February 1, 1957

To the Graduate Council:

I am submitting herewith a thesis written by Frank W. Woods entitled "Natural Replacement of Chestnut by Other Species in the Great Smoky Mountains." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Botany.

Loyal E. Shanks
Major Professor

We have read this thesis and recommend its acceptance:

A. J. Sharp

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Accepted for the Council:

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Dean of the Graduate School

NATURAL REPLACEMENT OF CHESTNUT BY OTHER SPECIES IN THE GREAT SMOKY MOUNTAINS

A THESIS

Submitted to
The Graduate Council
of
The University of Tennessee
in
Partial Fulfillment of the Requirements
for the degree of
Doctor of Philosophy

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by

Frank W. Woods

March 1957

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INTRODUCTION

The chestnut (Castanea dentata (Marsh.) Borkh.) was once among the largest of our hardwood trees. It reached greatest size in the mountains of eastern Tennessee and western North Carolina (Sargent, 1933) where it was known to reach a height of 120 feet and have a stem diameter of eight feet, five feet above the ground. Throughout most of its range, however, it attained an average height of 80 to 100 feet and a diameter of two to four feet (Pinchot, 1907). It was found in nearly every state east of the Mississippi and in Canada and ranged from sea level in Massachusetts to elevations over 5,000 feet in Tennessee and North Carolina. Many floras list it as having occurred in Florida and southern Alabama, but these reports have not been confirmed by herbarium specimens.

Chestnut grew on a wide variety of well-drained soils. "Richness" of soil was not so important as good drainage and abundant light, for it was somewhat intolerant of shade (Pinchot, 1907). Good soil aeration was also a requisite for optimum growth.

The wood of chestnut was light, moderately strong, elastic and coarse-grained. It was used for cabinet work, cooperage, fence posts, telegraph poles, ties, and mine timbers. Its high tannin content made it highly desirable for manufacturing tannin extract, and large quantities were so used.

In 1904 the chestnut blight caused by the fungus Endothia parasitica was discovered in New York City. It had been introduced to this country from Asia on Asiatic chestnuts several years earlier and by the time it was recognized as a potential hazard it was already established in southern New England and probably uncontrollable even at that early date (Anonymous, 1954; Gravatt, 1949).

The fungus is pathogenic on all species of American and European Castanea, although in varying degrees. The sticky conidiospores are carried for long distances by insects, birds and animals (Heald and Studhalter, 1914), while the ascospores may be blown by wind (Metcalf, 1912). Details of its spread, virulence, and maleffects have been widely publicized.

The spores of the fungus germinate on an open wound in the bark and result in a growth of mycelium throughout the bark, cambium, and outer sapwood. It spreads concentrically in the tree, girdling the stem and killing the tree above the girdle. On smooth bark that has been infected sunken areas appear which are soon covered with orange, yellow, or reddish brown masses of conidia about the size of a pinhead. Leaves above the girdle soon wither and die, but may remain on the dead tree in winter. After the limbs or trunks die small brownish clusters of ascospores may be produced (Metcalf, 1912).

The causal fungus, Endothia parasitica, was monographed by Shear, et al. (1917). Another early and important contribution to the understanding of the chestnut blight is found in the Proceedings of the Pennsylvania Chestnut Blight Conference (Pearson, 1912). Practically

no aspect of the disease was neglected by its students with the result that a large literature was built up in a few years. Even such minutiae as the longevity of pycnospores in soil were studied in detail (Heald and Gardner, 1914). Beattie's (1914) "Bibliography of the Chestnut Tree Blight Fungus" includes a comprehensive list of the early literature on the disease and the causal organism.

Wherever chestnut trees were killed by the blight, an opening was created in the forest canopy. During the course of this study, 2569 such openings were examined. They were found to vary in size with the width and height of the crowns and the density of chestnut trees in the stands. Significant environmental changes were brought about in the immediate vicinity of the dead and dying trees. Light and temperature at the soil surface were increased and root competition for soil water was decreased. The natural closure of these openings by other species of trees in the Great Smoky Mountains National Park has been the subject of this study.

When a chestnut tree is infected by the blight fungus, death is not sudden. At first, a few small limbs die. This is followed by the death of more and larger limbs, until finally, the entire tree succumbs. This slow demise of the tree may take place over a period of two to ten or more years. The higher the elevation in the Great Smokies, the slower the death of the chestnut and consequent release of associated trees. During this period, the crowns of co-dominants expand, the growth rate of the seedlings and saplings established prior to the blight (advance reproduction) increases, and new seedlings may become established.

As Aughanbaugh (1935) points out, closure of the canopy in the chestnut openings created by the slow death of the chestnut is decidedly different from closure of openings created by cutting. The slow death of the blight-killed chestnuts makes it possible for adjacent trees to adjust gradually to the new conditions and occupy much of the space which was left vacant.

LITERATURE

Several intensive studies of chestnut replacement have been made in other regions of the United States. Five of these, by Korstian and Stickel (1927a; 1927b), Aughanbaugh (1935), Keever (1953), and Nelson (1955) are particularly pertinent.

In southern New England Korstian and Stickel (1927a; 1927b) found nine or more taxa replacing chestnut. These were Quercus primus, Q. rubra, Q. alba, Acer rubrum, Fraxinus americana, Quercus coccinea, Q. velutina, Acer saccharum and Carya spp. They noted a loss of Betula lenta in stands where chestnut was blight-killed. Also, Acer saccharum entered into the stand composition where it had previously been absent. This is the only record where sugar maple plays a significant role in the succession following chestnut. The major roles of Quercus rubra and Q. primus in replacing chestnut were stressed.

Aughanbaugh (1935) studied 1618 chestnut openings in Pennsylvania. He found that of the reproduction established prior to the blight, 13 species attained an abundance of one per cent or more. In order of decreasing abundance, these were: Quercus primus, Acer rubrum, Quercus coccinea, Nyssa sylvatica, Sassafras albidum, Robinia pseudoacacia, Quercus velutina, Q. alba, Q. rubra, Carya glabra, Betula lenta, and Pinus rigida. It should be noted that hickory is far down the list. Aughanbaugh's studies also indicate a trend from an oak-chestnut association to an oak association-complex. He found no evidence that an oak-hickory association was in the making. He says that "Under natural forest conditions, the species replacing chestnut comprise those that formerly most closely associated with it." In practically every locality red maple and chestnut oak were the two leading replacement species.

Keever (1953) investigated stands containing chestnut in Macon County, North Carolina. This is near the southern limits of the former oak-chestnut association. The relatively greater abundance of hickory and the smaller number of species which comprise the overstory trees imply a less mesic habitat than those of the Smokies. Fifteen dominant tree species were found in the Macon County study. These were tallied, in order of total density and frequency of occurrence in the six stands studied. In order of density, they were Quercus primus, Q. rubra var. borealis, Carya glabra, (including C. ovalis), Quercus alba, Acer rubrum, Betula lenta, Pinus strobus, Robinia pseudo-acacia, Oxydendrum arboreum, Quercus coccinea, Liriodendron tulipifera, Halesia carolina, Nyssa sylvatica and Sassafras albidum. This combination of species may be more representative of the oak-hickory association than of the oak association-complex which seems to be developing in other regions.

