak and chestnut oak. Other important species were white oak, red maple, white ash (_Fraxinus americana_), sugar maple (_Acer saccharum_) and hickories. In southeastern Pennsylvania, Aughanbaugh (1935) also found that the former associates of chestnut were the most common replacement species, mainly chestnut oak and red maple.

More recent studies in northern forests indicate regeneration patterns different of those previously mentioned. Good (1968), studying replacement of the chestnut in the Highlands of New Jersey, found that although the canopy was dominated by oaks, they have had declining success in reproducing themselves for many years. Mesic species such as beech, sweet birch, and red maple were more important than they had been in the pre-blight forest.

Approximately 50 years after the blight and extensive lumbering, Mackey and Siveck (1973) studied a former oak-chestnut forest in the Allegheny Mountains of western Pennsylvania. The dominant species reported, based on importance value, were black cherry (_Prunus serotina_), red maple, sugar maple, black oak, sweet birch, and black gum (_Nyssa sylvatica_). Gradual elimination of black cherry and older individuals of several species indicated that this forest would continue to change throughout the next few decades.

Replacement of chestnut has been intensively studied in southern forests. Some of these studies were completed within 30 years after the blight had infested the region (Keever, 1953; Nelson, 1955; Woods and Shanks, 1959), others were finalized within 50 years after the blight (West, 1970; Skeen, 1973; Stephenson, 1974; Flora, 1977; Karban, 1978). Two investigations analyzed changes in permanent plots 20 years and 50 years following the blight (Thor and Summers, 1971; McCormick and Platt, 1980). A computer model has been developed to simulate the forest dynamics associated with loss of chestnut (Shugart and West, 1977). Several additional studies report observations about chestnut replacement in southern areas (Brown, 1950; Whittaker, 1956; Barclay, 1957; Thomas, 1966; Mowbray and Oosting, 1968; Martin, 1971; Golden, 1974; West, 1974; Stamper, 1976; Schmalzer, 1978).

In the former oak-chestnut communities of the Cumberland Mountains of Kentucky, Braun (1950) observed that chestnut oak was favored by the death of chestnut. The hickories also, mainly pignut (Carya glabra) and shagback (Carya ovata), were increasing and, in some places, an oak-hickory forest would replace the original forest. Sugar maple and white oak were growing rapidly in more mesic conditions. These vegetation patterns were also reported by Schmalzer (1978) in cove communities of the Cumberland Plateau in Tennessee. Besides chestnut blight, human settlements and logging have long perturbed these communities. In such cases, chestnut oak, white oak and northern red oak were the dominant chestnut replacement species in oak communities. In more mesic communities, sugar maple or hickories might have been important replacement species.

In the Great Valley of east Tennessee, Martin (1971) suggested that chestnut oak and white oak were the major species that replaced chestnut. Thor and Summers (1971) analyzed changes in forest composition of logged and blighted stands between 1936 and 1967. Trees increasing sharply in density were red maple, sugar maple, black gum, and beech. Black oak, chestnut oak, and virginia pine (Pinus virginiana) had a marked basal area increase. The authors reported that chestnut oak and black oak would dominate most of the sites studied. They predicted that sugar maple would be an important replacement tree on mesic sites while on xeric sites there would be a mixture of pines, red maple and black gum.

In Johnson County, Tennessee, Barclay (1957) reported that forests formerly dominated by chestnut included sweet birch, white ash and white basswood (*Tilia heterophylla*) as associated species in mesic stands. In xeric stands, chestnut was associated with chestnut oak, pitch pine (*Pinus rigida*) and pignut hickory. West (1970) analyzed replacement of chestnut in disturbed secondary forests in east Tennessee. In stands disturbed only by the blight, black oak and white oak were dominant species in the canopy. Yellow poplar was dominant in logged stands. Northern red oak and red maple were found in most post-chestnut forests. Skeen (1973) studied a mature mesic north-slope forest in east Tennessee. The most important chestnut replacement species based on biomass and reproduction, were beech, hickories, black oak and sugar maple.

West (1974), using data of continuous forest inventories, indicated that post-chestnut stands of the continuously logged ridge and valley of East Tennessee were dominated by a mixture of oaks, red maple, and pitch pine. The author observed that the lack of northern red oak reproduction might indicate a decrease of the importance of this tree in some areas.

Shugart and West (1977) found that post-chestnut simulated forests of east Tennessee resulted in a short-term increase in red maple, hickories, and black oak and a long-term increase in white oak and chestnut oak.

In the Jefferson National Forest located in the Appalachian Mountains of Virginia, Braun (1950) reported that red oak and white oak were the principal associates of chestnut on the slopes of Salt Pond

Mountain. She suggested that the future forest might be one dominated by northern red oak because of the high reproduction of this species. On the southwest slope of adjacent Beanfield Mountain, McCormick and Platt (1980) studied the species composition of a former oak-chestnut forest between 1939 and 1970. They found that northern red oak, chestnut oak, and white oak persisted as co-dominants species for a quarter century following the blight. By 1970, pignut hickory had the highest importance value of any species on the forest, red maple had invaded clearings, and sugar maple was dominant in mixed mesophytic forest at low elevations. The authors concluded that replacement of the chestnut-oak forest had required at least a half century of succession and had resulted in an oak-hickory association with pignut hickory, northern red oak, and chestnut oak as dominants. White oak, red maple, and sugar maple occur as subdominant species.

The importance of hickory species in chestnut replacement has not been observed for other forest stands studied in Virginia. Stephenson (1974) based upon overall importance value, reported that chestnut oak, northern red oak, red maple, scarlet oak, and white oak were the dominant species in former chestnut stands of the Jefferson National Forest. Chestnut oak was the leading dominant on southern stands, while on northern ones it was codominant with northern red oak. In Shenandoah National Park, Karban (1978) analyzed southeast slopes on a former oak-chestnut forest which had been surveyed by Braun (1950) before the blight. Results showed that northern red oak, sugar maple, chestnut oak, and sweet birch had increased in percent composition of the forest canopy. The author, based on an association test, reported that red oak was the only species significantly associated with chestnut stumps.

According to Braun (1950) the oak-chestnut association reached its best development in the Southern Appalachians (Southern Blue Ridge). She observed that in many sites oaks were replacing chestnut; in some, yellow poplar had increased; in others, more mesic and shade-tolerant species were favored. In Macon County, North Carolina, Keever (1953) studied stands where chestnut was formerly abundant. Fifteen species were found in the forest canopy. In order of density, the six most important taxa were chestnut oak, northern red oak, hickories, white oak, red maple, and sweet birch. Chestnut oak and northern red oak were the most important trees on north-facing slopes, while hickories dominated on south slopes. The author considered that although the communities were successional ones, they would probably develop into an oak-hickory forest.

On permanent plots established in 1934 at the Coweeta area of western North Carolina, Nelson (1955) found that yellow poplar had been the most important chestnut replacement. Hickories and red maple also showed evidences of replacing chestnut. The author observed that northern red oak had decreased in both basal area and density, and species such as sourwood, cucumber magnolia (Magnolia acuminata), yellow birch (Betula lutea), and hemlock (Tsuga canadensis) were invading sites where they had previously been absent. The same plots were remeasured in 1969-72 and data were reported by Flora (1977). This study, using data of plots in which chestnut comprised at least 50% of the basal area in 1934, indicated that chestnut oak, red maple, and yellow poplar made largest increase in basal area; dogwood (Cornus florida) and sweet birch showed largest increase in density. Canopy dominants were chestnut oak, red maple, northern red oak, hickories, and yellow poplar.

Mowbray and Oosting (1968) found that chestnut was replaced by the already present oaks, chestnut oak and northern red oak, in the Thompson Gorge of the Blue Ridge, North Carolina. Stamper (1976) studying the vegetation of Beech Mountain, North Carolina, identified four chestnut replacement forests: mixed oak, northern red oak, red maple and white ash forest types. Red maple was the leading associate of chestnut oak and northern red oak in the mixed oak replacement forest. In addition to the loss of chestnut, grazing and logging have also disturbed these replacement forests.

In Chilhowee Mountain, Tennessee, Thomas (1966) observed that northern red oak, white oak, chestnut oak, yellow poplar, black gum and hickories were the most important species on sites that were once covered with almost pure chestnut woods. Red maple was the most important species in the sapling and seedling categories.

In the former chestnut oak-chestnut forests of the Great Smoky Mountains National Park, Whittaker (1956) observed that the death of chestnuts permitted heavy reproduction of suppressed trees, and had favored small tree species such as red maple, sourwood, and dogwood. Woods and Shanks (1959) studied 2569 gaps and 79 stands in order to determine what species were replacing chestnut. They found that chestnut oak, northern red oak, and red maple comprised 46 percent of the total individuals replacing chestnut. In the most mesic conditions such species as hemlock, silverbell (_Halesia carolina_) and yellow poplar were often favored, while in dry positions sourwood, scarlet oak, and pitch pine were replacing chestnut. The authors concluded that the former oak-chestnut forest association was in the process of developing into an oak association complex, in which chestnut oak and northern red oak would be particularly important.

This trend has generally been observed, although with some variations, by more recent works in the Smokies. Golden (1974) studying the vegetation pattern in the Central portion of the Smokies, reported that red maple, chestnut oak, northern red oak, and sourwood were the most common species which had replaced chestnut. Flora (1977) analyzed two former chestnut stands in the eastern part of the Park. On a northeast slope, the most abundant species were red maple, silverbell, and northern red oak. On a south slope, red maple, northern red oak, and hickories were the most numerous. In both stands northern red oak was dominant in basal area, and an abundant reproduction of both red maple and northern red oak was observed.

It may be concluded from the studies reviewed that there are variations in the vegetation patterns associated with the elimination of chestnut. These variations may be explained on the basis of temporal limitations of the studies, environmental differences of the region and sites analyzed, former abundance of chestnut, and amount of pre- and post-chestnut blight disturbance.

Braun (1950) points out that only after several generations of forest trees could an equilibrium be reached, and the dominant chestnut replacement species be determined. Most of the studies analyzed were done during the first few decades of succession, and the results are therefore limited. In general, chestnut was replaced by an oak complex (Wood and Shanks, 1959) soon after the blight, but in Virginia (McCormick and Platt, 1980) this oak association was replaced by an oak-hickory forest approximately 50 years after the blight. Shugart and West (1977) suggested that forest composition will continue to shift throughout 100 to 200 years until replacement species revert back to a status similar to the pre-blight forest.

Although oak species have persisted as canopy dominants since the blight, there are variations in their importance as a result of differences in environmental conditions. For example, black oak seems to be more important than northern red oak at low elevations (West, 1970; Thor and Summers, 1971). Hickories (Keever, 1953; Nelson, 1955; McCormick and Platt, 1980), red maple (West, 1974; Golden, 1974), and sweet birch (Good, 1968; Mackey and Sivec, 1973) appear to be important replacement species in several sites of the former oak-chestnut forests.

Chestnut replacement was also affected by the former abundance of chestnut. Stands with high abundance of chestnut were rapidly replaced by species such as hemlock; while in stands where chestnut was less abundant, a more gradual replacement of chestnut occurred (Wood and Shanks, 1959).

It is important to note that vegetation patterns after the loss of chestnut was modified by disturbances other than blight. For example, species such as yellow poplar were favored in sites disturbed by logging (Nelson, 1955; West, 1970). Because of these several important variables, it is difficult to identify a single pattern or process of chestnut replacement which can be extrapolated beyond a site specific basis.

This particular study provides an opportunity to compare results and interpretations with those of Woods and Shanks based upon examination of the same area a quarter century ago. This study establishes an additional baseline for future studies of longer term succession in this area.

CHAPTER III

THE STUDY AREA

Location

The Great Smoky Mountains National Park in eastern Tennessee and western North Carolina comprises 227,076 ha. of complex topography and a wide range of elevations. Sampling sites for this study were located in the eastern part of the Park, between Texas Creek and Indian Camp Creek in Sevier and Cocke Counties, Tennessee, and in the vicinity of Mount Sterling Gap in Haywood County, North Carolina (Figure 1). These sites were selected in an effort to sample the same sites, or sites very similar to those sampled by Woods and Shanks in 1957.

Although chestnut might be found at elevations from below 2000 ft. to above 5000 ft. (Woods and Shanks, 1959), this study was restricted to an elevation range between 2000 to 4000 ft. It was considered that this elevation range would include the most important forest types in which chestnut was abundant.

The area is mapped on the Jones Cove, Mount Guyot, and Cove Creek Gap 7.5 minute topographic quadrangle maps of the U. S. Geological Survey.

Climate

Climate of the Smokies varies from a humid mesothermal at low elevations to perhumid microthermal at high elevations (Thornthwaite, 1948; Shanks, 1954).

