# REPLACEMENT OF OAK-CHESTNUT FORESTS IN THE GREAT SMOKY MOUNTAINS[1]

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Abstract. Former oak-chestnut forests in the Great Smoky Mountains National Park were inventoried approximately 50 years after the chestnut blight. Thirty-eight sample plots ranged from 700 to 1400 M elevation in the eastern portion of the Park. Objectives were: (1) to determine present species composition of forests previously dominated or co-dominated by chestnut, (2) to identify replacement forest types, (3) to examine relationships of site factors to the success of replacement tree species, (4) to project continued successional trends, and (5) to compare results with results and predictions of earlier studies of chestnut replacement in the same area.

A half century following the blight six distinct successional forests occur on sites which formerly supported four forest types co-dominated by oaks and chestnuts. These successional forests are classified as: silverbell-red maple, hemlock-hardwood, northern red oak-silverbell, chestnut oak, red maple-oak, red maple-sourwood. Elevation and moisture are the factors most responsible for differnces in chestnut replacement. Chestnut is being replaced by the same species that were earlier associates. Under mesic conditions, chestnut is being rapidly replaced by northern red oak, hemlock and silverbell. Under xeric conditions where recovery is slower, chestnut oak and sourwood are important replacement species. Overall, red maple is the most important replacement species. It is hypothesized that over the next century the importance of oak species and hemlock will increase. The relative importance of sweet birch, black locust, sassafras and sourwood should diminish in the near future. A more gradual decline is expected in the importance of red maple, silverbell and Fraser magnolia.

These conclusions are consistent with those of Woods and Shanks (1959) and with long term projections of Shugart and West (1977).

Keywords: Chestnut replacement, forest recovery.

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## 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 begun to eliminate chestnut as an important component of southern Appalachian deciduous forests.

At intermediate elevations in the Great Smoky Mountains National Park (GSM) chestnut forests were widespread, almost regardless of slope, exposure and steepness (Braun, 1950). In submesic and subxeric stands described by Whittaker (1956), chestnut comprised 30-60 percent of the canopy stems. Whittaker described four vegetation types which were co-dominated by oaks and chestnut. At elevations below 1225-1400 M chestnut oak-chestnut heath and chestnut oak-chestnut forests occurred on almost all slopes except those facing south and southwest. Above these elevations northern red oak-chestnut forests occupied sub-mesic sites. White oak-chestnut forests occupied more xeric sites.

Objectives of this study were: 1) To determine present species composition of forests formerly dominated or co-dominated by chestnut, 2) to identify replacement forest types, 3) to examine relationships of site factors to the success of replacement tree species, 4) to project continued successional trends, and 5) to compare results with results and predictions of earlier studies of chestnut replacement in the same area.

## METHODS

### Study Sites

All sites were located in the eastern part of the GSM, 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). Although chestnuts occurred at elevations below 700 M to above 1700 M (Woods and Shanks, 1959), this study was restricted to a range between 700 to 1400 M. This range includes forest types in which chestnut was most abundant and includes the same areas sampled by Woods and Shanks a quarter century earlier. An effort was made to locate the same sites or sites very close to those studied by Woods and Shanks (1959). Field work was conducted from July through September, 1980. Criteria used for site selection included: 1) evidence (stumps, logs, or living sprouts) that chestnut had been abundant in the pre-blight forest; 2) sites which allowed a wide distribution of plots among elevations, aspects, and topographic positions; and 3) no appreciable evidence of disturbance by cutting, fire, or other agents. Only in the most xeric sites was there evidence of compounding influences of fire or other factors.

### FIELD SAMPLING

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 in draw and ridge locations were sampled using smaller plots (20 x 30 = 0.06 ha) which better matched the terrain. Sampling procedures followed guidelines described by the Uplands Field Research Lab (1978) for the vegetation survey of the GSM. Twenty-three of the thirty-eight 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. Ground cover estimates and percent canopy cover were estimated to the nearest 10%. Species composition of the shrub layer was also recorded. Nomenclature follows that of Radford et al. (1986). Common names follow Shanks and Sharp (1963).