Nelson's (1955) studies of chestnut replacement in the highlands area of western North Carolina show that about 11 taxa are most important in replacing chestnut. These are Carya spp., Liriodendron tulipifera, Quercus velutina, Q. primus, Acer rubrum, Q. alba, Betula lenta, Quercus rubra, Robinia pseudoacacia, Quercus coccinea, and Aesculus octandra. This study was carried out in a mountainous region with a generally southern exposure. The large proportion of hickories exceeds that found by Keever (1953) and places it in the oak-hickory association which she recognizes. It is of interest that Nelson found Oxydendrum arboreum, Magnolia acuminata, Betula alleghaniensis, and Tsuga canadensis invading some sites where they were not present when chestnut was present. This

indicates a current trend toward a more mesic habitat. Nelson concluded that "the trend to date indicates that chestnut is being replaced primarily by the advancement of species which were codominant with chestnut and secondarily by invasions and the advancement of subordinate species."

Other investigations of chestnut replacement (Richards, 1917; Illick, 1921; Spaeth, 1920; Nicholas, 1925), have generally been based on reconnaissance rather than actual sampling and treat only the commercially important species. Results of these studies are in general harmony with the more intensive quantitative studies.

It may be inferred from these studies, including the one by the author, that seven dominant taxa welded the former oak-chestnut forest association into a unit. These were Castanea dentata, Quercus prinus, Q. rubra, Q. alba, Q. coccinea, Acer rubrum, and Carya spp. Two other species, Quercus velutina and Betula lenta were also abundant throughout most of the oak-chestnut forest region. The hickories were generally not abundant and there seems to be little justification for including them in naming the probable future regional replacement of the oak-chestnut association.

THE STUDY AREA

The study of chestnut replacement reported herein was carried out in the Great Smoky Mountains of eastern Tennessee and western North Carolina. Some of the peaks are among the highest in the eastern U. S., with Clingman's Dome culminating at an elevation of 6,643 feet (King and Stupka, 1950). The terrain is steep, with mountain streams cascading and plunging down steep mountain valleys. The soils are thin, rocky, and often poorly developed.

Kendeigh (1942) described the principal study area, in a list of research areas in the National Parks, as follows:

> Great Smoky Mountains National Park. 8. Biotic Succession Area. Probably the largest stand of dead mature chestnut in the park, between Indian Camp Creek, Texas Creek, the Pinnacle Lead and the Park Line, approximately 3800 acres. Altitude approximately 2000-6300 feet. Comprises a complex of several vegetative cover types, conforming in a general way to varying altitudinal limits in drainage basins. Spruce on highest ridges, and oak-chestnut on lower ridges. Lower parts of drainages are chiefly cove hardwoods, with northern hardwoods predominating in upper positions of valleys and slopes. Includes several old burns with reproduction 1-20 years old, also some grassland, Yellow Pine Hardwoods, and heath balds. Also a limited amount of White Pine Hardwoods.

The forests of the Great Smokies are within the Oak-Chestnut Association, as mapped by Braun (1950), with the cove forests strongly related to her Mixed Mesophytic Association. While she could find no sharp boundary between the chestnut, chestnut-yellow poplar, and oak-chestnut communities of the mesic slopes and the highly mesophytic communities of the coves, she pointed out that the typical representatives of each situation are quite different. The gradual transitions between cove and slope stands are difficult to describe and account for many

unusual species combinations. Generally, however, stand boundaries follow natural topographic features, with those on southern exposures more sharply defined than northern ones.

Whittaker (1956) described the vegetation of the Smokies in detail, and suggested that Braun's Mixed Mesophytic concept is somewhat less applicable there than in the Cumberland Mountain region. He believed that the expression embraces too broad and heterogeneous a group of species. These differences in opinion on the status of the highly mesophytic cove forests, and their transitional types to ridges and slopes indicate the complex nature of the forests of the Smokies.

The climate of the Smokies may be described as perhumid, falling into a rain forest classification (Thornthwaite, 1931; Shanks, 1954). Annual rainfall at the highest elevations is in excess of 80 inches and at the lowest elevations about 60 inches. The five year mean of June temperatures at the base of the mountains was 71°F, with temperatures above 5000 feet averaging 10-15°F cooler (Shanks, 1954). Under these cool moist conditions, plant growth is luxuriant and many species reach their maximum recorded size in the Great Smoky Mountains.

METHODS

Thirty-five stands were intensively studied using a species check list (Figure 1), and a form (Figure 2). Each stand was given a reference number, then the location, elevation, aspect, and per cent slope were recorded. Humus type and soil type were listed. Following this, the height and distribution pattern of shrubs, herbs, and tree reproduction were entered. Tree-canopy height was measured with an Abney level and per cent coverage was estimated.

The pre-blight forest type was determined from the remaining dominant and co-dominant trees, plus the chestnut trees indicated by stumps and snags. The forest type at the time of study was also recorded. Probable future types were projected on the basis of the composition and character of existing reproduction. Size of the stand was estimated and increment borings made to determine the approximate date of release. Any evidence concerning fire history, such as faces and scars, was noted.

Detailed data were recorded for 387 openings on the form shown in Figure 3. The condition of the dead chestnut and its diameter breast high (d.b.h.) were recorded. When cut, an attempt was made to determine its age by counting growth rings. The per cent of the opening filled by other species, the height of the replacing species, and the stand position of these species were entered. Data on the species filling in the gap included distance from the dead chestnut, height, and d.b.h. Species composition, height, and coverage in per cent was recorded for the shrub layer. Qualitative data were taken for tree seedlings and the herbaceous layer. The predetermined categories simplified qualitative observations

and a systematic examination of the stands and individual openings provided equally dependable quantitative and qualitative data.

A total of 2569 openings in 79 stands was studied. Data recorded for these openings included replacing species, elevation, slope, and aspect.

Chestnut trees were not distributed evenly over the Great Smokies, but were highly concentrated in some places, and absent in others. In extending this study to locations outside the principal study area (between Indian Camp Creek and Texas Creek) those areas were chosen in which chestnut was most abundant, to provide the maximum amount of information for the time spent.

The usage in scientific names follows Little's (1953) Check List, except for Carya ovalis, which Little includes in Carya glabra. For shrubs, herbs, grasses and other plants not in this check list, Gray's Manual of Botany (Fernald, 1950) was used.

Stand types were named according to the method used in the Society of American Foresters' (1954) classification. Each type was required to be "distinctive and easily separated from other types which most closely resemble it." Many of the stand types recognized in this study would be classed as "subtypes" of the listed S.A.F. forest types. The area covered by most stands was greater than five acres, which was regarded as large enough for complete expression in any topographic situation. However, a few were between one and five acres in size and one ridgetop stand covered less than one acre.

RESULTS

Stands

Fifty-one species of trees were found in the 35 stands containing chestnut (Table 1). The mesic nature of these stands is indicated by the high degree of presence of Tsuga, Liriodendron, Magnolia fraseri, Halesia, Betula lenta, Tilia, Quercus rubra and Acer saccharum. Half of the 16 most characteristic associates of chestnut in these stands are mesophytes. This large array of associated species identifies chestnut as a member of the rich cove forests in the Appalachian-centered oak-chestnut forest region as well as a dominant of the oak-chestnut forests for which the region is named (Braun, 1950).