Mean annual precipitation, based on 54 years of data for

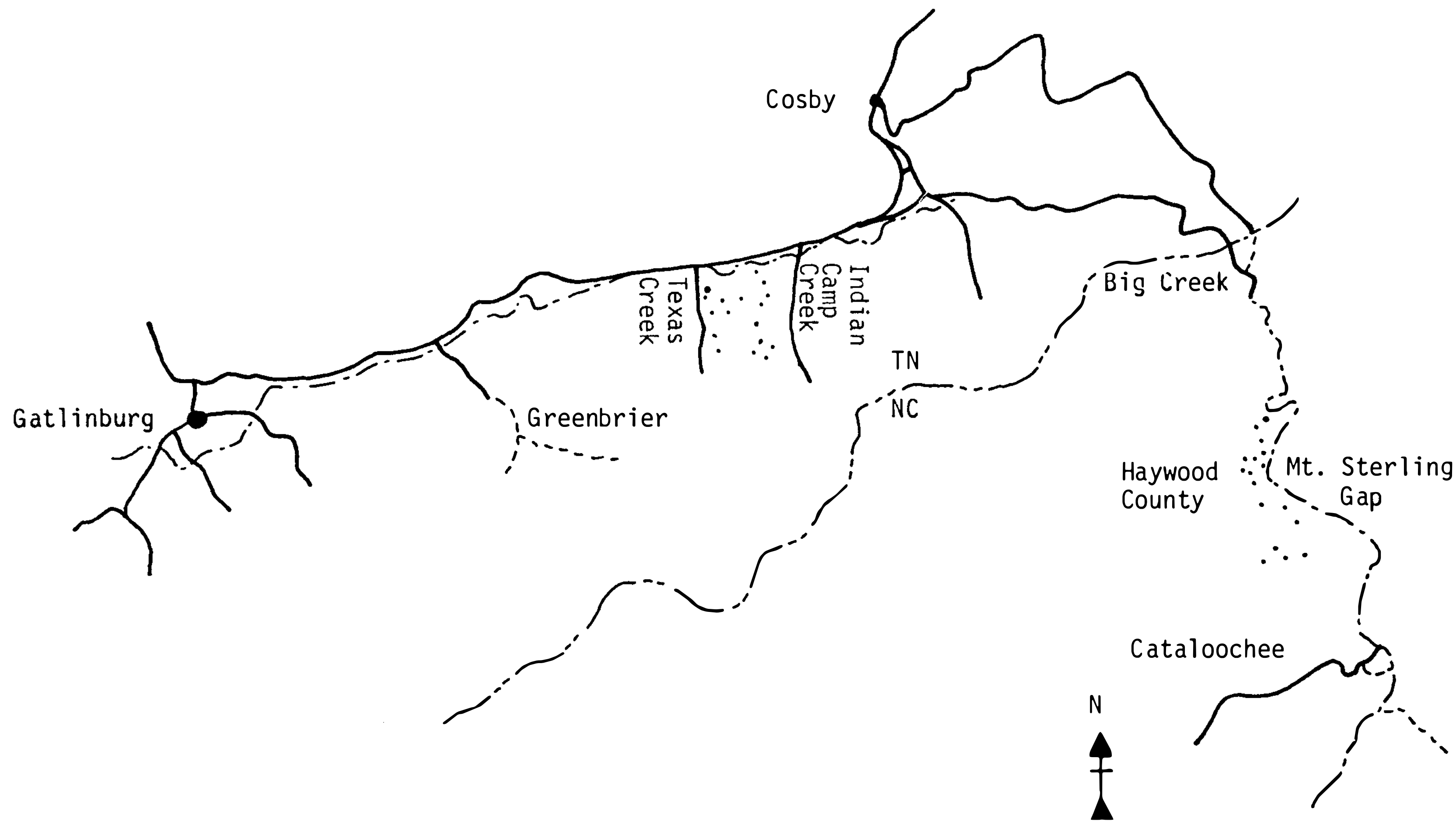

Figure 1. Locations of Sample Plots in the Great Smoky Mountains National Park.

Gatlinburg, Tennessee (1454 ft.), is 140.5 cm. (55.31 inches), while for Clingmans Dome, North Carolina (6250 ft.) it is 209.3 cm. (82.40 inches), based on 25 year records (Tennessee Valley Authority, 1979). Precipitation maxima occur in March and in July-August, and minima occur in September-October.

Mean maximum temperatures in the Smokies occur in June through August, and mean minima occur in December and January. Mean annual temperature at Gatlinburg is 13.3°C (56.8°F) with a mean maximum of 21.4°C (70.6°F) and a mean minimum of 6.1°C (42.9°F) (U. S. Dept. of Commerce, 1965). As elevation increases, temperature decreases at an average rate of 0.41°C/100 m. (2.23°F/1000 ft.), so that high elevations average 5.5-8.3°C (10-15°F) cooler than the base of the mountain during the growing season (Shanks, 1954).

Climatic and microclimatic variations, as a result of an altitudinal gradient and of the topographic complexity, contribute significantly to the biotic diversity of the Great Smoky Mountains.

Substrate

The Smoky Mountains are a segment of the Unaka Mountains of the Blue Ridge Province (Fenneman, 1938). Most of the Smokies are formed by late Precambrian sedimentary rocks of the Ocoee Series, which have been complexly folded and faulted internally and metamorphosed by heat and pressure (King et al., 1968).

Sample sites were located north and east of the Greenbrier Fault, which carries younger rock material over older. Low and middle elevation sites are overlain by three formations of the Snowbird Group: The Pigeon Siltstone formation of argillaceous material intermingled with abundant grains of quartz and feldspar, the Roaring Fork Sandstone formation composed of dark-colored fine-grained sandstone interbedded with silty and argillaceous rocks, and the Longarm Quartzite formation of dominantly light and medium- to coarse-grained feldspathic quartzite and arkose (King et al., 1968).

Sites at higher elevations were on Thunderhead Sandstone formation of the Great Smoky Group. This formation is composed principally of blue tinted quartz and potassic feldspar grains (King et al., 1968).

Detailed soil information is not available for the Great Smoky Mountains. General soil descriptions are based on the soil survey of Sevier County (Hubbard et al., 1956) and Haywood County (Goldston et al., 1954). Survey maps include most of the mountain slope soils in the residual Ramsey series, while some low elevation sites are placed within the Jefferson series.

Ramsey soils were developed from weathering of quartzites, sandstone, and conglomerates. They are shallow, poorly developed, excessively drained, low in water-holding capacity, strongly acid and relatively infertile (Hubbard et al., 1956; Goldston et al., 1954). Within the Ramsey series, sampled sites were on several soil types; predominantly Ramsey loam and Ramsey stony loam.

Some sampled sites were within the map unit named Rough mountainous land (Ramsey material). This is a miscellaneous land type, characterized by very steep slopes, with 20 to 70 percent of the surface occupied by bedrock outcrops and boulders with Ramsey soil material in the intervening spaces (Hubbard et al., 1956).

The Jefferson series is represented by sites located at the base of upland slopes. Those soils were formed from local alluvium and colluvium washed from the Ramsey soils of the uplands. Soil type was a stony fine sandy loan occurring on gently slopes, characterized by low fertility, strongly acid, low water-supplying capacity, and stoniness (Hubbard et al., 1956).

Vegetation

The Great Smoky Mountains support a wide variety of forest vegetation, as an expression of topographic, altitudinal and microclimatic variability. According to Braun (1950), forests of the Smokies are within the Oak-Chestnut Forest Region of the Deciduous Forest Formation, with forests located in coves and lower north slopes related to the Mixed Mesophytic Association. Mixed mesophytic forests were widespread in the early Holocene, but they were restricted to favorable ravines and slope habitats in the mid-Holocene due to an increasingly warm climate. At this time oak-chestnut forests became dominant (Delcourt and Delcourt, 1980).

Several studies have described and analyzed in detail the vegetation types of the Smokies (Cain et al., 1937; Whittaker, 1956; Golden, 1974). Whittaker (1956) described fifteen vegetation types which were, with some exceptions, fully continuous with one another. At low elevations the sequence of types from mesic sites to xeric was: cove forest, northern red oak-pignut hickory forest, chestnut oak-chestnut forest, chestnut oak-chestnut heath, and pine forests. Low to middle elevation coves and lower slopes are occupied by cove hardwood forests, characterized by a mixture of species such as *Tsuga canadensis*, _Halesia carolina_, _Aesculus octandra_, _Tilia heterophylla_, _Acer saccharum_, _Betula allaghaniansis_, and _Fagus grandifolia_ (Cain, 1943; Whittaker, 1956). Forests of middle and low elevation slopes were dominated by _Quercus prinus_ and _Castanea dentata_ (Whittaker, 1956).

Original vegetation of the Smokies has been modified by several disturbance factors. The elimination of chestnut trees by the blight and yellow pines by the southern pine beetle (Kuykendall, 1978) have caused drastic recent changes in the composition of large forest stands. Areas of second-growth due to fires, set by man and by lightening, logging and cutting are extensive. However, since 1934 with the establishment of the Great Smoky Mountains National Park this large forest area has been protected from human disturbance.

CHAPTER IV

METHODS

Field Data Collection

Field work was conducted from July through September, 1980.

Sampling sites were selected using topographic maps and field reconnaissance. Criteria used for site selection were: (1) evidence (stumps, logs, or living sprouts) that chestnut had been abundant in the pre-blight composition of the forest; (2) that the sites showed no appreciable evidence of disturbance by cutting, fire, or other agents; and (3) that the sites allowed a wide distribution of plots among elevations, aspects, and topographic positions. An effort was made to locate the same sites or sites very similar to those studied by Woods and Shanks (1959).

Thirty-three sites were sampled using rectangular plots of 20 x 50m (0.1 ha), with the long side perpendicular to the slope. In addition five sites of reduced size, particularly in draw and ridge positions, were sampled using plots of 20 x 30m (0.06 ha), for a total of 38 plots.

In general, sampling procedures followed guidelines described by the Uplands Field Research Lab (1978) for the vegetation survey of the Great Smoky Mountains National Park. In each site, the central point of the 20-meter side of the left hand facing downhill was randomly located. From that point, plot corners were located and borders were marked with flagging tape. Twenty-three plots (20 x 50m) were permanently marked with metal stakes.

In each plot, all stems greater than 1cm in diameter at breast height (dbh) were tallied by species and their diameters were recorded. Diameters of chestnut stumps or logs were measured to the nearest 5cm. Cover estimates to the nearest 10% and species compositions were recorded for the shrub layer. Percent of canopy cover was estimated to the nearest 10%.

Taxonomic determination was made in the field when possible. Unknown or uncertain species were collected and later identified. Nomenclature follows that of Radford et al. (1968). Common names follow Shanks and Sharp (1963).

Slope angles were measured using a clinometer, from upper and lower edges to plot center. The two readings were averaged. Aspect was measured from plot center using a hand held compass. Elevation of each plot was measured with a pocket altimeter which was checked frequently against topographic landmarks. Location of each plot was recorded on U. S. Geological Survey 7.5 minute topographic maps.

Surface rock cover was estimated to the nearest 10%. Soil depth up to 85 cm was measured using a soil auger. If obstructions were encountered at less than 85 cm two additional probes were made, and measurements were averaged. Evidence of past disturbance, such as cut stumps or fire scars, was recorded.

Data Preparation

Chestnut diameters at breast height were estimated from stump diameters using equations developed by Vimmerstedt (1957).

Aspect was transformed following the method of Beers *et al*. (1966). This transformation resulted in a maximum value of 2.0 for northeast aspects and a minimum value of 0.0 for southwest aspects.

Microtopographic position was derived from topographic maps, as an index based on the distance of the plot to the nearest ridge divided by the total distance from slope base to ridge. A ridge position was 0%, and a draw position was 100%. The same procedure was used in relation to the predominant ridge and draw and was denominated macrotopographic position (Golden, 1974).

Data Analysis

Computer analysis was performed at The University of Tennessee Computer Center utilizing the IBM 360/65 and the DEC-10 computers.

Data were submitted to a computer program prepared by the Uplands Field Research Lab personnel. The program calculates absolute and relative densities and basal areas, and importance values [IV = (RD + RBA)/2] for each species on each plot. Modifications to this program were made in order to apply it to the 20 x 30m plots, and to get data consistent with the 20 x 50m plot data.

Forest types based upon tree species importance values were determined using a program written by Post and Shepherd (1974).

Descriptive statistics, and correlations among and between vegetation and environmental variables were calculated using programs of the Statistical Analysis System (SAS Institute 1979). Discriminant analysis was performed on both vegetation and environmental data through the program of the Statistical Package for the Social Sciences (SPSS) from Nie et al. (1975).

CHAPTER V

RESULTS AND DISCUSSION

General Site and Vegetation Characteristics of the Former Chestnut Forests

Evidence of chestnut occurrences were found on several topographic positions, from draws and protected slopes to xeric sites such as open slopes and ridges. The 38 sample plots were evenly distributed by elevation, 29% occurred between 2000 ft. and 2700 ft., 34% between 2700 ft. and 3400 ft., and 37% between 3400 ft. and 4000 ft. Chestnut was found on a wide range of aspects and slope angles, 57% of the samples had northerly aspects and 42% had southerly aspects. Slope angles varied from 5 to 83%, with an overall mean of 50%. Sixty-six percent of the plots had soils less than 85 cm deep.

