To the Graduate Council:

I am submitting herewith a thesis written by David E. Flora entitled "The American Chestnut As An Allelopath." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology.

Frank W. Woods

Frank W. Woods, Major Professor

We have read this thesis
and recommend its acceptance:

Clifford C Hamber

Edward Buchner

Accepted for the Council:

L Evans Roth

Vice Chancellor
Graduate Studies and Research

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THE AMERICAN CHESTNUT AS AN ALLELOPATH

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

David E. Flora

June 1977

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ABSTRACT

Evidence is presented that the American chestnut (*Castanea dentata* (Marshall) Borkh.) was an allelopath. Substances of known allelopathic potential including condensed tannins, hydrolyzable tannins, and associated substances gallic acid, ellagic acid, pyrocatechin, pyrogallic acid and acetic acid are found in American chestnut wood and bark.

Water extracts from leaves of chestnut and three other species were used to conduct germination tests using radish seeds. American chestnut, sugar maple (*Acer saccharum*, Marshall), and American beech (*Fagus grandifolia*, Ehrhart) extracts caused a significant reduction in germination. Northern red oak (*Quercus rubra* L.) extract did not.

Changes in the composition of chestnut stands since the blight were studied, utilizing data collected at Coweeta Hydrologic Laboratory, Franklin, North Carolina, and in the Great Smoky Mountains National Park. Stands formerly with a large basal area of chestnut are now mixed oak stands, with mesic species such as cherry birch (*Betula lenta*) and hemlock (*Tsuga canadensis* (L.) Carr.) increasing. Understory and herbaceous species are similar to those present before the blight, with the addition of some mesic herbaceous species.

The almost complete dominance of American chestnut on certain sites cannot be explained by its rapid growth and wide ecological amplitude alone. The release by chestnut of one or more toxins that inhibit formation of mycorrhizae, slow decay of leaf litter, inhibit seed germination, or inhibit the growth of other plants directly seems likely.

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CHAPTER I

INTRODUCTION AND OBJECTIVES

The American chestnut (*Castanea dentata* (Marshall), Borkh.) was one of the most widely distributed forest species in the eastern United States until the first of this century. It ranged throughout deciduous forests of the eastern half of the United States. In Tennessee it was most abundant on the slopes of the Unaka Mountains, and probably reached greatest development in the Smokies, reaching a height of 30 meters, and a diameter of over two meters. It was found on mesic to xeric sites, but was most abundant on slopes and ridgetops at elevations 550 to 1070 meters, sometimes comprising more than 60% of the basal area. Chestnut was important economically, furnishing long-lasting timber for barns and fences, nuts for human and animal consumption, and tannins for the tanning industry (Ashe 1911).

A pathogenic fungus (*Endothia parasitica* (Murr.), P. and W. Anderson), an Ascomycete, introduced into this country from Asia in 1904, spread rapidly from its point of discovery in New York, and by the mid-1930's had eliminated chestnut as an important forest species throughout its range. Since chestnut has a strong sprouting capacity (Ashe 1911), it continues to sprout but is killed back with regularity.

The demise of chestnut and trends in succession after the blight have been studied, but since it has not existed as a dominant tree for over one-half century, many aspects of its ecology have not been studied and may never be well understood. One explanation for its sucess as a species is the probability that the chestnut was a strong allelopath.

An allelopath is a plant from which substances which are phytotoxic or phytostatic are released into its environment by root exudation, leaching from bark and leaves, volatilization, or release following the death of the plant or loss of its organs. The term allelopathy was coined by Molisch (1937) to include interactions between plants, both beneficial and harmful. Muller (1966), Rice (1974) and others have used the term only as related to detrimental effects.

The hypothesis to be examined in this paper is that chestnut was successful in occupying a wide range of habitat and site conditions because it was strongly allelopathic, chemically inhibiting the growth of potential competitors. Implicit is the understanding that it had a wide range of ecological amplitude, which alone will not explain its ubiquitous occurrence and great abundance.

Three approaches were used to demonstrate allelopathy in chestnut. Tests of the effects of chestnut leaf extract on seed germination were conducted. Changes in stand composition since the chestnut blight were documented, and changes in the understory of chestnut stands since the chestnut blight were studied.

Nomenclature and authority primarily follows Radford, Ahles, and Bell (1964), *Guide to the Vascular Flora of the Carolinas*, and secondly, Rehder (1927), *Manual of Cultivated Trees and Shrubs*.