The shrubs in stands with chestnut (Table 2), often formed a very important stratum. Rhododendron maximum, for example, was present in 60 per cent of all stands that were studied. At one extreme, it was found as an understory to hemlock, chestnut, and hardwoods in very mesic habitats, sometime reaching a height of 15 to 20 feet. At the other extreme it was found in pine-chestnut-heath types as an associate of the more abundant Kalmia latifolia. Kalmia was characteristic of dry southern exposures as a dense understory to Pinus rigida and scattered chestnuts. Here, no chestnut replacement occurred and a pitch pine-heath resulted.

Shrubs and trees which never reach dominant or co-dominant canopy status were grouped together because of their overlap in range of height and similar role in the structure of the stand. Rhododendron, never of tree form, was often larger than Cornus florida and Aralia spinosa, which are normally small trees in an inferior stratum.

TABLE I

OCCURRENCE OF TREE SPECIES IN 35 STANDS CONTAINING CHESTNUT

Species	Number of Stands	Percent of Stands
Acer rubrum	30	86
Tsuga canadensis	29	83
Liriodendron tulipifera	24	69
Magnolia fraseri	23	66
Quercus prinus	20	57
Halesia carolina var. monticola	19	54
Acer pensylvanicum	18	51
Aralia spinosa	17	49
Betula lenta	17	49
Fraxinus americana	16	46
Cornus florida	15	43
Quercus rubra	15	43
Quercus velutina	15	43
Tilia heterophylla	15	43
Acer saccharum	13	37
Nyssa sylvatica	13	37
Oxydendrum arboreum	12	34
Sassafras albidum	10	29
Betula alleghaniensis	9	26
Robinia pseudoacacia	9	26
Aesculus octandra	8	23
Acer spicatum	7	20
Fagus grandifolia	7	20
Magnolia acuminata	7	20
Magnolia tripetala	7	20
Ilex opaca	6	17
Hamamelis virginiana	5	14
Carya tomentosa	5	14
Carya ovalis	4	11
Picea rubens	4	11
Prunus serotina	4	11
Amelanchier laevis	3	9
Carya glabra	3	9
Quercus coccinea	3	9
Pinus pungens	2	6
Pinus rigida	2	6
Prunus pensylvanica	2	6
Quercus alba	2	6
Quercus falcata	2	6

TABLE I (CONTINUED)

OCCURRENCE OF TREE SPECIES IN 35 STANDS CONTAINING CHESTNUT

Species	Number of Stands	Percent of Stands
Celtis occidentalis	1	3
Carya ovata	1	3
Cladrastis lutea	1	3
Juglans cinerea	1	3
Juglans nigra	1	3
Quercus muehlenbergii	1	3
Carya cordiformis	1	3
Pinus strobus	1	3
Diospyros virginiana	1	3
Liquidambar styraciflua	1	3
Ostrya virginiana	1	3
Morus rubra	1	3

TABLE II

OCCURRENCE OF SHRUBS AND SMALL TREES
IN 35 STANDS CONTAINING CHESTNUT

Species	Number of Stands	Percent of Stands
Rhododendron maximum	21	60
Kalmia latifolia	16	46
Pyrularia pubera	15	43
Aralia spinosa	12	34
Cornus florida	12	34
Sassafras albidum	10	29
Vaccinium spp.	9	26
Calycanthus fertilis	8	23
Clethra acuminata	7	20
Hamamelis virginiana	7	20
Lindera benzoin	7	20
Rubus spp.	7	20
Euonymus americanus	6	17
Euonymus obovatus	6	17
Ilex montana	6	17
Viburnum acerifolium	5	14
Hydrangea arborescens	5	14
Rhododendron (Azalea) spp.	4	11
Cornus alternifolia	3	9
Rubus canadensis	3	9
Sambucus canadensis	3	9
Amelanchier arborea	2	6
Gaultheria procumbens	2	6
Itea virginica	2	6
Rhododendron calendulaceum	2	6
Campsis radicans	2	6
Viburnum alnifolium	2	6
Rhododendron catawbiense	1	3
Rhus copallina	1	3
Viburnum cassinoides	1	3

While some shrubs may be quite large, others, such as Epigaea repens and Gaultheria procumbens are low and semi-procumbent. Viburnum alnifolium is a representative of the highest elevations, while Rhus copallina was found at lowest elevations.

The importance of such species as Medeola virginiana, Mitchella repens and Goodyera pubescens emphasizes the northern aspect of the flora (Table 3). Even though most of the species characterize mesic habitats, a few indicate more xeric sites, e.g., Coreopsis major and Aster linariifolius. The death of the chestnut undoubtedly created favorable light and soil moisture conditions for some invading species of low herbs.

Of the vines found in stands with chestnut, Smilax rotundifolia was most often present, with Parthenocissus quinquefolia second (Table 4). Determining the abundance of vines presented special difficulties. Per cent ground cover, number of stems per unit area, and the other usual methods of expressing abundance quantitatively were not applicable, and the vines were never so abundant as to merit special attention.

Ferns and fern allies in stands with chestnut included Adiantum pedatum, Asplenium platyneuron, Athyrium thelypteroides, Botrychium dissectum, B. obliqum, B. virginianum, Dennstaedtia punctilobula, Dryopteris spinulosa var. intermedia, D. noveboracensis, Osmunda cinnamomea, Polypodium polypodioides, P. virginianum, Polystichum acrostichoides, Pteridium aquilinum var. latiusculum, Lycopodium lucidulum and L. obscurum. Ferns were sometimes an important part of the ground cover, often being very abundant and luxuriant. Dryopteris

spinulosa var. intermedia is one of the taxa most likely to be present. On very dry, well-drained slopes, all fern species are scarce.

Individual Openings

A total of 5,046 individual replacement trees was found in the 2569 chestnut openings. This included 182 openings in which there was no evidence of replacement. Three species comprised 46 per cent of the replacements: Quercus primus, Q. rubra, and Acer rubrum (Table 5). These are also three of the most abundant species in other parts of the former oak-chestnut forest region (Korstian and Stickel, 1927a; Aughanbaugh, 1935; Keever, 1953; Nelson, 1955).

Tsuga canadensis and Halesia carolina var. monticola, comprising eleven per cent of the replacements, again strongly emphasize the mesic nature of the forest stands with chestnut found in the Great Smokies (Table 5). These two species and the low abundance of Carya spp. set these stands apart from those studied by Keever (1953) and reveal the wide ecological amplitude of chestnut.

Oaks comprised 41 per cent of all replacements, with no other genus approaching this high degree of abundance. This is probably a fair representation of the normal degree of association in the oak-chestnut region.

Three species had the greatest degree of presence in chestnut openings and were also most abundant: Quercus primus, Q. rubra and Acer rubrum (Table 6). The dominance of this trio is underlined by the drop from Acer rubrum (22 per cent), to Tsuga (9 per cent).