Simple linear correlations among site variables are reported in Table 1. Micro and macrotopographic position of the plots were correlated as expected. Shallow soils were generally found on ridges, upper slopes or on draw positions. These sites were associated with rock outcroppings or colluvial material, specially on southern aspects. These observations explain the negative correlations between rock cover and soil depth, and transformed aspect.

Canopy cover varied from fairly closed on mesic sites to open on xeric slopes, accounting for the positive correlation between aspect and percent of canopy cover. A moderate to heavy shrub layer was common in most samples. The shrub layer was dominated mainly by *Rhododendron maximum* and/or *Kalmia latifolia*. Other shrub species found

Table 1. Correlations Among Site Variables[a]

	Microtopographic Position[b]	Aspect[c]	Soil Depth (cm)	Canopy Cover (%)
Macrotopographic Position[b]	0.65**			
Rock Cover (%)		-0.39*	-0.62**	
Canopy Cover (%)		0.38*		
Shrub Cover (%)	-0.34*			-0.51**

[a]Only correlations significant at P = 0.01** or P = 0.05* are reported.

[b]Relative position from ridge (0) to draw (100).

[c]Aspect transformed following the method of Beers et al. (1966).

frequently were Pyrularia pubera, Clethra acuminata and Vaccinium spp. The percent of cover of this shrub layer tended to decrease with proximity to draw positions and to increase in samples with an open canopy.

In general sites analyzed were characterized by small stems less than 40 cm in diameter, with scattered larger stems. Tree basal areas (stems greater than 10 cm dbh) per sample ranged from 12.4 to 45.2 m^2ha. Tree densities varied from 310 to 880 stems/ha.

The former abundance of chestnut was estimated from remaining stumps and logs. Chestnut tree basal areas varied from 9.4 to 41.5 m^2/ha. Living chestnut sprouts occurred at 21 plots.

A total of thirty-three tree species occurred in the samples studied (Table 2). Mesic species and those with intermediate moisture tolerance were most frequently associated with chestnut. Northern red oak (Quercus rubra), silverbell (Halesia carolina), Fraser magnolia (Magnolia fraseri), and hemlock (Tsuga canadensis) were characteristic species under mesic conditions. In intermediate to dry slopes, sourwood (Oxydendron arboreum), chestnut oak (Quercus prinus), and black locust (Robinia pseudoacacia) were common chestnut associates. Red maple (Acer rubrum) was a constant associate of chestnut in almost all plots studied. Combinations of these tree species were common everywhere. This great variety of species associations indicates that chestnut had a very wide ecological amplitude in the Smokies. In general, a similar array of chestnut-associated species was reported by Woods and Shanks (1959), although they found a higher frequency of mesic species.

Correlation among importance values of species which occur with 45% or greater frequency and between those and the site variables were

Table 2. Frequency of Tree Species in 38 Plots Containing Chestnut

Species	Frequency (%)
Acer rubrum	97
Quercus rubra	82
Oxydendrum arboreum	76
Quercus prinus	74
Betula lenta	61
Halesia carolina	53
Magnolia fraseri	53
Robinia pseudoacacia	53
Nyssa sylvatica	50
Tsuga canadensis	45
Acer pensylvanicum	34
Liriodendron tulipifera	29
Acer saccharum	26
Amelanchier laevis	26
Quercus velutina	26
Carya glabra	21
C. tomentosa	18
Quercus coccinea	18
Cornus florida	16
Pinus rigida	16
Magnolia acuminata	13
Quercus alba	13
Ostrya virginiana	11
Sassafras albidum	8
Tilia heterophylla	8
Castanea dentata	5
Pinus strobus	5
Aesculus octandra	3
Fagus grandifolia	3
Fraxinus americana	3
Hamamelis virginiana	3
Ilex opaca	3
Prunus serotina	3

calculated (Table 3). Silverbell was positively correlated with Fraser magnolia. Both species were characteristic of the most mesic sites and sites with a closed forest canopy. Chestnut oak importance value was negatively correlated with the importance value of silverbell. Chestnut oak is considered a subxeric species (Whittaker, 1956), which occurs mainly on middle and upper slope positions. The importance value of this species decreased with elevation. Golden (1974) observed a similar trend in chestnut oak basal area. The importance value of red maple decreased with an increase of slope angle. Steep slopes were generally dominated by chestnut oak and northern red oak.

Small trees formed dense understories in most former chestnut forests, mainly in submesic to subxeric conditions. Black locust was positively correlated with sweet birch. These species were reported by Woods and Shanks (1959) as abundant in the large openings created by the death of chestnut. Sourwood was positively correlated with black gum (*Nyssa sylvatica*). Both species are subxeric trees (Whittaker, 1956) that are associated with xeric slopes. This relation was also reported by DeYoung (1979) in white pine-hardwood types of the Smokies.

Basal area of chestnut stumps increased with elevation. Wood and Shanks (1959) reported that chestnut was persisting at higher elevations with much greater tenacity than at low altitudes. Large chestnut logs and extant stumps were common at higher elevations, mainly near Mt. Sterling Gap.

Tree composition data of each sample plot were averaged to obtain an overall present composition of former chestnut forests (Table 4). Species with the highest mean importance values were red maple, chestnut oak, northern red oak, silverbell, and sourwood. These five tree species

Table 3. Correlations Among Species, and Between Species and Site Variables[a]

	Halesia carolina[b]	*Oxydendrum arboreum*	*Robinia pseudoacacia*	Elevation	Slope Angle (%)	Microtopographic Position[c]	Canopy Cover (%)	Shrub Cover (%)
Acer rubrum					-0.41			
Betula lenta			0.46					
Halesia carolina							0.41	-0.56
Magnolia fraseri	0.48							
Nyssa sylvatica		0.47						
Quercus prinus	-0.49			-0.45		-0.48		
Chestnut stumps[d]				0.44				

[a]Only correlations significant at P = 0.01 are reported.

[b]Species importance values were utilized as vegetation variables.

[c]Relative position from ridge (0) to draw (100).

[d]Basal area.

Table 4. Present Average Composition of the Former Chestnut Forests (N = 38)[a]

Species	Trees[b] Importance Value	Trees[b] Relative Basal Area	Trees[b] Relative Density	Saplings[c] Relative Density	Subsaplings[d] Relative Density
Acer rubrum	21.5	18.5 ± 1.9[e]	24.5 ± 2.2[e]	25.7	10.1
Quercus prinus	17.0	20.6 ± 3.5	13.4 ± 2.5	2.0	1.9
Q. rubra	11.8	15.8 ± 3.0	7.9 ± 1.2	1.0	P
Halesia carolina	7.7	6.5 ± 2.0	9.0 ± 2.3	3.6	10.4
Oxydendrum arboreum	6.9	4.7 ± 0.7	9.2 ± 1.3	6.9	5.7
Tsuga canadensis	3.9	2.9 ± 1.1	4.9 ± 1.7	14.3	13.2
Betula lenta	3.9	3.4 ± 1.0	4.4 ± 1.1	1.4	P
Magnolia fraseri	3.1	2.8 ± 0.9	3.4 ± 0.8	3.4	3.9
Pinus rigida	2.6	3.1 ± 1.5	2.2 ± 1.1	P	-
Nyssa sylvatica	2.6	3.0 ± 1.1	2.1 ± 0.5	5.9	4.8
Liriodendron tulipifera	2.5	3.0 ± 1.3	2.0 ± 0.9	P	1.3
Robinia pseudoacacia	2.2	2.2 ± 0.5	2.3 ± 0.6	P	P
Carya glabra	1.9	2.6 ± 1.2	1.2 ± 0.6	P	P
Quercus velutina	1.8	2.5 ± 1.0	1.2 ± 0.4	P	P
Acer pensylvanicum	1.6	P	2.4 ± 1.0	5.6	10.7
Quercus alba	1.3	1.8 ± 1.3	P	P	P
Acer saccharum	1.1	1.0 ± 0.5	1.2 ± 0.4	5.3	5.3
Pinus strobus	1.0	1.1 ± 1.1	P	P	P
Carya tomentosa	P	P	1.1 ± 0.4	P	P
Cornus florida	P	P	1.2 ± 0.7	6.5	5.9
Fagus grandifolia	P	P	1.2 ± 1.2	P	P
Hamamelis virginiana	P	P	P	6.3	10.2
Ostrya virginiana	P	P	P	2.0	P
Amelanchier laevis	P	P	P	1.5	1.4
Castanea dentata	P	P	P	P	5.8

[a]All species which reached more than 1% in any parameter reported. Data are mean values.

[b]Stems greater than 10 cm. dbh.

[c]Stems 3-9 cm. dbh.

[d]Stems less than 2 cm. dbh.

[e]Standard error.

P = Present but less than 1%.

made up over 60% of the mean basal area and density. In the sapling (3-9 cm dbh) and subsapling (less than 2 cm dbh) categories, the most abundant species with possibilities of becoming canopy trees were red maple, hemlock, sourwood, silverbell, sugar maple (Acer saccharum), and black gum.

Overall species composition includes aggregation of vegetation data from sites with different environments, and consequently vegetation patterns on sites with similar environmental conditions are concealed. In order to determine how the chestnut replacement species were related under similar environmental conditions, sample plots were divided into two categories using the gradient index derived by Golden (1974). This index placed each plot along a moisture gradient scale on the basis of slope position (microtopographic position), slope azimuth and slope angle. According to this index, sample plots placed on draw position, and those on lower and protected slopes were categorized as mesic (mesic to submesic). Plots mainly located on southerly exposure, and on middle slope to ridge were classified as xeric (subxeric to xeric).

Eighteen tree species with mean importance values over 1% were found on mesic sites (Table 5). Three species shared the highest mean importance values. They were red maple, northern red oak, and silverbell. Other important species were chestnut oak, hemlock, and sourwood. Red maple was important on the basis of its high density, while less abundant northern red oak reached the highest dominance in terms of basal area. The most important species were well represented in sapling and subsapling stems, with the exception of chestnut oak and northern red oak.

On xeric sites, thirteen species reached over 1% in mean importance value (Table 6). Chestnut oak and red maple were the leading

Table 5. Composition of the Former Chestnut Forests on Mesic Plots (N = 23)[a]

Species	Trees[b]			Saplings[c]	Subsaplings[d]
	Importance Value	Relative Basal Area	Relative Density	Relative Density	Relative Density
Acer rubrum	21.5	19.3 ± 2.8[e]	23.8 ± 3.4[e]	16.3	5.4
Quercus rubra	14.2	20.1 ± 4.4	8.3 ± 1.6	1.0	P
Halesia carolina	12.2	10.4 ± 3.1	14.1 ± 3.3	5.6	15.0
Quercus prinus	7.9	9.7 ± 2.6	6.1 ± 1.5	P	P
Tsuga canadensis	5.8	4.3 ± 1.8	7.4 ± 2.6	20.5	16.3
Oxydendrum arboreum	5.3	3.5 ± 0.8	7.0 ± 1.6	5.3	3.7
Betula lenta	4.3	3.9 ± 1.2	4.8 ± 1.3	1.5	P
Magnolia fraseri	4.0	3.8 ± 1.4	4.2 ± 1.2	4.3	5.3
Liriodendron tulipifera	3.9	4.7 ± 2.0	3.1 ± 1.5	P	1.8
Carya glabra	2.7	3.7 ± 1.9	1.8 ± 1.0	P	P
Acer pensylvanicum	2.5	1.4 ± 0.6	3.6 ± 1.6	6.8	12.7
Nyssa sylvatica	2.5	3.2 ± 1.6	1.8 ± 0.7	2.3	P
Robinia pseudoacacia	1.9	1.9 ± 0.5	1.9 ± 0.5	P	P
Acer saccharum	1.7	1.6 ± 0.8	1.9 ± 0.6	8.2	8.4
Quercus alba	1.6	2.2 ± 2.0	P	P	P
Q. velutina	1.5	2.4 ± 1.5	0.8 ± 0.4	P	P
Fagus grandifolia	1.4	P	2.0 ± 2.0	1.0	P
Cornus florida	1.1	0.5 ± 0.3	1.8 ± 1.2	8.6	7.5
Oxtrya virginiana	P	P	1.2 ± 1.0	3.3	1.4
Hamamelis virginiana	P	P	P	7.6	9.2
Amelanchier laevis	P	P	P	1.5	P
Castanea dentata	P	P	P	P	3.9
Tilia heterophylla	P	P	P	P	1.3

[a]All species which reached more than 1% in any parameter reported. Data are mean values.

[b]Stems greater than 10 cm. dbh.

[c]Stems 3-9 cm. dbh.

[d]Stems less than 2 cm. dbh.