CHAPTER II

CHESTNUT AS A SUSPECT ALLELOPATH

American chestnut leaves, wood, and bark contain several substances know to have allelopathic effects. Most important of these growth inhibitors are various tannins and their derivatives, which occur in the wood, bark, and leaves (Griffith 1921).

Greaves (1918) stated that tannin in the bark of American chestnut is of the catechol type, and that in the wood is of the pyrogallol type. Both are condensed tannins, which are polymers of catechins or flavan-3, 4-diols. Condensed tannins inhibit nitrifying bacteria (Rice and Pancholy 1973), and can slow the decomposition rate of organic matter in soil (Benoit and Starkey 1968 a,b).

Hydrolyzable tannins are also found in American chestnut as are their breakdown products, gallic acid and ellagic acid (Griffith 1921). They are divided into several groups, one of which, the gallotannins, break down to form gallic acid. Gallic acid, ellagic acid, and hydrolyzable tannins have been shown to be inhibitory to nitrogen-fixing and nitrifying bacteria (Rice 1965). Hydrolyzable tannins are usually found in leaves and fruit, while condensed tannins are found in heartwood and bark (Swain 1965).

The tannin content of American chestnut wood is high compared to that of other hardwoods. Nelson and Gravatt (1929) give the tannin content of chestnut sapwood as 2 to 4%, and that of the bark and heartwood as 7 to 12%. Wise and Jahn (1952) found the tannin content of chestnut wood to be 9%, as compared to 2.0 to 3.3% for oaks.

Tannins may serve to defend against insects, (Feeney 1970), herbivores, and fungi (Whittaker 1970). It is thought that tannins inhibit the action of enzymes through their ability to combine with proteins and polysaccharides (Grant 1976).

The resistance of chestnut species to the chestnut blight has been in part related to the kinds of tannins in bark. American chestnut and Japanese chestnut (*C. crenata*, Sieb. and Zucc.) have low and intermediate blight resistance respectively, and have a mixture of catechol and pyrogallol tannins in their bark. Chinese chestnut (*Castanea mollissima* Bl.) is highly resistant to the blight, and its bark contains pyrogallol tannins (Nienstaedt 1953). Tannins have been shown to be concentrated in infected areas of American chestnut trunks (Penn. Chestnut Tree Blight Commission 1913).

Pyrocatechin and pyrogallic acid are associated with chestnut tannin (Gayley 1920). These compounds are phenols and are very likely inhibitory (Rice, personal communication).

Acetic acid is a component of the tannin of American chestnut (Griffith 1921). Acetic acid inhibits germination (Evenari 1949), and is a contributor to soil toxicity (Patrick 1971).

The high tannin content of American chestnut leaves, wood and bark, coupled with the potential for leaching or exudation of these substances, makes it highly likely that chestnut releases tannins and their derivatives into its environment. The known inhibitory effects of these substances, suggest that American chestnut has the chemical potential to be an allelopath of a high order.

CHAPTER III

METHODS AND MATERIALS

Germination Tests

Approximately 10 grams of fresh leaves of American chestnut, northern red oak (*Quercus rubra L.*), sugar maple (*Acer saccharum* Marshall), and American beech (*Fagus grandifolia* Ehrhart) were collected and placed in one hundred milliliters of distilled water. The containers of water and leaves were then placed on a shaker overnight.

Germination tests were made on filter paper in 15 Petri dishes, with 100 radish seeds in each dish. Each of the four extracts was used to water three dishes, and three dishes were used as a control. Each dish was watered with 10 milliliters of one of the leaf extracts or distilled water.

Free toxins in nature are generally thought to be shortlived. They are rapidly broken down or altered by soil microbes (Woods 1960, Winter 1961). Therefore germination was counted after only 24 hours.

Chestnut Stand Studies: Coweeta Hydrologic Laboratory

The Southeastern Forest Experiment Station, United States Forest Service conducted timber inventories at Coweeta Hydrologic Laboratory in Franklin County, North Carolina to establish stand density and growth. The laboratory is located in the Nantahala National Forest in southwestern North Carolina. Stand conditions are similar to those in the Smokies but are at different elevations.