TABLE III

OCCURRENCE OF HERBACEOUS GROUND COVER IN 35 STANDS CONTAINING CHESTNUT

Species	Number of Stands	Percent of Stands
Medeola virginiana	16	46
Mitchella repens	15	43
Solidago spp.	15	43
Galax aphylla	14	40
Dioscorea spp.	13	37
Goodyera pubescens	10	29
Desmodium spp.	9	26
Viola spp.	9	26
Trillium spp.	7	20
Actaea pachypoda	6	17
Pilea pumila	6	17
Arisaema atrorubens	5	14
Polygonatum biflorum	5	14
Smilacina racemosa	5	14
Tipularia discolor	5	14
Aster spp.	4	11
Epigaea repens	4	11
Galium spp.	4	11
Gaultheria procumbens	4	11
Geranium maculatum	4	11
Gerardia laevigata	4	11
Hepatica acutiloba	4	11
Oxalis montana	4	11
Tiarella cordifolia	4	11

Species in 10 per cent or fewer stands included: Aletris farinosa, Campanula divaricata, Cimicifuga racemosa, Conopholis americana, Clintonia spp., Coreopsis major, Cymophyllus fraseri, Disporum lanuginosum, Eupatorium rugosum, Habenaria fimbriata, Impatiens pallida, Monarda didyma, Panicum spp., Ranunculus recurvatus, Scutellaria spp., Streptopus spp., Uvularia perfoliata.

TABLE IV

OCCURRENCE OF VINES IN 35 STANDS CONTAINING CHESTNUT

Species	Number of Stands	Percent of Stands
Smilax rotundifolia	21	60
Parthenocissus quinquefolia	15	43
Rhus radicans	10	29
Vitis spp.	8	23
Smilax glauca	4	11
Aristolochia durior	7	20
Campsis radicans	2	6
Clematis spp.	1	3

TABLE V

RELATIVE ABUNDANCE OF MAJOR TREE SPECIES REPLACING CHESTNUT BASED ON 5046 INDIVIDUALS

Species	Number of Individuals	Abundance in Percent
Quercus prinus	859	17
Quercus rubra	828	16
Acer rubrum	678	13
Tsuga canadensis	287	6
Halesia carolina var. monticola	231	5
Oxydendrum arboreum	228	4
Robinia pseudoacacia	204	4
Quercus coccinea	192	4
Liriodendron tulipifera	181	4
Betula lenta	148	3
Quercus alba	116	2
Fagus grandifolia	99	2
Cornus florida	97	2
Pinus rigida	90	2
Quercus velutina	90	2
Pinus pungens	76	1
Nyssa sylvatica	74	1
Betula alleghaniensis	64	1
Acer saccharum	51	1
Carya glabra	49	1
Acer pensylvanicum	46	1
Pinus echinata	40	1
Sassafras albidum	33	1
All other species	285	6

TABLE VI

OCCURRENCE OF MAJOR REPLACEMENT SPECIES IN CHESTNUT OPENINGS BASED ON 2569 OPENINGS

Species	Number of Openings	Percent of Openings
Quercus prinus	626	24
Quercus rubra	625	24
Acer rubrum	576	22
Tsuga canadensis	221	9
Oxydendrum arboreum	208	8
Halesia carolina var. monticola	191	7
Robinia pseudoacacia	185	7
Liriodendron tulipifera	161	6
Quercus coccinea	157	6
Betula lenta	126	5
Quercus alba	101	4
Cornus florida	92	4
Quercus velutina	82	3
Fagus grandifolia	73	3
Nyssa sylvatica	73	3
Pinus rigida	59	2
Betula alleghaniensis	58	2
Pinus pungens	54	2
Acer saccharum	48	2
Acer pensylvanicum	46	2
Carya glabra	43	2
Sassafras albidum	30	1
Pinus echinata	26	1
Tilia heterophylla	26	1

After this drop, the decrease in occurrence of replacement species is gradual and more readily understood. In less mesic habitats than those at the Smokies, species such as Pinus pungens, Carya glabra, Quercus coccinea, and Sassafras albidum would be much more important.

Response of Suppressed Trees to Release

Suppressed trees, which had grown in no case over ten feet from the bases of overtopping chestnuts, were bored to obtain increment cores for study. Annual rings dating from 1920 to the date of sampling were measured to the nearest 1/1000 inch with a micrometer and hand lens. The width of each annual ring was converted to per cent of total growth, based on the years since 1920, for each tree. Annual percents for a series of trees were averaged to give data depicted in Figure 4. Cores not showing a definite increase in radial growth following chestnut death were not used. Hemlock, chestnut oak, and northern red oak, in that order, yielded the best data for dating the progress of the blight in the Great Smokies. These species also showed the most vigorous and consistent response to release.

Response of other species to release from chestnut dominance appears to have been generally a five stage process:

(1) A six to eight year period of slightly increased growth during which time crowns of co-dominants were probably filling out. Chestnuts were dying in this period.

(2) A five to eight year period of greatly accelerated growth. This was apparently a response to the enlarged crowns.

(3) A one to four year period of rapid decrease in growth rate.

(4) A two to four year period of slightly accelerated growth.

(5) Beginning of a normal decline in growth rate as the released trees increased in size.

It appears that response to release from the chestnut began in 1925 or 1926. This is in general agreement with local and regional observations.

The sharp drop-off in growth immediately after or before the peak response years is not readily explained. It cannot be explained on a climatic basis because all three species dropped in different years. Possibly, the first major increase is the result of increased crown growth, while the secondary increase is due to the subsequent expansion of the root system.

All suppressed trees did not respond to release from suppression by chestnut by increasing in radial growth. Some species, such as Halesia and Tilia showed very little or no response to release. This was also true of Rhododendron maximum.

Ecological Situations

Chestnut was found at elevations from below 2,000 feet to above 5,000 feet (Table 7). All major replacement species were found below 3,000 feet, but above this elevation species dropped out at varying altitudes. Cornus florida was not found in association with chestnut at elevations over 3,500 feet. Liriodendron was not found higher than 4,000 feet and Quercus velutina not over 4,500 feet, while Q. prinus and Tsuga extended up to 5,000 feet.

TABLE VII

ALTITUDINAL DISTRIBUTION OF MAJOR CHESTNUT REPLACEMENT SPECIES IN 2569 CHESTNUT OPENINGS (ONE OR MORE INDIVIDUALS PER OPENING)

Species	Elevation in thousands of feet			
	1.5-2.5	2.5-3.5	3.5-4.5	4.5-5.5
	Percent of each species			
Quercus primus	41	41	15	3
Quercus rubra	16	23	22	39
Acer rubrum	36	35	11	18
Tsuga canadensis	33	59	5	3
Oxydendrum arboreum	33	47	17	3
Halesia carolina var. monticola	13	67	15	6
Robinia pseudoacacia	18	47	25	10
Liriodendron tulipifera	29	46	15	0
Quercus coccinea	2	62	36	0
Betula lenta	14	52	15	18
Quercus alba	33	28	37	3
Cornus florida	74	26	0	0
Quercus velutina	58	40	2	0
Fagus grandifolia	4	26	3	67
Nyssa sylvatica	32	58	10	0
Openings with no replacements	7	42	24	27
Distribution of samples	28	44	16	12

Quercus rubra and Fagus grandifolia were the species in chestnut openings found most often above 5,000 feet. Both species are found in essentially pure stands on the tops of ridges and in saddles at these elevations, with chestnut typically on the slopes around the edges. While beech and chestnut may often be associated at higher elevations, this is generally not true at lower elevations, where beech is found only in deeply shaded and consistently moist sites.