Surface rock cover was estimated to the nearest 10%. Soil depth up to 85 cm was measured. Evidence of past disturbance, such as cut stumps or fire scars, was recorded. Chestnut diameters at breast height were estimated from stump diameters using equations developed by Vimmerstedt (1957). Slope angles, aspect and elevations were measured and the location of each plot was recorded on topographic maps retained by the Uplands Laboratory of the GSM. 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 and macrotopographic positions were derived from topographic maps, and expressed as an index based on the distance of the plot to the nearest ridge divided by the total distance from slope base to ridge. The value of a ridge position was 0%, and that of a draw position was 100% (Golden, 1974). This index placed each plot along a moisture gradient on the basis of slope position (microtopographic position), slope asimuth and slope angle. According to this index, sample plots placed on draw locations, and those on lower and protected slopes were categorized as mesic (mesic to submesic). Plots located on southerly exposures, and on middle slopes to ridge were classified as xeric (subxeric to xeric).

### Data Analysis

Data were submitted to a computer program that calculates absolute and relative densities, basal areas, and importance values {IV = (RD + RBA)/2} for each species in each plot. Data from 20 x 30m plots were adjusted to obtain values comparable to those from 20 x 50m plots. Descriptive statistics, and correlations among and

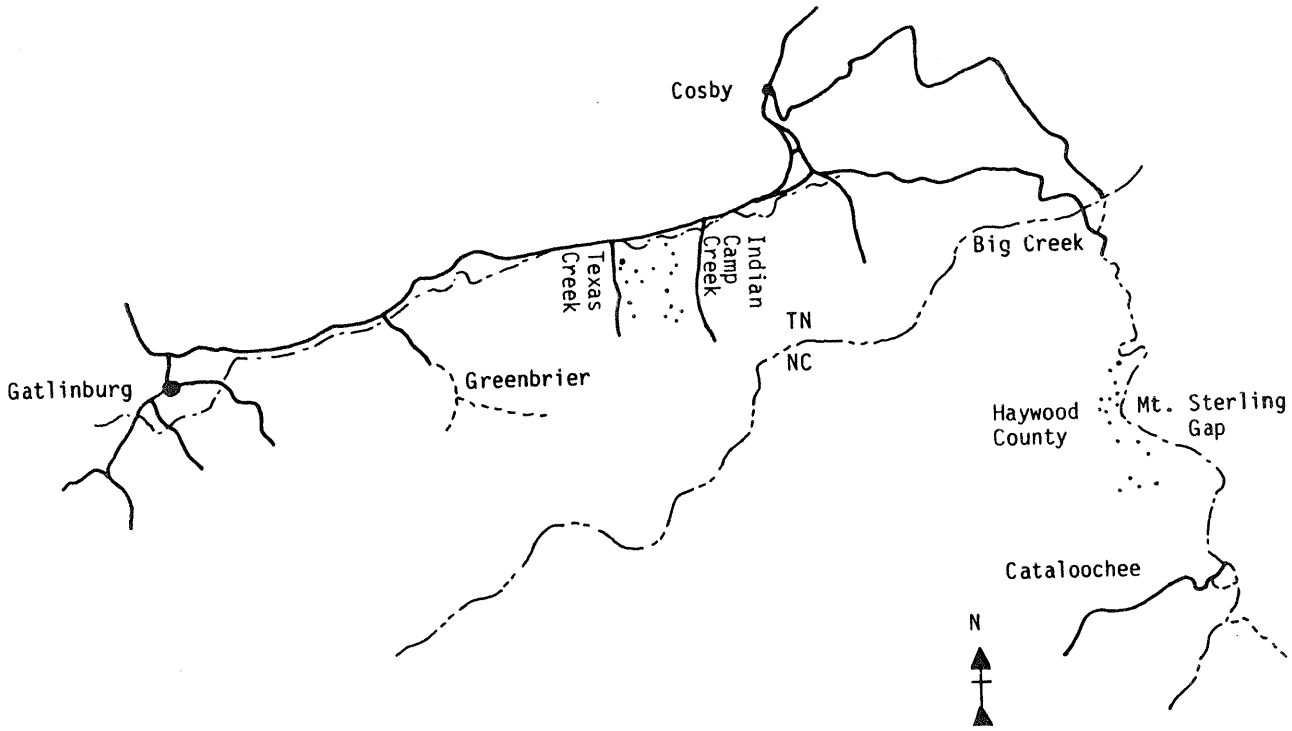


**Figure 1. Locations of Sample Plots in the Great Smoky Mountains National Park.**

between vegetation and site 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).

Orloci's (1967) hierarchical agglomerative clustering technique was used to determine replacement forest types on sites formerly dominated by chestnut. This technique permits the investigator to group samples considered to have similar chestnut replacement patterns. Importance values of tree species, which occurred in at least 5% of the total sample, were used in the cluster analysis. Golden (1974), Kuykendall (1978), and DeYoung (1979) previously used this technique to segregate and classify plant communities in the GSM.

Discriminate analysis based upon vegetation and environmental variables was used to check the success of the classification derived by cluster analysis. The purpose was to weigh and linearly combine discriminant variables in such a way as to maximize separation of groups (Nie et al., 1975; Pielou, 1977). Hinkle (1978) and Schmalzer (1978) used discriminant analysis to distinguish between community types of the Cumberland Plateau in Tennessee. DeYoung (1979) used discriminant analysis to identify soil moisture as the major factor responsible for segregation of white pine and hardwood forest types in the GSM.