Permanent fifth-acre plots were established in 1934-35 and re-measured in 1969-72. Species, diameter breast height, and number of stems were recorded. Plots in which chestnut comprised 50% or more of the basal area (total of 78) or less than 10% of the basal area (total of 75) in 1934-35 were used in the analysis presented here. It was felt that a clearer picture of successional trends since the blight could be obtained utilizing plots with the extremes of chestnut concentration rather than all of the data available. Plots with a basal area greater than 50% chestnut will hereafter be referred to as "chestnut plots," and those with a basal area less than 10% chestnut as "non-chestnut plots."

Total stems per hectare by dbh class and total basal area per hectare for each species were tabulated for all plots. Percentages of stems and basal area for each species were then calculated. Some shrub species, including Mountain laurel (*Kalmia latifolia* L.) and species of rhododendron (*Rhododendron* spp.), were not counted in the 1930's so they were not included in total figures in the 1960's. Azimuth, elevation, percent slope, and slope position were determined for each plot.

Chestnut Stand Studies: Great Smoky Mountains National Park

Field work was conducted in two former chestnut stands in the eastern end of Great Smoky Mountains National Park, east of Mt. Sterling. One site is on the northeast slope of a spur ridge beside the Mt. Sterling Trail, at about 1280 meters elevation. The second is southeast of the first, near the Asbury Trail on Scottish Mountain. It is on a south sloping ridgetop at about 1220 meters.

Trees were measured on 5 fifteenth-acre plots on each site. Diameters of trees over one inch in diameter breast height were measured and basal area computed.

Seedling and herbaceous vegetation were sampled in spring and in early fall, with 12 plots, each four square meters, being taken on each site. Species frequency was calculated for each species.

CHAPTER IV

RESULTS

Germination Tests

Table 1 contains a summary of results of bioassays. Means of the numbers of germinated radish seeds were separated using Duncan's New Multiple-Range Tests (Steel and Torrie 1960).

Northern red oak extract produced a slight reduction in germination that was not significantly different from the control (Table 1). This might have been expected for a species not known to be allelopathic.

Sugar maple extract produced germination significantly lower than the control. Sugar maple roots are known to produce a growth inhibitor that adversely affects yellow birch (*Betula lutea* Michaux f.)(Tubbs 1970). Gallic acid and ellagic acid in particular were cited by Smith (1976) as exudates of both sugar maple and yellow birch, which also have been shown to inhibit nitrification (Rice and Pancholy 1973).

American beech extract caused a significant reduction in germination. This is in agreement with Smith (1976), who found a higher level of organic acids exuded by the roots of beech than by sugar maple and yellow birch.

American chestnut extract also caused a significant reduction in germination. Chestnut leaves apparently produce a germination inhibitor that can be leached from mature leaves.

TABLE 1

Germination of Radish Seeds as Affected by Leaf Extracts of Trees (Means Separated by DNMR[a])

Treatment (Extract)	Percentage Germination Test 1	2	3	Treatment Mean
Control	79	77	84	80
Quercus rubra	66	66	47	60
Acer saccharum	40	63	51	51
Castanea dentata	44	46	54	48
Fagus grandifolia	32	54	40	42

[a]Vertical lines represent mean separation using Duncan's New Multipl Range Test (Steel and Torrie, 1960). Treatments grouped together are not significantly different. Probablility level is 1%.

Chestnut Stand Studies: Coweeta Hydrologic Laboratory

Site descriptions of all plots were studied to determine whether topographic factors were related to high density of chestnut (Table 2). There was little difference in elevation, slope position, and percent slope. Generally, more chestnut plots (51) occurred on north and east than on south and west aspects (27), while more non-chestnut plots were found on south and west aspects (48) than on north and east (27). However, topography alone did not seem to determine whether a site was predominantly chestnut.

Table 3 reveals the rapid loss of chestnut, which averaged 60% of the basal area of chestnut plots in 1934-35, and only 3.6% in 1969-72. Table 4 shows a similar decline in chestnut stems, from 34.8 to 11.5%.

With the exception of sassafras (*Sassafras albidum* (Nuttall) Nees) (Table 3), all other species in chestnut plots increased in percent basal area following the loss of chestnut. Chestnut oak (*Quercus prinus* L.), northern red oak, and red maple (*Acer rubrum* L.) made largest gains in chestnut plots, while scarlet oak (*Quercus coccinea* Muench.), black oak (*Quercus velutina* Lam.), yellow poplar (*Liriodendron tulipifera* L.), sourwood (*Oxydendrum arboreum* (L.) DC.) and cherry birch (*Betula lenta* L.) had moderate increases.