Chestnut is persisting at higher elevations with much greater tenacity than at low altitudes. At elevations above 4,500 feet many sprouting chestnut trees were found, often with fruits. It is possible that the fungus is either not as pathogenic in this cooler environment as it is on lower slopes or that a race of chestnut found at higher altitudes is less susceptible than the populations further down the slope.

Aspect of each of the 2569 openings was studied (Table 8). It was found that the replacement species could be classified in three groups: (1) those primarily characteristic of a northerly aspect; (2) those mainly characteristic of a southerly aspect, and (3) those without a pronounced aspect correlation. Eastern and western aspects were not represented so often as others, and generally blended into either the northern or southern aspects, depending on such factors as slope and topographic position. Quercus primus, Q. rubra, Q. alba were representative of species with no strong topographic affinity. Among the 15 species represented in Table 8, Quercus coccinea was the only one on slopes with a pronounced southerly aspect. Among those characteristic

TABLE VIII

ASPECT DISTRIBUTION OF MAJOR CHESTNUT REPLACEMENT SPECIES
BASED ON 2569 OPENINGS (ONE OR MORE INDIVIDUALS PER OPENING)

Species	Direction of exposure							
	N	NE	E	SE	S	SW	W	NW
	Percent of each species							
Quercus prinus	17	13	9	14	13	12	8	14
Quercus rubra	17	10	11	12	16	13	14	9
Acer rubrum	25	12	7	8	13	9	13	14
Tsuga canadensis	34	16	4	6	13	7	21	0
Oxydendrum arboreum	26	10	9	11	7	10	10	18
Halesia carolina var.monticola	47	1	22	5	6	6	6	7
Robinia pseudoacacia	19	14	9	7	16	12	12	11
Liriodendron tulipifera	39	14	6	7	6	6	6	16
Quercus coccinea	6	5	13	10	28	23	12	3
Betula lenta	17	17	3	3	9	13	17	22
Quercus alba	22	4	13	12	14	16	8	11
Cornus florida	35	15	2	3	4	6	18	15
Quercus velutina	24	17	4	7	2	6	18	21
Fagus grandifolia	21	41	0	0	4	8	15	11
Nyssa sylvatica	26	12	8	14	18	3	10	10
Openings with no replacement	6	4	11	26	20	11	15	7
Distribution of samples	24	13	8	9	12	10	13	12

of northern exposures were Halesia, Liriodendron, Tsuga, Cornus florida and Fagus.

Chestnut was found on a wide range of slopes (Table 9), ranging from 0 to 90 per cent. Grades of 40 per cent were commonplace. The well aerated, rocky soil in which chestnut thrived is found on these slopes. Quercus rubra, Betula lenta, Fagus, and Nyssa were found with chestnut on very steep slopes more often than other species, particularly at high altitudes.

DISCUSSION

Closure of Chestnut Openings

Chestnut openings were re-occupied by three basic processes, their relative roles determined by the dominant trees and character of the understory in the immediate vicinity of the blighted trees and the density of chestnut trees in the stand. These three processes may be summarized as follows:

(1) Closure of the canopy by adjacent dominant and co-dominant trees in mature and over-mature stands. This process has probably been most important in stands where chestnut crowns did not occupy more than 30-40 per cent of the canopy and were sufficiently separate that openings did not overlap. In these openings expansion of the crowns of co-dominants has been generally faster than increase in size of the advance reproduction. However, complete closure in some over-mature stands has not been completed even after 25 years because of slow response to environmental change, due to low growth potential of the over-mature trees.

(2) Growth of advance reproduction. Suppressed seedlings and saplings present at the time of the death of the chestnut reacted most rapidly to the increased amount of light. Both radial growth of stems and height growth were accelerated.

(3) Growth of seedlings established subsequent to the death of the chestnut. This method of replacement has been most important in stands where chestnut was the predominant species and where chestnut crowns were contiguous or overlapped. The greatly increased light at

the soil surface permitted the survival of many seedlings which likely would have perished in the low light intensities typical of mature forests. Also, the reduced intensity of root competition for soil water may have been important even in the moist soils of the Smokies.

Pure or nearly pure stands of chestnut with a sparse herbaceous vegetation existed only on northern exposures. Stands on southern exposures with an equivalent density of chestnut were nearly always accompanied by a dense woody understory of Kalmia, Rhododendron, and Vaccinium in various mixtures.

Different replacement species responded differently to chestnut death. Quercus primus and Q. rubra, the two most abundant species replacing chestnut, were often dominants or co-dominants at the time of death. Upon the development of the chestnut openings, the crowns of these species increased in size and closed the openings from the side.

Tsuga canadensis replaced chestnut by all three of the basic processes and often a dramatic increase in the evergreen component of the forest stands resulted. If we assume that hemlock is more mesic than chestnut, it may be inferred that death of the chestnut has, in such places, led to accelerated forest succession in a mesic direction. Chestnut and Tsuga were found together in stands as low as 3350 feet.

Robinia pseudoacacia probably increased in abundance proportionally more than any other species following death of chestnut. It entered the new openings rapidly and was most abundant in those where several chestnuts had died. The great increase in abundance of black locust was followed shortly by a major outbreak in locust leaf-miners.

This caused a gradual weakening and decline of the black locust populations that was similar in slowness to the chestnut death. Secondary invasions by locust borers accelerated the decline of this species. As a result, black locust is rapidly resuming its subordinate place in the forests.

Acer rubrum is widely distributed throughout the forests of the Smokies at all altitudes. Seeds are shed in great abundance and germination percentage is usually high, so that young seedlings are numerous. However, mortality is great and usually only a very small fraction of these develop to maturity. When the chestnuts died, the openings in the canopy admitted more light than usual and a larger proportion of the seedlings survived. At the same time a larger proportion of the advance reproduction grew to maturity. Liriodendron and Betula lenta often responded in a manner similar to red maple by forming dense stands of saplings, especially in the very large openings. These stands are often found on very steep slopes.

Pinus rigida was often found growing with chestnut on dry southern exposures, usually with a dense understory of Kalmia. Upon death of the chestnut the heath became even more abundant. These were open stands, and there was no evidence that pine responded to release from chestnut.

Successional Trends Following Chestnut Death

Successional changes from the former oak-chestnut and cove forest types resulted from various combinations of the species replacements discussed in the foregoing section. As a basis for generalizations concerning present stages and predictions of probable future trends, 79

stands were studied in detail. To determine the "past type", the abundance of chestnut in stands prior to the blight was determined on the basis of dead trees, snags, stumps, and fallen trees still present. The "present type" was determined on the basis of trees present and alive at the time of the study. The "future type?" was forecast on the basis of persistent canopy dominants, seedling reproduction, transgressives, and the relative tolerance of the various species to low light intensities. For example, it was inferred that understory hemlock seedlings and saplings were probable future canopy dominants, because of the high shade tolerance of this species.

Prior to the blight, chestnut occurred in at least 27 distinct forest stand types in the Smokies. These included chestnut, red oak-chestnut, chestnut-pitch pine-heath, scarlet oak-chestnut, hemlock, hemlock-hardwoods, and mixed hardwoods.