Two weaknesses of this analytical procedure are that the 50% dispersion level for cluster analysis was subjectively chosen and that bias may be introduced into the discriminant analysis since calculations of classification functions were based on predetermined groups.

## RESULTS

### General Characteristics

Sample plots are evenly distributed by elevation, 29% occur between 700 M and 950 M, 34% between 950 M and 1200 M and 37% between 1200 M and 1400 M. Chestnut is found on a wide range of aspects and slope angles; 57% of the samples have northernly aspects amd 42% have southernly aspects. Slope angles vary from 5 to 83%, with an overall mean of 50%. Sixty-six percent of the plots have soils less than 85 cm deep.

Canopy cover varies from fairly closed on mesic sites to open on xeric slopes. A moderate to heavy shrub layer is common in most plots. The shrub layer is dominated by *Rhododendron maximum* and/or *Kalmia latifolia*. Other common shrub species are *Pyrularia pubera*, *Clethra acuminata* and *Vaccinium* spp.

Sites are 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 range from 12.4 to 45.2 $m^2$ha. Tree densities vary from 310 to 880 stems/ha. Former chestnut basal areas, estimated from remaining stumps and logs, varied from 9.4 to 41.5 $m^2$ha. Living chestnut sprouts occur in 21 plots. Basal area of chestnut stumps increases with elevation. Correlation between chestnut basal area and elevation is 0.44. Wood and Shanks (1959) reported that chestnut persisted at higher elevations with much greater tenacity than at low altitudes. Large chestnut logs and extant stumps are presently common at higher elevations, mainly near Mt. Sterling Gap.

A total of thirty-three tree species occur in the plots studied. Northern red oak (Quercus rubra), silverbell (Halesia carolina), Fraser magnolia (Magnolia fraseri), and hemlock (Tsuga canadensis) are characteristic replacement species on mesic sites. On intermediate to dry slopes, sourwood (Oxydendron arboreum), chestnut oak (Quercus prinus), and black locust (Robinia pseudoacacia) have most commonly replaced chestnut. Red maple (Acer rubrum) is an important chestnut replacement species in almost all plots studied. This great variety of species associations reflects the former wide ecological amplitude of chestnut in the GSM. A similar array of chestnut-associated species was reported by Woods and Shanks (1959), although they found a higher frequency of mesic species.