[e]Standard error.

P = Present but less than 1%.

Table 6. Composition of the Former Chestnut Forests on Xeric Plots (N = 15)[a]

Species	Trees[b] Importance Value	Trees[b] Relative Basal Area	Trees[b] Relative Density	Saplings[c] Relative Density	Subsaplings[d] Relative Density
Quercus prinus	31.0	37.2 ± 5.8[e]	24.8 ± 4.8[e]	4.6	4.4
Acer rubrum	21.4	17.3 ± 2.2	25.6 ± 1.9	40.2	17.4
Oxydendrum arboreum	9.5	6.6 ± 1.3	12.4 ± 2.2	9.4	8.8
Quercus rubra	8.2	9.2 ± 2.6	7.3 ± 1.9	P	P
Pinus rigida	6.6	7.7 ± 3.7	5.5 ± 2.6	P	-
Betula lenta	3.2	2.6 ± 1.8	3.8 ± 2.1	1.2	1.3
Robinia pseudoacacia	2.8	2.6 ± 1.2	3.1 ± 1.2	1.3	P
Nyssa sylvatica	2.7	2.8 ± 1.3	2.5 ± 0.6	11.3	10.8
Pinus strobus	2.6	2.9 ± 2.8	2.4 ± 2.2	P	P
Quercus velutina	2.2	2.7 ± 1.4	1.7 ± 0.7	1.2	1.0
Q. coccinea	1.9	2.2 ± 0.8	1.7 ± 0.6	P	-
Magnolia fraseri	1.8	1.2 ± 0.7	2.3 ± 1.2	2.0	1.7
Carya tomentosa	1.2	P	1.7 ± 0.9	1.0	P
Tsuga canadensis	P	P	1.2 ± 0.5	4.8	8.5
Quercus alba	P	1.2 ± 0.8	P	P	P
Halesia carolina	P	P	1.1 0.6	P	3.4
Acer pensylvanicum	P	P	P	3.8	7.6
Cornus florida	P	P	P	3.2	3.5
Amelanchier laevis	P	P	P	1.5	2.7
Castanea dentata	P	P	P	1.1	8.8
Carya glabra	P	P	P	1.1	P
Sassafras albidum	P	P	P	P	1.2

[a]All species which reached more than 1% in any parameter reported. Data are mean values.

[b]Stems greater than 10 cm. dbh.

[c]Stems 3-9 cm. dbh.

[d]Stems less than 2 cm. dbh.

[e]Standard error.

P = Present but less than 1%.

dominant species in terms of mean importance value, basal area and density. Other species achieving high mean importance values were sourwood, northern red oak, and pitch pine (Pinus rigida). Red maple made up over 50% of the mean sapling density. Northern red oak and pitch pine reached less than 1% of the mean relative density of saplings and subsaplings. The latter species was not represented in the subsapling category.

Live chestnut sprouts occurred in 52% of the plots considered as mesic, while they occurred in 60% of the xeric samples. Two species represented only on mesophitic sites were beech (Fagus grandifolia), hop horbeam (Ostrya virginiana). Scarlet oak (Quercus coccinea) and pinus species occur only on xeric sites.

Among the more important species, only red maple and sweet birch did not show noticeable differences in importance with respect to moisture conditions. Chestnut oak and sourwood were more important under xeric conditions. Pitch pine was a common chestnut associate under driest conditions. Northern red oak and other mesic species such as silverbell, hemlock, Fraser magnolia, and tulip poplar (Liriodendron tulipifera) were more important under favorable moisture conditions.

Replacement Forest Types

Analysis of plant communities has been one of the major objectives of plant ecology. Two main approaches have been proposed to conceive and interpret species associations and their distribution. One approach is to consider vegetation as composed of discrete and recognizable units susceptible to classification (Clements, 1936; Daubenmire, 1966). Another trend considers vegetation as a continuum population pattern along environmental gradients (Whittaker, 1956; McIntosh, 1967). It has been suggested that classification and gradient analysis are not antagonistic, but complementary approaches (Goodall, 1963; Whittaker, 1966).

In recent years, numerical techniques have increasingly been used in vegetation classification. In the Great Smoky Mountains National Park, Golden (1974) applied Orloci's (1967) clustering procedure to segregate and classify plant communities. The same technique was used by Kuykendall (1978) to determine replacement types on beetle-killed pine stands, and by DeYoung (1979) to identify white pine-hardwood types in the Smokies.

The present study used Orloci's (1967) hierarchical agglomerative clustering technique to determine replacement forest types formerly dominated by chestnut. In the agglomerative method, each sample is initially considered a separate group, each group is compared on the basis of all its attributes (species importance values). During each clustering cycle, pairs of groups with the smallest within-group dispersion are joined. This process continues until the whole set of samples is combined into a single group. The ultimate objective is to minimize the variance within groups and maximize that between groups (Goodall, 1978).

Importance values of tree species, which occurred in at least 5% of the total sample, were used in the cluster analysis. Cluster groups are represented in a hierarchical diagram or dendogram (Figure 2). The vertical axis represents within-group dispersion expressed as a percentage of total dispersion. Numbers at the base of the diagram represent the number of sample plots included in each group at the 20% dispersion level.

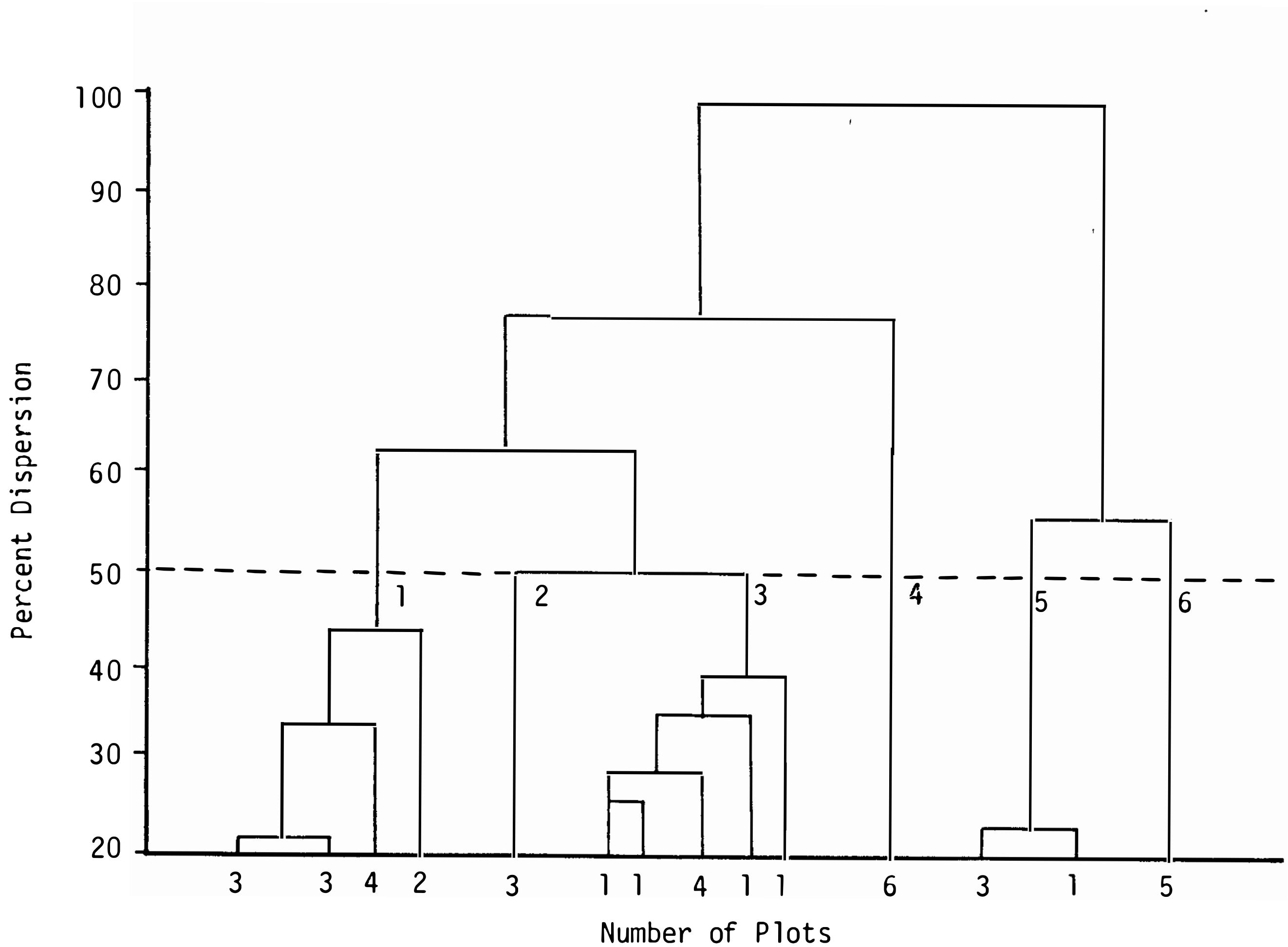

Figure 2. Classification Dendogram.

Key: 1 = red maple-oaks; 2 = hemlock-hardwood; 3 = red maple-sourwood; 4 = chestnut oak, 5 = silverbell-red maple; 6 = northern red oak-silverbell.

Cluster analysis provided an objective grouping of sample plots but the dispersion level at which to select the number of types was subjectively chosen. A 50% dispersion level was considered most consistent with the field observations to determine the major chestnut replacement patterns on the study area. Replacement forest types identified are red maple-oak, hemlock-hardwood, red maple-sourwood, chestnut oak, silverbell-red maple, and northern red oak-silverbell. As replacement types, these are successional stages and should not be considered as stable communities.

After determining replacement forest types, summary statistics were calculated for each type. Discussion of each type is given below generally in sequence from most mesic to most xeric. Composition of tree, sapling and subsapling categories of each type is given in the tables included within the discussion. Environmental variables for these types appear in the Appendix.

Silverbell-Red Maple Forest

The silverbell-red maple replacement forest occurs on mesic sites from cove to protected middle slopes, mainly on north aspects. Elevations range from 2950 to 3600 ft., with slope angles from 42 to 83%. Soil depths vary from 63 to 85cm, and have an average of 5% of rock cover (Appendix).

Sample plots consist of fairly closed canopies predominantly of trees less than 40cm in diameter with occasional larger trees. Tree basal areas range from 21 to 32 m^2/ha, averaging 27 m^2/ha. Tree densities vary from 340 to 880 stems/ha, averaging 600 stems/ha. A total of 10 species reach a mean importance value over 1% (Table 7). Silverbell

Table 7. Composition of the Silverbell-Red Maple Forest (N = 4)[a]

Species	Trees[b] Importance Value	Trees[b] Relative Basal Area	Trees[b] Relative Density	Saplings[c] Relative Density	Subsaplings[d] Relative Density
Halesia carolina	34.6	37.9 ± 6.0[e]	31.3 ± 3.7[e]	3.9	9.1
Acer rubrum	16.8	18.9 ± 6.9	14.7 ± 4.5	3.9	P
Magnolia fraseri	13.0	14.2 ± 5.4	11.8 ± 4.0	7.3	8.1
Tsuga canadensis	9.9	5.4 ± 3.2	14.5 ± 9.4	30.2	17.3
Acer pensylvanicum	8.1	4.6 ± 2.9	11.5 ± 8.4	23.8	25.1
Acer saccharum	5.4	6.2 ± 4.2	4.6 ± 2.6	15.5	25.6
Betula lenta	3.8	4.7 ± 2.0	2.8 ± 1.5	1.2	-
Robinia pseudoacacia	2.8	2.9 ± 1.0	2.7 ± 1.8	-	-
Quercus rubra	1.1	1.0 ± 0.8	1.1 ± 0.7	1.2	P
Tilia heterophylla	1.0	1.3 ± 1.3	P	-	5.7
Sassafras albidum	P	P	1.1 ± 1.1	-	-
Ostrya virginiana	P	P	P	5.7	-
Hamamelis virginiana	-	-	-	6.8	3.1
Aesculus octandra	-	-	-	P	3.9
Density (stems/ha)			600	815	932
Basal Area (m^2/ha)		26.6			
Chestnut Stump Density (Stems/ha)			202		
Chestnut Stump Basal Area (m^2/ha)		28.7			

[a]All species which reached more than 1% in any parameter reported. Data are mean values.

[b]Stems greater than 10 cm. dbh.

[c]Stems 3-9 cm. dbh.

[d]Stems less than 2 cm. dbh.

[e]Standard error.

P = Present but less than 1%.

has the highest mean importance value, relative basal area, and relative density. This species is dominant in three of the plots analyzed, and shares dominance with red maple in one plot. Red maple mixed with mesophitic species such as Fraser magnolia, hemlock, and sugar maple (Acer saccharum) is codominant in most sample sites. Besides silverbell and red maple tree species that occur with frequency of at least 75% were Fraser magnolia, striped maple (Acer pensylvanicum), sweet birch, and black locust (Robina pseudoacacia).