At times, the loss of chestnut from forest stands seemed to accelerate successional changes already in progress, the death of the chestnuts giving impetus to make the shift very rapid rather than gradual. The most extreme example of this type of change was the shift from "pure" chestnut to hemlock, without an intermediate successional stage. This was made possible by the availability of hemlock seed from nearby hemlock stands. Some hemlock-hardwoods stand types, in which the hardwoods were largely chestnuts, also moved directly into a hemlock type. In other shifts from chestnut to hemlock, several intermediate successional stages are apparent: hemlock-hardwood, red maple, and chestnut oak-red maple. Still other former oak-chestnut stands seem to be moving toward hemlock with a yellow poplar intermediate stage.

On other sites the yellow poplar does not seem likely to be replaced by another species within the forseeable future. Mixed hardwood stands have sometimes shifted to a rather stable hemlock-hardwood type.

The above examples are all indicative of the trend in the most mesic habitats of chestnut in the Great Smoky Mountains. Associated mesophytes were generally favored by the removal of chestnut dominance. The shift is most striking where hemlock is involved as a replacement, and a change from deciduous to evergreen forest is now in progress. However, in the modal and drier habitats the residual stands following death of chestnut took several other courses.

In many cases, chestnut was replaced immediately by types which included red maple, apparently due to the abundant and widely dispersed seed supply of this species. However, there is no evidence from either these successional stands or stabilized old stands in the region that red maple will persist as a "climax" type.

Some stands changed composition only to the extent that chestnut was lost. These included mixed oak-chestnut, chestnut oak-chestnut, chestnut oak-chestnut-heath, chestnut oak-pitch pine-heath, red oak-chestnut-heath, and scarlet oak-chestnut. Chestnut in these stands was a co-dominant, and was less abundant than the accompanying dominants, so that changes were less radical. The pitch pine-chestnut-heath combination reveals chestnut on perhaps its most xeric site--well drained, steep, rocky, slopes with a southern exposure. In these locations heath, mainly Kalmia latifolia, increased more than the pine after the chestnut death.

Management of Blighted Stands

Many foresters have expressed concern as to the effects of losing chestnut from the forests of the eastern United States and several types of problems have been recognized. One of the major problems at the outset of the blight was devaluation of forest land (Ziegler, 1920). The silvicultural problems, dealing with sustained management and chestnut replacement, have been explored (Retan, 1918). Other writers have explored other economic aspects of chestnut replacement (Barnes, 1917; Toumey, 1914; Perry, 1922).

At an early date, Frothingham (1924) acknowledged the inevitable loss of chestnut in the southern Appalachians and proposed several types of studies designed to expedite management of blighted stands. These suggestions were subsequently implemented as follows:

(1) Determination of rate and character of spread of the fungus. Cravatt and Marshall (1926) studied this aspect of the disease and made prognostications which turned out to be very good. They said that by 1935 nine-tenths of the counties in the southern United States would have reached the 80 per cent infection stage. This was the case.

(2) Utilization of blighted trees. Studies such as those by Cruikshank et al. (1951) and Baxter and Gill (1931), on the utilization of dead chestnut for tannin production have been helpful in this respect.

(3) Studies of natural replacement. The works of Keever (1953), Nelson (1955), and Korstian and Stickel (1927a; 1927b) have yielded valuable information on this aspect of the problem.

(4) Studies of cultural replacement. In some regions, planting has been recommended (Richards, 1914; Illick, 1921). However, in spite of the vast areas of chestnut lost in the southern Appalachians, there has been very little planting. Now, since most of the gaps have been closed by natural processes, it is apparent that planting is not practical.

In retrospect, there have been very few and feeble attempts in the southern Appalachians to manage blighted stands from the standpoint of timber production. In the ten or fifteen years while chestnut death was acknowledged to be inevitable in the southern Appalachians, economic conditions were not such that a large quantity of the undiseased chestnut could be absorbed by the lumber and acid-wood market. After the blight, the stricken trees were too numerous to be used immediately, and they were soon degraded for lumber use by wood borers.

Recovery of the Chestnut

A number of writers found indications that the chestnut may develop an immunity or resistance to the blight (Collins, 1920; Illick, 1925; Hodson, 1920; Wilber, 1926). Aughanbaugh (1930) made an intensive study of this subject and concluded "it now appears possible that it [chestnut] may eventually recover its rightful position as one of our most important forest trees." However, in the same year Perry (1930) reported that chestnut sprouts infected with the blight failed to develop into trees. Recurring reports from local areas in the southern Appalachians that chestnut is "coming back" have not been confirmed in any case. No optimistic reports have appeared in more recent studies.

While root systems, with their short-lived crops of sprouts, may continue to live for many years, no healthy trees were seen during the course of the present study. The fact that some sprouts bear fruits, especially at higher altitudes, is no indication of acquired immunity. Today, it appears that the American chestnut is, indeed, a doomed species.

There can be no hope that, once all of the blighted trees are dead, the source of the fungus will be removed and American chestnut can be reintroduced. The fungus is parasitic or saprophytic on a number of other species of American trees, although never so virulent as on Castanea dentata (Anonymous, 1954). Post oaks have been more seriously harmed than any species other than chestnut (Anonymous, 1954). Also many varieties of Asiatic chestnuts have been introduced which are blight resistant but will harbor the fungus indefinitely.

Breeding for Blight Resistance

Great efforts have been made in the United States to develop blight-resistant American-Asiatic hybrid chestnut trees which will make high quality timber and fill the ecological niche once occupied by American chestnut (Clapper, 1950; Diller, 1950; Graves, 1949; Clapper, 1944). Nut production has also been regarded as an important aspect of the breeding program, although this has seldom been a paramount objective. Breeding work was begun by the U. S. Department of Agriculture in 1909. Even though many blight-resistant hybrids have been developed and show promise, none have approached the grandeur of the American parent. Another problem seems to lie in the poor frost hardiness of the hybrids. The Asiatic chestnut is readily winter-killed, a characteristic usually

transmitted genetically. Breeding for disease resistance is also being carried on in Europe, where the blight has attacked the indigenous species, Castanea sativa (Pavari, 1949).

Nearly 50 years of chestnut breeding work has not seen the production of an acceptable hybrid for introduction as a forest tree. It is to be hoped that fundamental genetic work can be successfully carried out before the source of Castanea dentata genetic material is unavailable.

It should also be recognized that even if an acceptable hybrid were available, the time is past when chestnut can be re-established in our forests simply and easily. The openings have, for the most part, healed and drastic measures would undoubtedly be required to make stand conditions favorable for chestnut re-establishment.

SUMMARY

(1) Prior to the beginning of this century, chestnut (Castanea dentata) was one of the most important forest trees in the eastern United States. It ranged from New England to Georgia, reaching greatest abundance and best form in the mountains of Tennessee and North Carolina. In 1904, the chestnut blight was discovered in New York. Within the next 40 years, the causal fungus (Endothia parasitica) introduced from Asia on blight-resistant species of chestnut, virtually eliminated chestnut as a member of the deciduous forest complex of the eastern United States.

(2) Being a great distance from the center of spread, chestnut trees in the forests of the southern Appalachians were among the last to be attacked by the blight. To determine what tree species are replacing chestnut in the Great Smoky Mountains of North Carolina and Tennessee, 2569 openings in the forest canopy created by the death of the trees and 79 stands, in which chestnut had been a component, were studied.