On non-chestnut plots total basal area increased from 21 square meters per hectare to 26 (Table 5), while on chestnut plots it decreased from 32 square meters per hectare to 26. The most abundant species on non-chestnut plots were pitchpine (*Pinus rigida* Miller), scarlet oak, chestnut oak, black oak and hickories (*Carya* spp.) in both inventories.

TABLE 2

Topography of Coweeta Inventory: 1934-35[1]

		Chestnut more than 50% of basal area No. of Plots	Chestnut less than 10% of basal area No. of Plots
Azimuth			
Degrees	Aspect		
315-360 and 0-45	north	32	9
45-135	east	19	18
135-225	south	13	38
225-315	west	14	10
		78	75
Elevation			
Meters			
610-914		32	48
914-1219		40	23
1219-1402		6	4
		78	75
Position on Slope			
Valley and Cove		10	10
Lower Slope		15	22
Middle Slope		43	35
Upper Slope		8	7
Ridge		2	1
		78	75
Percent Slope			
1-29		5	12
30-59		39	35
60-99		34	28
		78	75

[1] Data From Coweeta Hydrologic Laboratory, U.S. Forest Service Timber Cruise.

TABLE 3

Changes in Basal Area per Hectare Based on 78 Fifth-acre Plots: Chestnut More Than 50% of Basal Area in 1934-35

Species	1934-35		1969-72		Change	
	M^2	%	M^2	%	M^2	%
Castanea dentata	19.05	60.0	0.88	3.6	-18.17	-56.4
Carya spp.	1.81	5.7	1.97	8.0	+ 0.16	+ 2.3
Quercus prinus	1.77	5.5	4.08	10.5	+ 2.31	+ 5.0
Acer rubrum	1.45	4.6	3.09	12.5	+ 1.64	+ 7.9
Quercus rubra	1.10	3.4	2.84	11.5	+ 1.74	+ 8.1
Quercus coccinea	1.00	3.1	1.55	6.3	+ 0.55	+ 3.2
Liriodendron tulipifera	0.76	2.4	1.67	6.7	+ 0.91	+ 4.3
Cornus florida	0.71	2.2	1.16	4.7	+ 0.45	+ 2.5
Robinia pseudo-acacia	0.67	2.1	0.84	3.4	+ 0.17	+ 1.3
Nyssa sylvatica	0.66	2.1	0.79	3.2	+ 0.13	+ 1.1
Quercus velutina	0.57	1.8	1.14	4.6	+ 0.57	+ 2.8
Oxydendrum arboreum	0.44	1.4	0.96	3.9	+ 0.52	+ 2.5
Quercus alba	0.33	1.0	0.69	2.8	+ 0.36	+ 1.8
Tsuga canadensis	0.04	0.1	0.21	0.7	+ 0.17	+ 0.6
Amelanchier arborea	0.04	0.1	0.18	0.7	+ 0.14	+ 0.6
Acer pennsylvanicum	0.06	0.2	0.20	0.8	+ 0.14	+ 0.6
Sassafras albidum	0.18	0.5	0.13	0.5	- 0.05	0.0
Betula lenta	0.26	0.8	0.74	3.0	+ 0.48	+ 2.2
Magnolia sp.	0.07	0.2	0.20	0.8	+ 0.13	+ 0.6
Acer saccharum	0.05	0.2	0.17	0.8	+ 0.12	+ 0.6
Prunus spp.	0.10	0.3	0.19	0.8	+ 0.09	+ 0.5
Magnolia acuminata	0.09	0.3	0.17	0.7	+ 0.08	+ 0.4
Betula lutea	0.07	0.2	0.28	1.2	+ 0.21	+ 1.0
Others	0.57	1.8	2.06	8.3	+ 1.49	+ 6.5
Total	31.85	100.0	26.19	100.0	- 5.66	0.0

[1]Data from Coweeta Hydrologic Laboratory, U. S. Forest Service Timber Cruise.