Species with 45% or greater frequencies of occurrence were analyzed for correlation with other species and site variables. Occurrence of silverbell and Fraser magnolia are positively correlated with mesic sites and sites with closed canopy. The importance value of chestnut oak decreases with elevation, confirming reports of Golden (1974). Importance of red maple decreases with an increase of slope angle. Steep slopes are generally dominated by chestnut oak and northern red oak. Black locust and sweet birch (Betula lenta) form dense understories in former chestnut forests on submesic to subxeric sites. Woods and Shanks (1959) reported these species as being abundant in large openings created by the death of chestnuts. Sourwood and black gum (Nyssa sylvatica) are associated with xeric slopes as previously reported by Whittaker (1956) and by DeYoung (1979)

When data from all sample plots are aggregated to obtain an overall present composition (Table 1) of former chestnut forests, red maple, chestnut oak, northern red oak, silverbell, and sourwood account for over 60% of total mean basal area and

Table 1. 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%.

density. In the sapling and subsapling categories, the most abundant replacement species are red maple, hemlock, sourwood, silverbell, sugar maple (Acer saccharum), and black gum.

Eighteen tree species (importance values over 1%) occur on mesic sites (Table 2). Red maple, northern red oak, and silverbell predominate. Red maple has high densities, while northern red oak has a high basal area. Chestnut oak and northern red oak have few saplings or subsaplings.

Of the thirteen species occupying xeric sites (over 1% importance value) chestnut oak and red maple are dominant (Table 3). Over 50% of the saplings are red maple. Saplings of northern red oak and pitch pine are scarce.

Live chestnut sprouts occur in 52% of the mesic plots and in 60% of the xeric plots. Beech (Fagus grandifolia) and hop horbeam (Ostrya virginiana) occur only on mesic sites while scarlet oak (Quercus coccinea) and pinus species occur only on xeric sites. Importance of red maple and sweet birch do not differ with respect to moisture conditions.

## Replacement Forests

Six replacement forest types were identified (Figure 2). Site variables for each appear in Table 4. Each forest type is a successional stage, occuring after only 50 years of a recovery process that may require 200 years.

### 1. Silverbell-Red Maple Forest

Silverbell-red maple replacement forests occur on mesic cove sites and north facing middle slopes at elevations ranging from 1030 to 1260 M, with slope angles from 42 to 83% (Table 4). Tree species that occur with a frequency of at least 75% include silverbell, red maple, Fraser magnolia, striped maple (Acer pensylvanicum), sweet birch, and black locust (Robina pseudoacacia). The shrub layer is dominated by Rhododendron maximum and includes Clethra acuminata, Hydrangea arborescens, and Pyrularia pubera.

### 2. Hemlock-Hardwood Forest

Hemlock-hardwood forests occur from 900-1400 M on protected but steep middle and lower slopes with deep soils and northern to western aspects (Table 4). Hemlock shares dominance with sweet birch and beech. Other important species are red maple, sourwood, Fraser magnolia, and silverbell. The shrub layer has 40-70% cover and is dominated by Rhododendron maximum.

Table 2. Composition of the Former Chestnut Forests on Mesic Plots (N = 23)[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 | 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 3. 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%.

3. Northern Red Oak-Silverbell Forest

The northern red oak-silverbell replacement forest occurs from 1325 to 1400 M, on middle to upper northern slopes and on lower slopes of southeast aspects (Table 4). Northern red oak comprise over 50% of the basal area. Silverbell and red maple are abundant as small trees. Other important species include sweet-birch hop hornbeam (Ostrya virginiana), hemlock, cucumber tree (Magnolia acreminata), Fraser magnolia, chestnut oak, and sugar maple. A significant shrub layer is lacking.