(3) A total of 5046 trees of 51 species were found in the 2569 openings studied. The most abundant species replacing chestnuts in the Great Smokies were found to be Quercus prinus (17% of all individuals), Q. rubra (16%), Acer rubrum (13%), Tsuga canadensis (6%), Halesia carolina var. monticola (5%), Oxydendrum arboreum (4%), Robinia pseudoacacia (4%), Quercus coccinea (4%), Liriodendron tulipifera (4%), Betula lenta (3%), Quercus alba (2%), Fagus grandifolia (2%), Cornus florida (2%), Pinus rigida (2%), and Quercus velutina (2%). The three leading species,

Quercus prinus, Q. rubra, and Acer rubrum comprised 46 per cent of the total individuals. Quercus, comprising a total of 41 per cent of all replacements, was the most abundant genus.

(4) In some stands, especially the very mesic cove types, the removal of chestnut resulted in more mesic forest types, generally including Tsuga canadensis and often Liriodendron tulipifera, Magnolia fraseri, Halesia carolina var. monticola, Tilia heterophylla and Acer saccharum. On the dry slopes and ridges chestnut is usually being replaced by species more xeric than itself.

(5) The death of chestnuts attacked by the blight was not sudden, but gradual. Occupation of the canopy and soil space once filled by chestnut was usually begun by canopy expansion of co-dominants, growth of advance reproduction, or seedling growth even before the blighted trees were dead. Increment cores revealed that suppressed trees generally took nine to 15 years to reach maximum yearly growth increment following release. Increased annual growth began in approximately 1925-1926, indicating the arrival date of the fungus in the Great Smoky Mountains.

(6) No indication was found that the chestnut will "recover" or regain its former position as a dominant. Forest management practices in regions which once contained chestnut should be predicated on this premise.

(7) The results of this study are in general agreement with those obtained in New England, Pennsylvania, and elsewhere in North Carolina. The unifying taxa that welded the former oak-chestnut

association into a unit were Castanea dentata, Quercus prinus, Q. rubra, Q. alba, Q. coccinea, Acer rubrum, and Carya spp. Carya was of minor importance in the forests of the Great Smoky Mountains. Because chestnut is being replaced mainly by various species of oak, mainly Quercus prinus and Q. rubra, it is believed that the former oak-chestnut forest association will eventually develop into an oak association-complex.

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APPENDIX A

TABLE IX

DISTRIBUTION BY SLOPE CLASSES OF MAJOR CHESTNUT REPLACEMENT SPECIES
(BASED ON PRESENCE OF ONE OR MORE INDIVIDUALS IN AN OPENING)

Species	Slope in Percent											
	0-5	5-10	10-15	15-20	20-25	25-30	30-40	40-50	50-60	60-70	70-80	80-90
	Percent of species											
Quercus prinus	4	9	10	6	8	5	12	18	9	0	11	8
Quercus rubra	2	8	5	8	7	4	11	16	11	3	4	19
Acer rubrum	5	9	12	7	8	5	9	17	8	2	4	14
Tsuga canadensis	4	10	24	6	15	2	13	11	7	0	5	3
Oxydendrum arboreum	11	15	15	7	10	4	9	12	5	1	5	5
Halesia carolina var. monticola	1	0	12	4	7	2	18	25	12	0	5	14
Robinia pseudoacacia	3	6	8	9	3	5	10	26	14	2	4	9
Liriodendron tulipifera	1	6	22	14	11	2	9	17	9	1	1	6
Quercus coccinea	2	3	5	5	10	8	8	27	7	0	0	3
Betula lenta	4	4	13	13	7	6	13	3	8	0	3	21
Quercus alba	11	17	17	10	5	5	3	17	4	7	1	3
Cornus florida	21	5	15	1	12	4	9	10	2	0	4	16
Quercus velutina	13	13	18	6	14	4	9	12	3	0	4	4
Fagus grandifolia	0	4	15	8	8	3	7	21	7	0	1	26
Nyssa sylvatica	7	12	16	3	4	11	7	15	5	0	1	18
Openings with no replacement	3	1	4	3	3	4	10	14	11	17	29	0
Distribution of samples	6	8	13	7	8	5	10	17	8	2	5	11

APPENDIX B

Check list of trees, shrubs, and herbs of the GSMNP number _____.

Trees

____ Acer rubrum
____ " pensylvanicum
____ " saccharum
____ " spicatum
____ Aesculus octandra
____ Amelanchier laevis
____ Betula lenta
____ " alleghaniensis
____ Carya cordiformis
____ " glabra
____ " ovalis
____ " ovata
____ " tomentosa
____ Fagus grandifolia
____ Fraxinus americana
____ Halesia carolina
____ Hamamelis virginiana
____ Ilex opaca
____ Juglans cinerea
____ " nigra
____ Juniperus virginiana
____ Liriodendron tulip-.
____ Magnolia acuminata
____ " fraseri
____ " tripetala
____ Nyssa sylvatica
____ Oxydendrum arboreum
____ Picea rubens
____ Pinus pungens
____ " rigida
____ " strobus
____ " virginiana
____ Platanus occidentalis
____ Prunus pensylvanica
____ " serotina
____ Pyrus malus
____ Quercus lba
____ " coccinea
____ " falcata
____ " montana
____ " rubra
____ " velutina
____ Robinia pseudoacacia
____ Salix nigra
____ Tili heterophylla
____ Tsuga canadensis

Shrubs and small trees

____ Aralia spinosa
____ Aronia melanocarpa
____ Calycanthus fertilis
____ Campsis radicans
____ Carpinus caroliniana
____ Clethra acuminata
____ Cornus alternifolia
____ " florida
____ Crataegus spp.
____ Euonymus americana
____ " obovatus
____ Gaylussia baccata
____ " ursina
____ Hydrangea arborescens
____ Ilex montana
____ " " mollis
____ Kalmia latifolia
____ Leucothoe catesbaei
____ " recurva
____ Lindera benzoin
____ Lonicera japonica
____ Lyonia ligustrina
____ Ostrya virginia
____ Parthenocissus quin.
____ Pyralaria pubera
____ Rhus radicans
____ Rhododendron calen.
____ " catawb.
____ " maximum
____ Rubus canadensis
____ " odoratus
____ " spp.
____ Rosa _____
____ Sambucus canadensis
____ Smilaxglauca
____ " rotundifolia
____ Sassafras albidum
____ Vaccinium _____
____ Viburnum acerifolium
____ " alnifolium
____ " cassinoides
____ Vitis spp.

Herbs and grasses

____ Actaea alba
____ Andropogon scop
____ Ascyrum hyper
____ Aster spp.
____ Campanula divar
____ Caulophyllum thal
____ Conopholis
____ Chrysopsis gram
____ Cimicifuga race
____ Danthonia compres
____ Desmodium _____
____ Dioscorea _____
____ Diphylleia cymosa
____ Epigaea repens
____ Galax aphylla
____ Gaultheria procum
____ Geranium maculatu
____ Gerardia spp.
____ Goodyera pubescens
____ Hepatica acutilob.
____ Lilium superbum
____ Lycopodium obs
____ " lucid
____ Medeola
____ Mitchella repens
____ Oxalis montana
____ Panicum
____ Sedum ternatum
____ Senecio rugelia
____ Solidago _____
____ Stellaria pubera
____ Tipularia discolor
____ Trillium _____
____ Viola rotundifolia

____ Adiantum pedatum
____ Asplenum _____
____ Athyrium asplenoi
____ " thalictr
____ Botrychium dissec
____ " oblicu
____ " virgin
____ Dennstaedtia punct
____ Drypopteris interm
____ " noveb
____ Osmunda cinnamome
____ Polypodium poly
____ " virginia
____ Polystichum acros
____ Pteridium latiusc

Figure 1. Form used to record species present in stands formerly containing chestnut.