TABLE 4

Changes in Stems per Hectare Based on 78 Fifth-acre Plots: Chestnut More Than 50% of Basal Area in 1934-35.[1]

Species	1934-35		1969-72		Change	
	M^2	%	M^2	%	M^2	%
Castanea dentata	1053	34.8	218	11.5	- 835	-23.3
Acer rubrum	304	10.0	308	16.3	+ 4	+ 6.3
Carya spp.	267	8.8	159	8.4	- 108	- 0.4
Cornus florida	260	8.6	343	18.1	+ 83	+ 9.5
Quercus prinus	198	6.5	146	7.7	- 52	+ 1.2
Liriodendron tulipifera	107	3.5	75	4.0	- 32	+ 0.5
Nyssa sylvatica	103	3.4	58	3.1	- 45	- 0.3
Quercus coccinea	78	2.6	39	2.1	- 39	- 0.5
Sassafras albidum	71	2.3	19	1.0	- 52	- 1.3
Oxydendrum arboreum	68	2.2	71	3.7	+ 3	+ 1.5
Robinia pseudo-acacia	67	2.2	27	1.4	- 40	- 0.8
Quercus rubra	67	2.2	41	2.2	- 26	0.0
Quercus alba	34	1.1	21	1.2	- 13	+ 0.1
Quercus velutina	32	1.1	23	1.2	- 9	+ 0.1
Betula lenta	28	0.9	70	3.5	+ 42	+ 2.6
Acer pennsylvanicum	25	0.8	36	1.9	+ 11	+ 1.1
Acer saccharum	21	0.7	32	1.7	+ 11	+ 1.0
Amelanchier arborea	16	0.5	30	1.6	+ 14	+ 1.1
Tsuga canadensis	3	0.1	19	1.0	+ 16	+ 0.9
Others	235	7.7	159	8.4	- 76	+ 0.7
Total	3037	100.0	1894	100.0	-1143	0.0

[1]Data from Coweeta Hydrologic Laboratory, U. S. Forest Service Timber Cruise.

TABLE 5

Changes in Basal Area per Hectare Based on 75 Fifth-acre Plots: Chestnut Less Than 10% of Basal Area in 1934-35.[1]

Species	1934-35		1969-72		Change	
	M^2	%	M^2	%	M^2	%
Pinus rigida	3.05	14.8	2.90	11.2	- 0.15	- 3.6
Quercus coccinea	2.94	14.2	3.77	14.5	+ 0.83	+ 0.3
Quercus prinus	1.84	8.9	2.74	10.6	+ 0.90	+ 1.7
Quercus velutina	1.31	6.4	1.71	6.6	+ 0.40	+ 0.2
Carya spp.	1.09	5.3	1.35	5.2	+ 0.26	- 0.1
Acer rubrum	0.93	4.6	1.80	6.9	+ 0.87	+ 2.3
Quercus alba	0.93	4.6	1.20	4.6	+ 0.27	0.0
Castanea dentata	0.95	4.6	0.18	0.7	- 0.77	- 3.9
Betula lenta	0.88	4.3	0.85	3.2	- 0.03	- 1.1
Liriodendron tulipifera	0.83	4.0	1.55	6.0	+ 0.72	+ 2.0
Nyssa sylvatica	0.78	3.8	0.72	2.8	- 0.06	- 1.0
Quercus rubra	0.64	3.1	0.94	3.6	+ 0.30	+ 0.5
Tsuga canadensis	0.57	2.8	1.36	5.2	+ 0.79	+ 2.4
Cornus florida	0.47	2.3	0.67	2.6	+ 0.20	+ 0.3
Robinia pseudo-acacia	0.42	2.0	0.37	1.4	- 0.05	- 0.6
Oxydendrum arboreum	0.40	1.9	1.01	3.9	+ 0.61	+ 2.0
Tilia heterophylla	0.36	1.8	0.67	2.6	+ 0.31	+ 0.8
Castanea pumila	0.33	1.6	0.05	0.2	- 0.28	- 1.4
Fraxinus americana	0.30	1.4	0.09	0.4	- 0.21	- 1.0
Aesculus octandra	0.24	1.2	0.35	1.4	+ 0.11	+ 0.2
Sassafras albidum	0.22	1.1	0.11	0.3	- 0.11	- 0.8
Quercus falcata	0.22	1.1	0.07	0.3	- 0.15	- 0.8
Betula lutea	0.21	1.0	0.78	3.0	+ 0.57	+ 2.0
Others	0.66	3.2	0.72	2.8	+ 0.06	- 0.4
Total	20.57	100.0	25.96	100.0	+ 5.39	0.0

[1]Data from Coweeta Hydrologic Laboratory, U. S. Forest Service Timber Cruise.