4. Chestnut Oak Forest

Chestnut oak forests occur from 800 to 1050 M on middle and upper slopes, with west to east aspects (Table 4). Chestnut oak makes up over 55% of the basal area and over 40% of the density of small 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. A moderate to heavy shrub layer is dominated by Kalmia latifolia and/or Rhododendron maximum. Other species include Rhododendron calendulaceum, Clethra acuminata, Pyrularia pubera, and Vaccinium spp.

5. Red Maple-Oak Forest

Red maple-oak replacement forests occur from 700 M to 1350 M elevation on a variety of slopes and aspects (Table 4). Red maple, chestnut oak and northern red oak have the highest mean importance values. Other dominants include sourwood, black gum, black locust, sweet birch, and pitch pine (Pinus rigida). A heavy shrub layer is dominated by Rhododendron maximum and/or Kalmia latifolia. Otherfrequent shrubs are Lyonia ligustrina, Rhododendron calendulaceum, Pyrularia pubera, and Clethra acuminata.

6. Red Maple-Sourwood Forest

Red maple-sourwood replacement forests occur from 770 to 1270 M on lower to upper southern slopes (Table 4). Red maple is dominant and small sourwoods are abundant in all plots. Other important species which occur with frequencies of at least 62% are tulip poplar, white oak (Quercus alba), black oak, chestnut oak, sweet birch, northern red oak, black locust, and mockernut hickory (Carya tomentosa). A heavy shrub layer is composed of Kalmia latifolia, Rhododendron maximum, and Pyrularia pubera. More detailed descriptions are provided by Arends (1981).

Validation of Forest Classification

All replacement forest types identified using cluster analysis are significantly

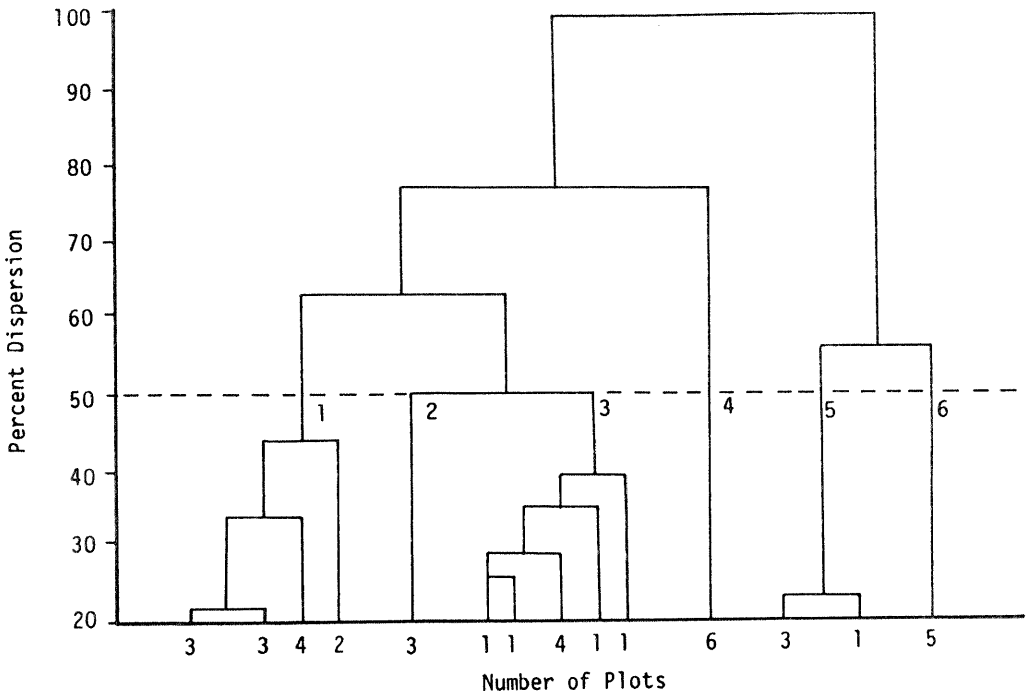


**Figure 2. Classification Dendogram.**

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

different from each other (Table 5). Classification success was very high (over 97%). The relative importance of site variables in segregating replacement forests may be interpreted from standardized coefficients of the discriminant functions (Table 6). Functions 1 and 2 explain over 82% of the total variability attributable to discriminant site variables. The prominent discriminating variables for the first function are elevation and canopy cover. The second function is related to shrub cover, angle of slope, and 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 is not an important variable in segregating chestnut replacement forests. This may be due to the fact that chestnut was formerly a dominant species in all study sites.