STAND ANALYSIS FOR STUDY OF PLANT SUCCESSION AFTER CHESTNUT DEATH

Date _____ Crew _____ Elevation _____ Stand No. _____

Location: _____

_____

Direction of slope: N NE E SE S SW W NW

Percentage slope: 0 5 10 15 20 25 30 35 40 50 60 70 80

Humus ____ in. deep. Mull: coarse- medium-fine- firm- twin
Mor: matted- laminated- granular- greasy- fibrous.

Soil type: _____

Outcrops and/or boulders: absent - sparce - plentiful - numerous.

SHRUBS				
Hvy	Lt	Pat	Ind	Abs
15				
10				
5				
3				
1				

HERBS				
Hvy	Lt	Pat	Ind	Abs
4				
3				
2				
1				
½				

REPRODUCTION				
Hvy	Lt	Pat	Ind	Abs
15				
10				
5				
3				
1				

Tree Layer
Coverage in %: 0 5 10 20 30 40 50 60 70 80 90 95 100

Canopy ht.: 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100 ____

STAND DATA
Former type: _____

Present type: _____

Future type: _____

Area of the type: less than 1 acre__; 1-5 acres__; over 5 acres__.

Date of release as determined from increment borings 19____.

Past history (owners, cutting, burning, farming) _____

_____

Notes. _____

_____

Figure 2. Form used for tabulating data on stands formerly containing chestnut.

TREE ANALYSIS FOR STUDY OF PLANT SUCCESSION AFTER CHESTNUT DEATH

Date_____ Crew_____ Total No._____ Plot No._____ Sample No._____

Tree condition: fallen - cut - standing
DBH, _____ inches. Age, _____ years.

Canopy is:(1)still open (at the time of death)
(2)occupied by: seedlings -saplings -shrubs -sprouts
suppressed -subdominant - odominant -dominant

Coverage in %: 0 5 10 20 30 40 50 60 70 80 90 95 100

Height: 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100 _____

SPECIES FILLING THE GAP ARE:

_____;____ft. to the base;___ft. high;___inches DBH.

_____;____ft. to the base;___ft. high;___inches DBH.

_____;____ft. to the base;___ft. high;___inches DBH.

Notes._____

_____

SHRUB LAYER
Coverage in %: 0 5 10 20 30 40 50 60 70 80 90 95 100

Height in feet: 0 1 2 3 4 5 6 7 8 9 10 12 14 16 18 20 22 24 26 28 30

Species._____

REPRODUCTION

_____ 3"6"1'2'4'8'16'32'
_____
_____
_____

A - abundant
C - common
O - occasional
R - rare

HERBACEOUS LAYER

	Hvy	Lt	Pat	Ind	Abs
4					
3					
2					
1					
½					

Species._____

_____

NOTES._____

Figure 3. Form used for tabulating data on individual trees replacing chestnut.

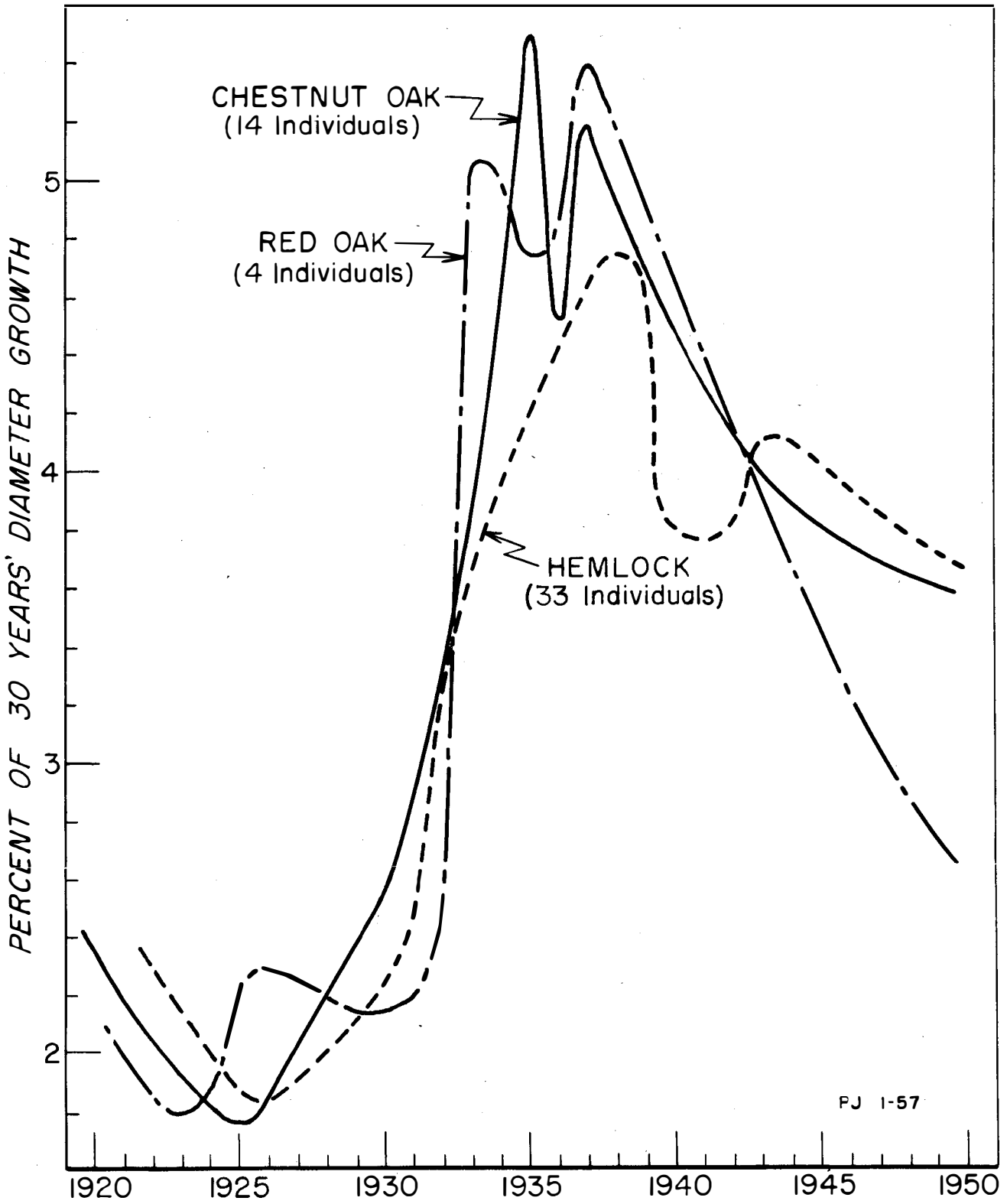

Figure 4.--Relative yearly diameter growth of 3 species of trees after release from chestnut competition.