Sapling and subsapling stems with high mean relative density values are hemlock, striped maple, sugar maple, and Fraser magnolia. These species, except for Fraser magnolia, together with silverbell and red maple occur as reproductive stems in all samples studied. Red maple makes up less than 1% of the mean subsapling density. Black locust does not occur in the reproductive categories and sweet birch is present only as sapling stems.

The shrub layer varies from 10 to 40% in cover. Rhododendron maximum is the dominant species on sites with moderate shrub cover. Other present shrubs are Clethra acuminata, Hydrangea arborescens, and Pyrularia pubera. Evidence of fire scars was observed in only one plot.

Basal area of chestnut stumps varies from 22 to 41 m^2/ha, averaging 28 m^2/ha. Chestnut stump density averages 202 stems/ha. The sample plot with the highest chestnut stump basal area occurs on a middle northern slope at 3300 ft. elevation. This plot has the highest tree density (880 stems/ha) of all 38 samples studied. Numerous chestnut logs and standing snags are still present. Individuals of red maple are the larger trees (>35cm dbh). Smaller trees are those of red maple, silverbell, Fraser magnolia, and hemlock in order of basal area. Hemlock makes up over 50% of the sapling density and shares dominance with sugar maple in the subsapling layer. Silverbell and Fraser magnolia are also important in the reproductive categories. In this plot chestnut was initially replaced by red maple and mesic species including silverbell and Fraser magnolia. Under these established trees, hemlock has developed because of its high shade tolerance (Fowells, 1965) and eventually will dominate other species. This pattern is similar in the other plots grouped in this replacement forest type. These observations and comparison of densities in the different diametric categories suggests that the silverbell-red maple replacement forest will likely become a hemlock-hardwood forest.

Forest types dominated or codominated by silverbell are very uncommon in the Smokies and elsewhere. Only one study (Golden, 1974) has described a silverbell-hemlock forest type in the central part of the Smokies. Red maple was also present. Minor evidences of former chestnut presence was observed in this forest type. Golden (1974) also described a community type dominated by red maple and sweet birch. The author considered this community as the most mesic chestnut replacement type and suggested that eventually it will be dominated by hemlock. In general, environmental conditions and vegetation composition of this type were similar to those described for the silverbell-red maple forest identified in the present study. However, in this study mesic species such as silverbell and Fraser magnolia are more important than sweet birch. Sweet birch is considered intolerant or of intermediate tolerance (Fowells, 1965), being favored only initially after the elimination of chestnut. Its reproduction is limited under an established canopy.

Hemlock-Hardwood Forest

Sample plots dominated by hemlock and a mixture of hardwoods occurred from 2550 to 4000 ft., on protected middle and lower slope positions. This forest type occurs on north and west aspects, on moderate to steep slopes. Soils are deep and no surface rock is exposed (Appendix).

The hemlock-hardwood replacement forest consists of small (<40cm) canopy trees with scattered larger trees. Canopy cover is moderate to fairly closed. Shrub layer varies from 40 to 70% in cover, dominated mainly by *Rhododendron maximum*. Tree basal areas range from 26 to 33 m^2/ha, averaging 29 m^2/ha. Tree densities vary from 680 to 780 stems/ha. Twelve species reach over 1% of the mean importance value (Table 8). Hemlock has the highest mean importance value. This species is dominant, in terms of importance value, in two of the sites and shares dominance with sweet birch and small trees of beech (*Fagus grandifolia*) at 4000 ft. altitude. The species that occur in all sample plots are hemlock, red maple, sweet birch, sourwood, Fraser magnolia, and silver-bell. Importance of red maple is due mainly to scattered large trees.

Sapling and subsapling mean relative densities are dominated by hemlock. This species makes up over 40% of the density of the reproductive categories in all samples studied. Witch hazel (*Hamamelis virginiana*) is abundant as subsapling stems. Important canopy species absent in the subsapling category are sweet birch, oak species, tulip poplar, and black gum (*Nyssa sylvatica*).

Chestnut stump basal areas vary from 24 to 29 m^2/ha, with an average of 27 m^2/ha. Chestnut stump density average 220 stems/ha.

Table 8. Composition of the Hemlock-Hardwood Forest (N = 3)[a]

Species	Trees[b] Importance Value	Trees[b] Relative Basal Area	Trees[b] Relative Density	Saplings[c] Relative Density	Subsaplings[d] Relative Density
Tsuga canadensis	25.2	22.5 ± 7.5[e]	27.9 ± 8.0[e]	50.2	50.4
Acer rubrum	12.4	15.7 ± 3.7	9.1 ± 1.6	10.3	1.0
Fagus grandifolia	10.5	5.9 ± 5.9	15.2 ± 15.2	6.7	5.7
Betula lenta	10.4	11.2 ± 7.5	9.6 ± 3.4	1.5	-
Quercus prinus	8.7	11.5 ± 5.9	5.9 ± 3.6	P	-
Oxydendrum arboreum	7.1	7.1 ± 3.2	7.1 ± 2.8	4.8	P
Magnolia fraseri	5.9	5.6 ± 2.7	6.1 ± 2.5	4.6	9.3
Halesia carolina	5.1	5.3 ± 1.9	4.9 ± 2.0	P	6.7
Quercus rubra	5.0	7.4 ± 5.4	2.6 ± 1.9	P	-
Liriodendron tulipifera	4.3	4.4 ± 4.4	4.3 ± 4.3	P	-
Nyssa sylvatica	1.4	1.0 ± 0.5	1.8 ± 0.9	1.2	-
Acer pensylvanicum	1.0	P	1.5 ± 1.5	1.2	P
Hamamelis virginiana	P	P	P	7.9	20.2
Amelanchier laevis	P	P	P	2.5	-
Ilex opaca	P	P	P	1.2	-
Acer saccharum	P	P	P	P	3.6
Ilex montana	-	-	-	3.6	-
Density (stems/ha)			727	863	383
Basal Area (m^2/ha)		29.0			
Chestnut Stump Density (Stems/ha)			220		
Chestnut Stump Basal Area (m^2/ha)		27.1			

[a]All species which reached more than 1% in any parameter reported. Data are mean values.

[b]Stems greater than 10 cm. dbh.

[c]Stems 3-9 cm. dbh.

[d]Stems less than 2 cm. dbh.

[e]Standard error.

P = Present but less than 1%.

The plot with the highest chestnut stump basal area is dominated in terms of importance value, basal area, and density by hemlock. Red maple and chestnut oak, with a few individuals, are also important in terms of basal area. Hemlock is dominant in the reproductive categories. Evidence of fire scars and cut chestnut stumps were observed in this plot.

Of this replacement forest type, red maple, sweet birch, and oaks seem to have been initially favored with the death of chestnut. Mesophytic species, especially hemlock, have subsequently become established and form a dense layer of small stems. Because of the high reproduction of hemlock in all samples grouped as hemlock-hardwood forest, and given its high degree of tolerance (Fowells, 1965), this species should eventually totally dominate this forest type. Species such as red maple, Fraser magnolia, and silverbell will likely be important associated species.

Wood and Shanks (1959) reported a shift from pure chestnut stands to hemlock. The authors also observed several intermediate successional stages from chestnut to hemlock, which included chestnut oak-red maple and hemlock-hardwood. These two intermediate stages are consistent with the replacement patterns observed on the sites analyzed in the present study.

Northern Red Oak-Silverbell Forest

The northern red oak-silverbell replacement forest type occurs from 3500 to 4000 ft., on middle to upper northern slopes and on lower slopes of southeast aspect. Slope angles range from 39 to 58%, and deep soils with absent surface rock are typical. A sample plot located on an upper slope has soils as deep as 58cm (Appendix).

Sample plots are characterized by small trees with frequently scattered larger trees (>60cm dbh) mainly of northern red oak. Canopy cover varies from 50 to 70%. Tree basal areas range from 30 to 45 m^2/ha with tree densities varying from 310 to 540 stems/ha. Mean basal area (36 m^2/ha) and mean density (460 stems/ha) are higher and lower respectively than in any of the other forest types. A heavy shrup layer dominated by Rhododendrum maximum occurs only in one sample plot. Other shrub species present in this forest type are Lyonia ligustrina and Rhododendrum calendulaceum.

Fourteen species achieve over 1% of the mean importance value (Table 9). Northern red oak makes up over 50% of the mean basal area. This species together with silverbell and red maple make up over 65% of the mean density. Northern red oak accounts for over 40% of the basal area of all plots grouped in this forest type. Silverbell and red maple occur abundantly as small trees. Other important trees that occur with frequencies of at least 60% are sweet birch, hop hornbeam (Ostrya virginiana), hemlock, cucumber tree (Magnolia acuminata), Fraser magnolia, chestnut oak, and sugar maple. Pignut hickory (Carya glabra) is present as a large tree (119cm dbh) in a single sample.

Sapling and subsapling stems with high mean relative density values are sugar maple, silverbell, hemlock, and hop hornbeam. These species together with northern red oak, red maple, sweet birch, cucumber tree, and striped maple occur as reproductive stems in at least 80% of the sample plots. Tulip poplar and black oak (Quercus velutina) are not

Table 9. Composition of the Northern Red Oak-Silverbell Forest (N = 5)[a]

Species	Trees[b] Importance Value	Trees[b] Relative Basal Area	Trees[b] Relative Density	Saplings[c] Relative Density	Subsaplings[d] Relative Density
Quercus rubra	34.0	52.4 ± 6.0[e]	15.6 ± 2.1[e]	1.4	1.5
Halesia carolina	21.9	11.7 ± 3.1	32.2 ± 5.8	15.0	34.0
Acer rubrum	16.2	13.5 ± 5.8	18.8 ± 5.4	6.9	6.3
Betula lenta	5.9	3.2 ± 1.8	8.6 ± 5.0	4.5	P
Ostrya virginiana	3.2	1.4 ± 0.7	4.9 ± 2.3	10.7	6.6
Tsuga canadensis	2.7	1.7 ± 1.0	3.7 ± 1.6	12.7	5.0
Carya glabra	2.7	4.9 ± 4.9	P	P	P
Magnolia acuminata	2.2	2.1 ± 1.1	2.4 ± 1.4	P	3.3
Magnolia fraseri	2.0	1.5 ± 1.0	2.6 ± 1.6	1.0	1.0
Quercus prinus	1.6	2.0 ± 0.8	1.2 ± 0.5	-	P
Acer saccharum	1.4	P	2.4 ± 1.2	21.5	14.3
A. pensylvanicum	1.4	P	2.3 ± 1.2	3.1	6.7
Robinia pseudoacacia	1.1	1.1 ± 0.9	1.1 ± 0.7	P	-
Liriodendron tulipifera	1.1	1.4 ± 1.0	P	-	-
Quercus velutina	P	1.4 ± 1.4	P	-	-
Fraxinus americana	P	P	P	4.2	2.3
Amelanchier laevis	P	P	P	2.3	2.3
Hamamelis virginiana	-	-	-	11.3	6.5
Tilia heterophylla	-	-	-	1.5	P
Castanea dentata	-	-	-	P	5.0
Ilex montana	-	-	-	P	1.0
Density (Stems/ha)			460	646	1264
Basal Area (m^2/ha)		35.9			
Chestnut Stump Density (Stems/ha)			180		
Chestnut Stump Basal Area (m^2/ha)		28.0			

[a]All species which reached more than 1% in any parameter reported. Data are mean values.

[b]Stems greater than 10 cm. dbh.

[c]Stems 3-9 cm. dbh.

[d]Stems less than 2 cm. dbh.

[e]Standard error.

P = Present but less than 1%.

represented in the reproductive categories. Chestnut oak and black locust do not occur in the sapling and subsapling categories, respectively.

Live chestnut sprouts occur in 80% of the sample plots. Chestnut stump basal areas vary from 20 to 39 m^2/ha, averaging 29 m^2/ha. Chestnut stump densities range from 100 to 220 stems/ha, averaging 180 stems/ha. The plot with highest chestnut stump basal area and density occurs at 4000 ft. altitude. Here, northern red oak and a single individual of pignut hickory are the largest trees (>55cm dbh). Smaller trees of silverbell and sweet birch are abundant and make up over 70% of the total density. Reproductive categories are dominated by sugar maple and silverbell. It would appear that at this plot northern red oak, formerly codominant with chestnut, increased its crown with the death of the chestnuts, but the larger openings left by chestnut were filled by silverbell and sweet birch. This pattern is similar in the other plots grouped in this forest type, although in some of them the chestnut gaps were filled by red maple more than sweet birch. Reproduction of northern red oak is low but it is present in 80% of the sample plots. This will likely guarantee its replacement. The high frequency and abundance of silverbell and red maple suggests that these species will continue as a part of the composition of this forest type.