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. The most mesic forests are grouped to the right of the figure. Elevation and moisture conditions are important site variables in segregating replacement forests along function one (DF-1). Overlap of site 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. Since these forest types are successional, some overlap of site conditions should be expected. 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 replacement forests (silverbell-red maple and hemlock-hardwood) chestnut previously formed almost pure stands. Here, the process of recovery has occurred rapidly. 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. Shrubs have likely limited the reproduction of oak species. The sequence of forest type centroids on the second function is not readily interpreted as an ecological gradient.

Continuing changes in species composition are expected in all replacement forests. Pioneer species such as sweet birch, black locust, and sassafras that were initially favored with the elimination of chestnut have low reproduction and

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

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

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

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 chestnut replacement forests.

## SUMMARY AND CONCLUSIONS

Thirty-three tree species occur on the sites analyzed. 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 a moisture gradient. Northern red oak, silverbell, and hemlock are most important under mesic conditions. Chestnut oak and sourwood are most important under xeric conditions.

Six successional forest types were identified in areas which supported four types of oak-chestnut forests prior to the chestnut blight. In the silverbell-red maple replacement forest, a high frequency of occurrence and abundant reproduction of hemlock suggest that this forest will eventually become a hemlock-hardwood forest. In the northern red oak-silverbell replacement forest northern red oak reproduction is low but sufficiently frequent that 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. In the chestnut oak forest, chestnut oak should continue to dominate but 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. Abundance of red maple in all diametric categories indicates that this species should continue to be an important species. Oak species are expected to continue to share dominance with red maple. The red maple-sourwood replacement forest is a product of slow succession on xeric sites. Red maple and sourwood initially filled canopy openings created by the loss of chestnut and were subsequently favored by the occurrence of fire.

Overall, red maple was the species most favored following the death of chestnut. Wide ecological amplitude, prolific seed production and dispersal enables this species to invade chestnut openings. The importance of red maple as a chestnut replacement species was also observed by Golden (1974) in the central portion

Table 5. 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.

Table 6. Standardized Coefficients of Site 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 |

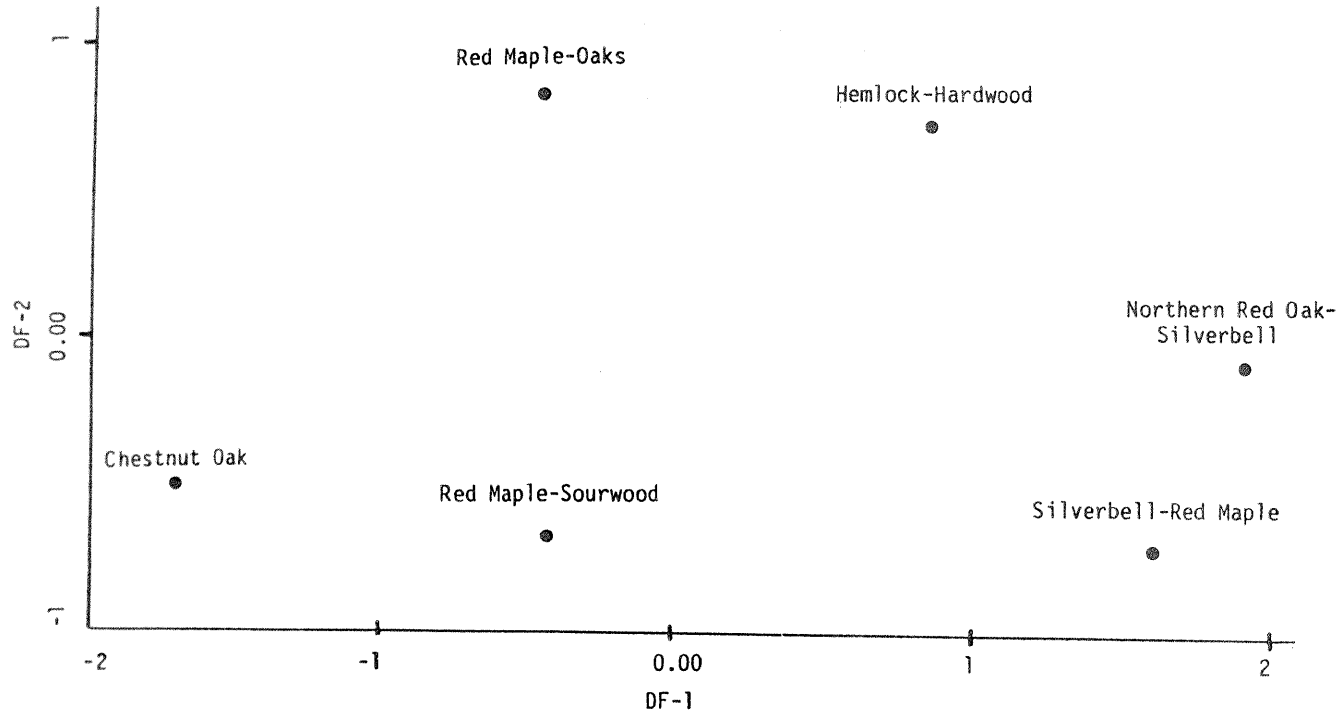


Figure 3. Centroids of Replacement Forest Types Along First Two Discriminant Functions Based on Environmental Variables.

of the Smokies. Red maple is expected to remain a part of the composition of replacement forests for a long time. However, the eventual role of red maple as a dominant species is not entirely clear since red maple is generally considered to be a successional species. At middle elevations there is no evidence of stabilized forests which 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 probably decrease in importance. Aok reproduction is low, probably due to competition with shrub species. Continued changes in species composition are expected in all these successional forests.

Woods and Shanks (1959) predicted that the former oak-chestnut forest association would eventually develop into an oak association-complex. Species composition of replacement forests identified in the present study indicates that oaks are common as persistent larger trees. However, there are variations in their importance as a result of the differences in site conditions. In the chestnut oak and red maple-oak forests, oak species have persisted as dominants but red maple has increased in importance and is codominant. In the most mesic replacement forests, where chestnut previously formed almost pure stands, hemlock and silverbell are presently more important than oaks. At higher elevations, northern red oak is persistent as a canopy dominant, but the largest openings left by chestnuts are being filled by silverbell and red maple.

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 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.

The chestnut blight is believed to be the most extensive and intensive disturbance of Appalachian hardwood forests in the past few centuries. Contemporary successional forests we have described are a response to that disturbance. Only in the most xeric sites was there evidence of compounding influences, such as fire, and fire itself cannot be disassociated from the influence of the blight. As atmospheric pollution and other anthropogenic stresses become increasingly extensive and intensive, it soon may become impossible to analyze site specific responses to individual stresses such as the chestnut blight.

Current understanding of species and

community ecology suggests that during the next century, in the absence of additional disturbance, oak species and hemlock will gradually increase in relative importance at the expense of red maple, silverbell and Fraser magnolia. A decline in the importance of sweet birch, black locust, sassafras and sourwood should be more immediate.

Results of this study, as well as those of others, warrant the following conclusions: a) Chestnut is being replaced in the GSM 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; e) The diversity of forest types has increased significantly (50%) since the chestnut blight. This is interpreted to be a temporary phenomenon since convergence of successional forests is to be expected. Although these conclusions are based upon studies of only a small portion of the Great Smoky Mountains National Park, sites were originally selected to include a great variety of conditions under which chestnut-oak forests flourished in the southern Appalachians.

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