In the central portion of the Smokies, Whittaker (1956) observed that submesic trees and _Halesia monticola_ were taking advantage of the death of the chestnut on stands dominated by northern red oak and chestnut. Golden (1974) reported red maple and silverbell as northern red oak associated species on stands with some evidence of previous chestnut occurrence.

Chestnut Oak Forest

Sample plots dominated by chestnut oak occur from 2300 to 3000 ft., mainly on middle and upper slopes, with west to east aspects. Slope angles vary from 25 to 75%. Most sample plots have soils deeper than 50cm with few or no surface rocks. Shallow soils with moderate rock cover occurred on upper slope positions (Appendix).

The chestnut oak replacement forest consists predominantly of small trees (<40cm). Canopy cover is generally open. Tree basal areas range from 18 to 31 m^2/ha, averaging 25 m^2/ha. Tree densities vary from 580 to 780 stems/ha, averaging 662 stems/ha. Most sample plots have a moderate to heavy shrub layer, dominated by *Kalmia latifolia* and/or *Rhododendron maximum*. Other frequent shrubs are *Rhododendron calendulaceum*, *Clethra acuminata*, *Pyrularia pubera*, and *Vaccinium spp*. Evidence of fire scars was observed on two of the sample plots.

Eight species achieve over 1% of the mean importance value (Table 10). Chestnut oak is the leading dominant. This species makes up over 55% of the basal area and over 40% of the density on most of the sample plots. Red maple and sourwood occur as small trees in all plots studied. Other important species that occur with frequencies of at least 66% are northern red oak, black gum, and Fraser magnolia.

Sapling and subsapling densities are dominated by red maple and sourwood. These species together with black gum occur as reproductive stems in all plots analyzed. Reproduction of chestnut oak is absent in only one plot, but it is only present as both sapling and subsapling stems in two plots. Other species that occur as reproductive stems in more than 66% of the samples are Fraser magnolia, silverbell, hemlock,

Table 10. Composition of the Chestnut Oak Forest (N = 6)[a]

Species	Trees[b]			Saplings[c]	Subsaplings[d]
	Importance Value	Relative Basal Area	Relative Density	Relative Density	Relative Density
Quercus prinus	50.6	56.7 ± 4.5[e]	44.6 ± 3.4[e]	2.0	1.5
Acer rubrum	17.3	13.7 ± 3.0	21.0 ± 1.7	53.0	23.0
Quercus rubra	13.2	14.9 ± 4.9	11.6 ± 3.7	P	P
Oxydendrum arboreum	8.8	5.6 ± 1.7	12.0 ± 3.0	11.8	11.6
Nyssa sylvatica	3.2	3.9 ± 2.8	2.4 ± 1.0	9.7	9.7
Magnolia fraseri	1.7	1.0 ± 0.6	2.4 ± 0.9	3.3	3.2
Halesia carolina	1.3	P	1.7 ± 1.2	1.1	8.1
Pinus rigida	1.1	1.7 ± 1.7	0.6 ± 0.6	P	-
Acer pensylvanicum	P	P	P	8.1	14.5
Tsuga canadensis	P	P	P	5.1	9.9
Cornus florida	P	P	P	1.4	1.1
Sassafras albidum	P	P	P	P	1.6
Amelanchier laevis	P	P	P	P	1.1
Hamamelis virginiana	-	-	-	2.6	13.5
Density (Stems/ha)			662	938	910
Basal Area (m^2/ha)		24.9			
Chestnut Stump Density (Stems/ha)			165		
Chestnut Stump Basal Area (m^2/ha)		18.9			

[a]All species which reached more than 1% in any parameter reported. Data are mean values.

[b]Stem greater than 10 cm. dbh.

[c]Stems 3-9 cm. dbh.

[d]Stems less than 2 cm. dbh.

[e]Standard error.

P = Present but less than 1%.

flowering dogwood (Cornus florida), service berry (Amelanchier laevis), and witch hazel. Reproduction of northern red oak is absent or of low density in most sample plots.

Chestnut stump basal areas vary from 9 to 23 m^2/ha, averaging 19 m^2/ha. Chestnut stump densities range from 100 to 300 stems/ha, averaging 165 stems/ha. Live chestnut sprouts occur in 66% of the samples, but they occur as subsapling stems only in two plots. In general, all plots grouped in this forest type have similar chestnut replacement patterns whether or not chestnut was formerly more important than chestnut oak. Chestnut oak has been occupying the place left by the dead chestnuts. Although its reproduction is low this species should remain as dominant. Red maple has also been favored by the elimination of chestnut and because of its great abundance it may increase in importance.

Golden (1974) described a chestnut oak community type in the central portion of the smokies. In that forest the second most important species was also red maple, which had a much higher frequency and relative density in the sapling category than chestnut oak.

Red Maple-Oak Forest

Sample plots grouped as red maple-oak replacement forest occur from 2000 to 3800 ft. This forest type occurs on flat to upper slope positions on north to east aspects, on middle to lower slopes with west aspects and on middle to upper southern slopes. Slope angles vary from 5 to 64%, and angles of 45% were commonplace. Most plots have deep soils with no surface rock. Plots with rocky surface occur on flat and upper slope positions (Appendix).

In general sample plots consist of trees less than 40cm in diameter with frequent larger trees. Canopy cover varies from open on xeric south-facing slopes to fairly closed on lower north-facing slopes. Tree basal areas vary from 12 to 34 m^2/ha, averaging 26 m^2/ha. Tree densities range from 410 to 770 stems/ha, averaging 621 stems/ha. Most sample plots have a heavy shrub layer, dominated by *Rhododendron maximum* and/or *Kalmia latifolia*. Other frequent shrubs are *Lyonia ligustrina*, *Rhododendron calendulaceum*, *Pyrularia pubera*, and *Clethra acuminata*. Evidence of fire scars was observed in three samples.

A total of twelve species achieve mean importance values over 1% (Table 11). Red maple, chestnut oak and northern red oak have the highest mean importance values. These three species share dominance in terms of importance value, relative basal area, and relative density on most plots grouped in this forest type. Besides the dominants, sourwood, black gum, black locust, and sweet birch occur with frequencies of at least 66%. Pitch pine (*Pinus rigida*) occurs in 33% of the samples, sharing dominance with red maple, and chestnut oak in two plots.

Mean sapling relative density is dominated by red maple. This species is the only one that occurs as sapling stems in all plots. Other important species that occur as sapling stems in more than 66% of the samples are hemlock, black gum, sourwood, and Fraser magnolia. Hemlock has the highest mean subsapling relative density. This species together with red maple, black gum, sourwood, and sweet birch occur as subsapling stems in more than 66% of the samples. Reproduction of chestnut oak and northern red oak is present in 50% of the sample plots. Pitch pine is absent in the subsapling category.

Table 11. Composition of the Red Maple-Oak Forest (N = 12)[a]

Species	Trees[b] Importance Value	Trees[b] Relative Basal Area	Trees[b] Relative Density	Saplings[c] Relative Density	Subsaplings[d] Relative Density
Acer rubrum	30.7	25.0 ± 3.6[e]	36.5 ± 3.5[e]	29.9	9.1
Quercus prinus	21.8	28.7 ± 4.3	15.0 ± 1.8	3.1	3.5
Q. rubra	12.0	15.5 ± 3.7	8.5 ± 2.2	1.2	P
Oxydendrum arboreum	8.4	5.2 ± 1.2	11.6 ± 2.4	8.5	8.0
Pinus rigida	6.9	7.8 ± 4.5	6.1 ± 3.2	1.0	-
Nyssa sylvatica	3.8	4.2 ± 2.7	3.5 ± 1.2	11.4	8.2
Robinia pseudoacacia	3.1	2.7 ± 0.7	3.6 ± 1.2	1.6	P
Betula lenta	2.4	2.1 ± 0.8	2.7 ± 1.0	P	1.4
Magnolia fraseri	1.9	1.2 ± 0.9	2.5 ± 1.5	4.5	5.2
Liriodendron tulipifera	1.5	2.0 ± 1.2	1.1 ± 0.5	P	1.2
Quercus velutina	1.2	1.2 ± 0.8	1.1 ± 0.7	P	P
Halesia carolina	1.2	P	1.6 ± 0.9	1.5	5.5
Tsuga canadensis	P	P	1.3 ± 0.6	13.2	14.3
Cornus florida	P	P	P	6.0	2.8
Acer pensylvanicum	P	P	P	2.3	12.6
Castanea dentata	P	P	P	1.7	12.3
Amelanchier laevis	P	P	P	1.3	P
Acer saccharum	P	P	P	1.2	P
Hamamelis virginiana	-	-	-	3.6	6.1
Ilex montana	-	-	-	2.8	4.4
Density (Stems/ha)			621	1027	1016
Basal Area (m^2/ha)		25.6			
Chestnut Stump Density (Stems/ha)			183		
Chestnut Stump Basal Area (m^2/ha)		20.8			

[a]All species which reached more than 1% in any parameter reported. Data are mean values.

[b]Stems greater than 10 cm. dbh.

[c]Stems 3-9 cm. dbh.

[d]Stems less than 2 cm. dbh.

[e]Standard error.

P = Present but less than 1%.

Live chestnut sprouts occur in 66% of the samples. Chestnut stump basal areas range from 9 to 41 m^2/ha, averaging 21 m^2/ha. Chestnut stump densities vary from 100 to 250 stems/ha, averaging 183 stems/ha. The plot with the highest chestnut stump basal area is dominated by northern red oak, red maple, and chestnut oak. These three species make up over 75% of the total basal area and density. Reproductive categories are dominated by red maple, and reproduction of oak species is low. On sites where chestnut is less abundant, persistent trees (>40cm dbh) of chestnut oak, northern red oak, and red maple are frequent. Here smaller trees of these three species are common. In more xeric sites the importance of northern red oak decreases, while red maple along with chestnut oak share dominance more frequently.

Red maple is usually considered a pioneer or subclimax species (Fowells, 1965). This species grows under a wide variety of environmental conditions in the Smokies. It was likely more favored by the elimination of chestnut than were oak species due to its ability to invade chestnut openings. Its high frequency and abundance in all diametric categories suggest that red maple will continue to be an important species in this forest type. Oak reproduction is low, but it does occur in 50% of the samples. Oaks should continue to share dominance with red maple in this forest type. Other species that may likely increase in importance are hemlock on most mesic sites, and black gum on most xeric ones.

In the Smokies, Whittaker (1956) observed that the death of the chestnuts had permitted heavy reproduction of species formerly limited by competition and shading. Forests formerly dominated by chestnut had by that time (1947) dense stands of submesic small trees, mainly red maple. Woods and Shanks (1959) also observed that chestnut was replaced by forest types which included red maple. Golden (1974) identified a chestnut replacement type dominated by red maple and northern red oak. He also identified red maple as the most abundant chestnut replacement species in the chestnut oak forest. The author concluded that red maple would likely remain as part of the composition of those forest types over a long period of time, if not indefinitely.

Red Maple-Sourwood Forest

Sample plots grouped as red maple-sourwood replacement forest occur from 2200 to 3625 ft., predominantly over 2900 ft. This forest type occurs mainly on lower to upper southern slopes. Slope angles vary from 34 to 74%. Most samples have soils with depths less than 50cm, with little to moderate occurrence of surface rocks (Appendix). A heavy shrub layer is common on most sample plots. This layer is mainly composed of Kalmia latifolia, Rhododendron maximum, and Pyrularia pubera.

Species composition and species size classes in these samples are highly variable, perhaps because of occurrence of fire, even though it was observed only on three samples. Plots consist of small trees, with occasional larger trees (>40cm) of red maple, black oak (Quercus velutina), pignut hickory, and tulip poplar. Tree basal areas range from 17 to 29 m^2/ha, averaging 24 m^2/ha. Tree densities vary from 450 to 710 stems/ha, averaging 610 stems/ha. Nineteen species reach over 1% of the mean importance value (Table 12). Red maple has the highest mean importance value. Small stems of sourwood occur abundantly in all sample plots. Other important species that occur with frequencies of at least 62% are tulip poplar, white oak (Quercus alba), black oak, chestnut oak,

Table 12. Composition of the Red Maple-Sourwood Forest (N = 8)[a]

Species	Trees[b] Importance Value	Trees[b] Relative Basal Area	Trees[b] Relative Density	Saplings[c] Relative Density	Subsaplings[d] Relative Density
Acer rubrum	20.5	16.5 ± 4.0[e]	24.5 ± 4.7[e]	27.2	12.5
Oxydendrum arboreum	11.0	7.6 ± 1.4	14.5 ± 2.6	9.6	6.2
Liriodendron tulipifera	7.1	8.9 ± 5.3	5.3 ± 4.0	1.1	4.2
Quercus alba	6.3	8.6 ± 5.6	3.9 ± 1.8	2.6	P
Q. velutina	6.1	8.9 ± 4.1	3.2 ± 1.1	1.0	1.1
Carya glabra	5.9	7.9 ± 4.8	3.9 ± 2.6	1.3	1.2
Quercus prinus	5.8	6.7 ± 2.4	5.0 ± 1.7	2.9	2.7
Betula lenta	5.0	4.3 ± 3.2	5.6 ± 3.8	1.4	1.2
Pinus strobus	4.7	5.3 ± 5.3	4.1 ± 4.1	1.1	-
Quercus rubra	4.5	4.4 ± 1.4	4.6 ± 1.9	P	P
Robinia pseudoacacia	3.9	4.0 ± 1.9	3.7 ± 1.6	P	P
Nyssa sylvatica	3.2	4.7 ± 2.4	1.7 ± 0.7	3.1	3.0
Carya tomentosa	3.0	2.1 ± 0.9	3.9 ± 1.5	2.2	2.0
Cornus florida	2.9	1.3 ± 0.8	4.6 ± 3.1	20.3	22.7
Quercus coccinea	2.0	2.5 ± 1.3	1.5 ± 0.9	-	-
Acer pensylvanicum	1.6	P	2.5 ± 1.8	2.7	4.1
Pinus rigida	1.3	1.6 ± 1.6	1.0 ± 1.0	-	-
Tilia heterophylla	1.2	1.1 ± 1.0	1.3 ± 1.2	1.2	P
Halesia carolina	1.1	P	1.3 ± 1.2	2.3	6.9
Magnolia fraseri	P	P	1.2 ± 1.2	1.0	P
Tsuga canadensis	P	P	1.0 ± 0.4	2.3	3.1
Amelanchier laevis	P	P	P	2.2	3.2
Acer saccharum	P	P	P	2.1	1.4
Hamamelis virginiana	-	-	-	9.4	15.9
Ilex montana	-	-	-	1.1	P
Castanea dentata	-	-	-	P	5.3
Density (Stems/ha)			610	924	1097
Basal Area (m^2/ha)		24.3			
Chestnut Stump Density (Stems/ha)			177		
Chestnut Stump Basal Area (m^2/ha)		18.7			

[a]All species which reached more than 1% in any parameter reported. Data are mean values.

[b]Stems greater than 10 cm. dbh.

[c]Stems 3-9 cm. dbh.

[d]Stems less than 2 cm. dbh.

[e]Standard error.

P = Present but less than 1%.

sweet birch, northern red oak, black locust, and mockernut hickory (Carya tomentosa). Mean sapling densities are highest for red maple and flowering dogwood. Besides these species, sourwood, witch hazel, black gum, hemlock, and pignut hickory occur as reproductive stems on 62% of the samples.

Chestnut stump basal areas vary from 11 to 28 m^2/ha averaging 19 m^2/ha. Chestnut stump densities range from 100 to 310 stems/ha. The plot where chestnut is least abundant has large trees (>40cm) of black oak, pignut hickory, and chestnut oak. Smaller trees of red maple and sourwood are abundant. Reproductive categories are dominated by red maple. It seems that chestnut openings which have not been closed by the larger trees are being filled by red maple and sourwood. Importance of these species seems to increase toward sites where chestnut was more abundant, but this pattern could be affected by the past occurrence of fire.

Whittaker (1956) observed that red maple, sourwood and flowering dogwood formed dense stands following the death of the chestnuts. In the present study red maple shared dominance with other taxa formerly associated with chestnut. Species composition of these plots should continue to change. Red maple will continue to be important because of its high abundance and ability to invade chestnut openings which have not been yet closed. In most mesic sites hemlock and tulip poplar will likely increase, and toward more xeric sites sourwood and black gum will be important.

Discriminant Analysis

Cluster analysis was used to group samples on the basis of their overall similarity in species composition. Sample groups (types) were determined from the dendrogram derived by the clustering procedure. This technique permits the investigator to group samples considered to have similar chestnut replacement patterns. Discriminant analysis based upon vegetation and environmental variables may be used to check the success of the classification derived by cluster analysis.

Discriminant analysis allows the investigator to distinguish between two or more groups of observations on the basis of a set of discriminating variables by which the groups are expected to differ. The basic purpose is to weigh and linearly combine discriminant variables in such a way as to maximize separation of the groups (Nie et al., 1975; Pielou, 1977). Discriminant functions are of the form: $Di = di_1Z_1 + di_2Z_2 + \ldots + dipZp$, where Di is the score on the discriminant function i, the d's are the weighting coefficients, and the Z's are the standardized values of p discriminant values (Nie et al., 1975). The number of functions that can be derived is equal to the number of discriminating variables or one less than the number of groups, whichever is smaller.

Each discriminant function represents an axis which describes the location of a group relative to the others. Functions are derived in order of decreasing importance, so that the first function represents the axis along which maximum separation of groups occurs. A discriminant function coefficient (dij) permits evaluation of the relative contribution of its associated standardized variable (Zj) to that function (Nie et al., 1975).

Classification functions for each group are derived after the discriminant functions have been calculated. These classification functions permit the investigator to check the success of the original classification derived by cluster analysis. If a larger proportion of misclassification occurs, then the selected variables are considered poor discriminators (Nie et al., 1975).

Discriminant analysis has been used in several vegetation studies. Hinkle (1978) and Schmalzer (1978) used discriminant analysis to distinguish between community types of the Cumberland Plateau in Tennessee. Here, types were distinct in terms of vegetation data and some overlap between types was revealed using environmental variables. DeYoung (1979), using discriminant analysis, found that the white pine-hardwood vegetation types of the Smokies were segregated by variables related to soil moisture conditions.

Discriminant analysis was used in the present study to determine the classification success of chestnut replacement forest types derived by clustering procedures. Species importance values in samples grouped by replacement forest types were used in the discriminant analysis. Bias may be introduced into the classification success since calculations of classification functions were based on predetermined groups.

Results of discriminant analysis using vegetation variables are given in Tables 13 and 14. All of the replacement forest types identified using cluster analysis were significantly different from each other. Classification success was very high (over 97%). One sample from the red maple-oak forest was reclassified as chestnut oak. Both replacement forest types were distinguished primarily by the lower importance values of chestnut oak in the red maple-oak forest type.

Table 13. Matrix of F-Values from Discriminant Analysis of Replacement Forest Types Using Species Importance Values[a]

Types	Silverbell-Red Maple	Hemlock-Hardwood	Northern Red Oak-Silverbell	Chestnut Oak	Red Maple-Oaks
Hemlock-Hardwood	5.47				
Northern Red Oak-Silverbell	6.97	7.92			
Chestnut Oak	14.73	6.64	10.84		
Red Maple-Oaks	16.25	5.49	11.80	3.41*	
Red Maple-Sourwood	19.70	6.61	19.60	11.93	6.27

[a]F-value at $\alpha = 0.005$ (d.f. 19, 14) is 4.09.

*Significant at $\alpha = 0.05$.

Table 14. Matrix of Classification Success from Discriminant Analysis of Replacement Forest Types Using Species Importance Values[a, b]

Actual Groups	Silverbell-Red Maple	Hemlock-Hardwood	Northern Red Oak-Silverbell	Chestnut Oak	Red Maple-Oaks	Red Maple-Sourwood
Silverbell-Red Maple	100					
Hemlock-Hardwood		100				
Northern Red Oak-Silverbell			100			
Chestnut Oak				100		
Red Maple-Oaks				8.3	91.7	
Red Maple-Sourwood						100

[a]Percent of grouped cases correctly classified: 97.3%.

[b]Values within the table are percentages of the plots in the replacement forest types.

Discriminant analysis was also performed using environmental variables. The purpose was to determine which environmental factors were most important in segregating the chestnut replacement forests. Environmental variables used in the analysis were: elevation, aspect, slope angle, microtopographic position, rock cover and soil depth. Canopy and shrub covers were also used in this analysis because of the effect of these variables on environmental factors such as light penetration, moisture conditions, etc. Chestnut stump basal area was also included in the analysis to determine if this variable was important in segregating the chestnut replacement forests. Significance tests were not used since with some of these variables it is not possible to assume multivariate normality.

The classification matrix (Table 15) indicated that the overall classification success was high. All samples identified as hemlock-hardwood and silverbell-red maple forest were well classified. Overlap in environmental characteristics occurred between all replacement forest types. Red maple-oak forest overlapped mainly with chestnut oak forest. Northern red oak-silverbell forest overlapped with the most mesic forest types: silverbell-red maple and hemlock-hardwood.

The relative importance of environmental variables may be interpreted from standardized coefficients of the discriminant functions (Table 16). Functions 1 and 2 explain over 82% of the total variability attributable to the discriminant environmental variables. The prominent discriminating variables for the first function were elevation and canopy cover. Percent of microtopographic position was also important in this function. The second function is related with shrub cover, angle of

Table 15. Matrix of Classification Success from Discriminant Analysis of Replacement Forest Types Using Environmental Variables[a, b]

Actual Groups	Silverbell-Red Maple	Hemlock-Hardwood	Northern Red Oak-Silverbell	Chestnut Oak	Red Maple-Oaks	Red Maple-Sourwood
Silverbell-Red Maple	100					
Hemlock-Hardwood		100				
Northern Red Oak-Silverbell	20	20	60			
Chestnut Oak				66.7	16.7	16.7
Red Maple-Oaks	8.3	8.3		16.7	58.3	8.3
Red Maple-Sourwood	12.5		12.5	12.5		62.5

[a]Percent of grouped cases correctly classified: 68.4%.

[b]Values within table are percentages of the plots in the replacement forest types.

Table 16. Standardized Coefficients of Environmental Variables

	DF-1	DF-2
Elevation	1.08	0.22
Slope angle	-0.24	-0.78
Microtopographic Position	0.39	0.50
Canopy Cover	0.70	-0.07
Rock Cover	-0.27	-0.37
Shrub Cover	0.09	0.86
Percent of Total Variance Explained	60.1	22.1

slope, and percent of microtopographic position. The sign of these coefficients determines whether the variable is making a positive or negative contribution to the discriminant score of the given function.

Chestnut stump basal area was not an important variable in segregating the chestnut replacement forests. This may be due to the fact that all sites studied were selected by the formerly high chestnut dominance as expressed by the remaining chestnut stumps.

The plot of group centroids (mean of the discriminant scores for the cases within a group) along the discriminant functions is shown in Figure 3. Replacement forest types are arrayed from chestnut oak to northern red oak-silverbell, with the most mesic forest types grouped to the right of the chart. This suggests that elevation and moisture conditions are important environmental variables in segregating these replacement forest types, although overlap of environmental conditions occurs between them. The sequence of forest type centroids on the second function is not readily interpreted as an ecological gradient. Along the first function, overlap of environmental conditions occurs between red maple-oak and red maple-sourwood. The latter forest type occurred predominantly in southern exposures and it was influenced by fire in addition to chestnut blight.

Environmental variables measured in this study were general factors which could conceal local or microenvironmental gradients. Variables such as soil moisture, nutrient content, pH, etc., might also contribute to the differentiation between forest types. However, since these forest types are successional after the elimination of chestnut, it should be expected that environmental conditions overlap occur

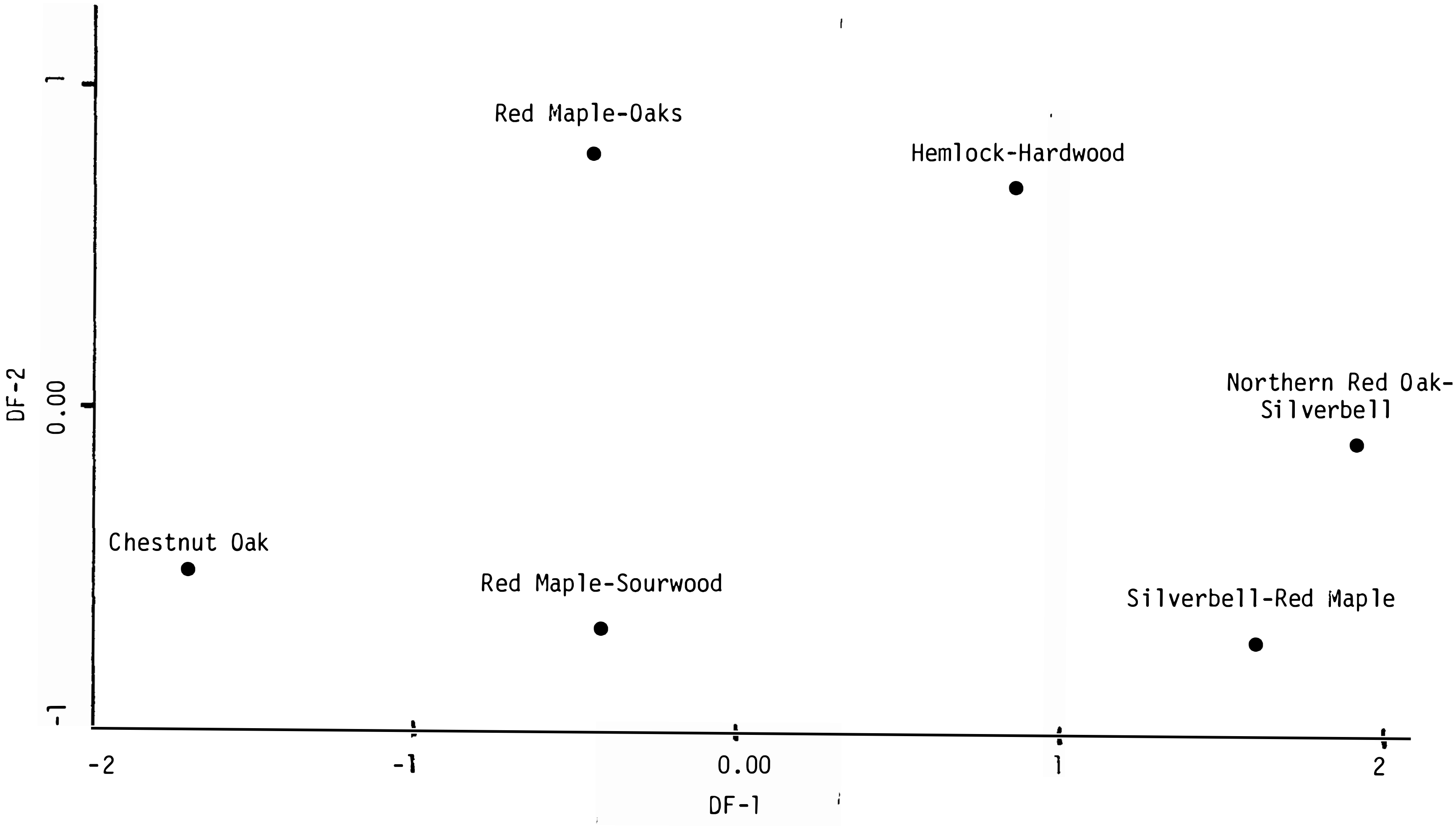

Figure 3. Centroids of Replacement Forest Types Along First Two Discriminant Functions Based on Environmental Variables.

between them. With the death of chestnut, original microenvironmental conditions were modified, canopy openings increased light penetration. Subsequently more xeric conditions prevailed. Species composition of these forest types is formed by persistent trees, which were codominant or dominant before the blight, smaller trees of those same species, and a great number of invader species.

In the most mesophytic forest types, silverbell-red maple and hemlock-hardwood, chestnut previously formed almost pure stands. Here, the process of recovery has occurred rapidly. That process was likely influenced by succession of species before the death of chestnut.

Recovery in xeric sites has been slow. In these sites, red maple and shrub species (Kalmia latifolia and/or Rhododendron maximum) seem to have been favored following the death of the chestnuts. Shrubs have likely limited the reproduction of oak species.

Red maple-oak forest together with the chestnut oak forest type conform to part of the Whittaker's former chestnut oak-chestnut communities. Whittaker (1956) observed that dense stands of small stems of red maple and other species were favored following the death of the chestnuts. Red maple shared dominance with chestnut oak and northern red oak in the red maple-oak replacement forest type.

Continuous changes in species composition are expected in all these replacement forest types. Pioneer species such as sweet birch, black locust and sassafras that were initially favored with the elimination of chestnut have low reproduction and will likely decrease in importance. Oak reproduction is low, but it has been observed that oak species have periodic peaks in reproduction (Fowells, 1965). High frequency of occurrence and successful reproduction of red maple indicate that this species will continue to play an important role in the composition of the chestnut replacement types.

CHAPTER VI

SUMMARY AND CONCLUSIONS

This study involved the analysis of data from 38 sample plots at elevations ranging from 2000 to 4000 ft. in the eastern portion of the Great Smoky Mountains National Park. This is the same area studied by Woods and Shanks (1959) a quarter century ago.

Forests formerly dominated or codominated by chestnut occur on a wide range of topographic positions, aspects, and slope angles. The former importance of chestnut was estimated from stumps, logs, and living sprouts. In all samples studied, persistent chestnut stumps made up over 25% of total basal area. Living chestnut sprouts occurred in most of the samples. Living sprouts that reached at least 1.4m in height occurred in 55% of the sample plots.

In general, plots consisted of small trees, less than 40 cm. in dbh, with scattered larger trees. Tree basal areas ranged from 12.4 to 45.2 m^2/ha. Former associates of chestnut such as chestnut oak, northern red oak, and red maple, are common as persistent large trees. Typical invader species such as sourwood, sweet birch, and black locust were frequently found.

Thirty-three species of trees were found in the sites analyzed. Species that occurred in at least 45% of the samples were red maple, northern red oak, sourwood, chestnut oak, sweet birch, silverbell, Fraser magnolia, black locust, black gum, and hemlock. This variety of chestnut associates indicates that chestnut had a very wide ecological amplitude in the Smokies.

Overall, species with the highest importance values (in all 38 plots analyzed) are red maple, chestnut oak, northern red oak, silverbell, and sourwood. These five species make up over 60% of the mean basal area and density. Red maple and hemlock are the most abundant species in the sapling and subsapling categories.

Among the more important species, only red maple and sweet birch do not show appreciable changes in importance across the moisture gradient. Northern red oak, silverbell, and hemlock are more important under mesic conditions. Chestnut oak and sourwood are more important under xeric conditions.

Species importance values were used to group sample plots into chestnut replacement forest types with the agglomerative clustering procedure described by Orloci (1967). Six forest types were identified at the 50% dispersion level.

A silverbell-red maple replacement forest occurs on mesic sites from coves to protected middle slopes, on northern aspects. Chestnut stump mean basal area exceeded that of all combined living taxa. Red maple and mesic species including silverbell and Fraser magnolia were initially favored following the death of the chestnuts. High frequency of occurrence and abundant reproduction of hemlock suggest that this forest type will eventually become a hemlock-hardwood type.

Sample sites dominated by hemlock and a mixture of hardwoods occur on protected middle and lower slope positions. Chestnut stump mean basal area was almost equal to that of all combined living taxa. Red maple, sweet birch, and oaks were initially favored with the elimination of chestnut. This forest type most likely will become dominated by hemlock.

A northern red oak-silverbell replacement forest occurs from middle to upper slopes at high elevations. Chestnut stump mean basal area was equivalent to 77.8% of the present tree basal area. Large chestnut openings, which were not closed by neighboring northern red oaks, are being filled by silverbell, red maple, and sweet birch. Northern red oak reproduction is low but frequent. This species should remain dominant. Silverbell and red maple should increase in importance and will continue to be part of the composition of this forest type.

Chestnut oak is the leading dominant in the chestnut oak forest type which occurs on middle and upper slopes. Chestnut stump mean basal area represented 76% of the current tree basal area. Chestnut oak occupies the place left by the dead chestnuts. Although its reproduction is low chestnut oak should continue to dominate this replacement forest. Red maple should increase in importance because of its high abundance in reproductive categories.

The red maple-oak forest is the most extensive chestnut replacement forest. This forest type occurs from lower to upper slopes over a variety of aspects. Chestnut stump mean basal area was equivalent to 80.7% of present tree basal area. Red maple, chestnut oak, and northern red oak were favored following the elimination of chestnut. Abundance of red maple on all diametric categories indicates that this species should continue to be an important species in the composition of this forest type. Although oak reproduction is low, oak species are expected to continue to share dominance with red maple.

A red maple-sourwood replacement forest occurs mainly on southern slopes. Chestnut stump mean basal area was equivalent to 79% of the living tree basal area. Red maple and sourwood were apparently favored in canopy openings created by the loss of chestnut. This replacement pattern may also be affected by the past occurrence of fire. Importance of red maple will likely increase because of its great abundance and ability to invade chestnut openings which have not yet been closed.

Discriminant analysis based upon vegetation data indicated that 97% of the samples were correctly classified. Discriminant analysis using environmental variables indicated that 68% of the samples were correctly classified. Elevation and moisture conditions (as determined by canopy cover and microtopographic position) appear to be important factors in separating the chestnut replacement forest types. Environmental conditions overlap between all the replacement forest types. This may be due to the successional status of these replacement forests and overlapping ecological amplitudes of the species.

In the present study, chestnut stump basal area was not an important variable in segregating the chestnut replacement forests. However, this may be due to the fact that all sites selected for study had high basal area of chestnut stumps.

Results of this study warrant the following conclusions: (a) chestnut is being replaced in the Smokies by the same species that were its earlier associates, mainly, red maple, chestnut oak, and northern red oak; (b) under the most mesic conditions, chestnut is being rapidly replaced by species more mesic than itself, such as hemlock, silverbell, and Fraser magnolia; (c) under the most xeric conditions, the process of recovery is slow, and red maple and sourwood have been favored by the death of chestnut; (d) former chestnut forests are being replaced by several forest types which include red maple as an important species.

According to the results of this study, red maple was the most favored species following the death of chestnut. Red maple's wide ecological amplitude, its prolific seed production and dispersal, and its ability to invade chestnut openings, explain why this species has been so successful in replacing chestnut. The importance of red maple, as chestnut replacement species, was also observed by Golden (1974) in the central portion of the Smokies. Red maple is expected to remain as part of the composition of the replacement forests for a long period of time. However, the future role of red maple as dominant species is not entirely clear since red maple is considered a characteristic species of successional stages. In the middle elevation Smokies there is no evidence of stabilized forests that include red maple as a dominant species (Woods and Shanks, 1959). Pioneer species such as sweet birch, black locust, and sassafras that were initially favored by the elimination of chestnut exhibit little or no reproduction and will likely decrease in importance. Oak reproduction is low. This is probably due to competition with shrub species and/or periodic reproduction. All observations suggest that continued changes in species composition are expected in all chestnut replacement forests.

Woods and Shanks (1959) predicted that the former oak-chestnut forest association would eventually develop into an oak association-complex. Species composition of the replacement forest types identified in the present study indicates that oaks are common as persistent large trees, however, there are variations in their importance as a result of the differences in environmental conditions and of the former abundance of chestnut. In the chestnut oak and red maple-oak replacement forests, oak species have persisted as dominants, however red maple has been increasing in importance and is now codominant with oak species. In the most mesic replacement forest types, where chestnut previously formed almost pure stands, species such as hemlock and silverbell are more important now than are oaks. At higher elevations, northern red oak is persistent as canopy dominant, but the large openings left by chestnuts are being filled by silverbell and red maple. Thus, these observations suggest that presently it is not possible to identify a single vegetation pattern related with the replacement of chestnut.

According to predictions of Shugart and West (1977), forest composition will continue to change throughout 100 to 200 years after the chestnut blight. Fifty years is indeed too short a time to determine with certainty which species will eventually dominate the composition of these forests. Therefore, subsequent and periodical studies are necessary to fully understand vegetation patterns related with the death of chestnut. Permanent plots marked in this study contribute to the continuity of these investigations.

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APPENDIX

Table A-1. Environmental Variables of the Replacement Forest Types, Means and Ranges of Data

	Silverbell-Red Maple (N = 4)	Hemlock-Hardwood (N = 3)	Northern Red Oak-Silverbell (N = 5)	Chestnut Oak (N = 6)	Red Maple-Oaks (N = 12)	Red Maple-Sourwood (N = 8)
Elevation (feet)	3312 2950-3600	3123 2550-4000	3860 3500-4000	2575 2300-3000	2984 2000-3800	3106 2200-3625
Aspect[a]	1.78 1.71-1.84	0.83 0.29-1.57	1.24 0.46-2.00	1.09 0.34-1.99	1.07 0.00-2.00	0.93 0.00-1.87
Microtopographic position[b]	69 60-80	62 50-70	55 5-83	27 0-44	57 13-100	51 0-100
Macrotopographic position[b]	84 62-98	79 70-96	63 5-97	48 9-93	74 36-100	58 0-100
Slope angle (%)	55 42-83	50 32-60	49 39-58	56 25-75	42 5-64	57 34-74
Rock cover (%)	5 0-10	0	0	7 0-30	7 0-30	17 0-40
Soil depth (cm)	77 63-85	84 81-85	78 58-85	56 30-85	61 30-85	56 28-85
Canopy cover (%)	75 70-80	67 50-80	62 50-70	57 40-60	53 30-70	59 40-70
Shrub cover (%)	22 10-40	60 40-70	28 10-80	63 30-90	61 10-90	49 0-80

[a]Aspect transformed following the method of Beers et al. (1966).

[b]Relative position from ridge (0) to draw (100).

VITA

Ernesto Arends was born in Durham, North Carolina, on July 31, 1952. He is a Venezuelan citizen. He attended high school in Caracas, Venezuela, and graduated in July 1970.

In March 1971 he entered the University of Los Andes, Merida, Venezuela. While studying, he worked as teaching assistant in the Botany Department during 1973-1976. He was awarded the 1973 and 1974 Professors Scholarship as best student of the Forestry School. He received a Forestry Engineer degree in May 1977.

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He is married to Marlene Morales from Caracas, Venezuela. They have a four-year-old son, Alejandro.