Red maple and yellow poplar showed large increases in basal area. Increases and decreases were about evenly divided between species.

Total stems in chestnut plots declined from 3037 per hectare to 1894. Red maple, hickories, chestnut oak, and dogwood (*Cornus florida* L.) had the most stems in both inventories (Table 4). American chestnut continued to have a high percentage of stems in the 1960's because of its large number of stump sprouts and seedlings. Northern red oak, though with a large basal area was not very abundant, and further declined in numbers between inventories. Cherry birch made a large gain in number of stems, and may become a more important species in chestnut plots.

Total stems in non-chestnut plots declined from 2699 her hectare to 1938 per hectare (Table 6). Hickories, red maple, yellow poplar, and blackgum (*Nyssa sylvatica* Marshall) were most numerous when remeasured. Oaks and hickories were important in non-chestnut plots, but other species were also abundant.

Chestnut Stand Studies: Great Smoky Mountains National Park

Ten species had stems one inch or greater at the Mt. Sterling site (Table 7). Red maple, silverbell (*Halesia carolina* L.), and northern red oak were most numerous, while cherry birch had increased in numbers since the death of chestnut.

Northern red oak had the largest total basal area, followed by chestnut oak and red maple (Table 7). Some oaks were 100 years old and greater, indicating that they were present when chestnut was present. Overall basal area was 23.2 square meters per hectare.

TABLE 6

Changes in Stems per Hectare Based on 75 Fifth-acre Plots: Chestnut Less Than 10% of Basal Area in 1934-35.[1]

Species	1934-35		1969-72		Change	
	No.	%	No.	%	No.	%
Liriodendron tulipifera	239	8.9	72	3.7	-167	- 5.2
Carya spp.	237	8.8	148	7.7	- 89	- 1.1
Nyssa sylvatica	221	8.2	120	6.2	-101	- 2.0
Acer rubrum	204	7.6	262	13.2	+ 58	+ 5.6
Castanea dentata	202	7.5	85	4.4	-117	- 3.1
Cornus florida	175	6.5	219	11.4	+ 44	+ 4.9
Quercus coccinea	169	6.3	94	4.9	- 75	- 1.4
Castanea pumila	146	5.4	22	1.2	-124	- 4.2
Pinus rigida	131	4.9	72	3.7	- 59	- 1.2
Quercus prinus	121	4.5	99	5.1	- 22	+ 0.6
Quercus velutina	108	4.0	54	2.9	- 54	- 1.1
Oxydendrum arboreum	98	3.5	135	7.0	+ 37	+ 3.5
Quercus alba	102	3.7	54	2.8	- 48	- 0.9
Betula lenta	81	3.0	53	2.7	- 28	- 0.3
Robinia pseudo-acacia	49	1.8	20	1.0	- 29	- 0.8
Sassafras albidum	42	1.6	33	1.6	- 9	0.0
Quercus rubra	31	1.2	23	1.2	- 8	0.0
Prunus spp.	30	1.0	4	0.2	- 26	- 0.8
Quercus falcata	28	1.0	2	0.1	- 26	- 0.9
Tsuga canadensis	21	0.8	97	5.0	+ 76	+ 4.2
Tilia heterophylla	13	0.5	110	5.7	+ 97	+ 5.2
Amelanchier arborea	12	0.4	23	1.2	+ 11	+ 0.8
Others	239	8.9	137	7.1	-102	- 1.8
Total	2699	100.0	1938	100.0	-761	0.0

[1]Data from Coweeta Hydrologic Laboratory, U. S. Forest Service Timber Cruise.

TABLE 7

Woody Stems Over 2.5 Centimeters Diameter Breast Height: Per Hectare: 1976: Mt. Sterling Site, Great Smoky Mountains.

Species	Basal Area		Stems	
	M^2	%	No.	%
Quercus rubra	18.12	78.1	59	15.9
Quercus prinus	2.19	9.4	30	7.8
Acer rubrum	1.70	7.3	111	29.4
Halesia carolina	0.74	3.1	82	21.6
Acer saccharum	0.34	1.4	22	5.9
Tsuga canadensis	0.04	0.2	15	3.8
Betula lenta	0.04	0.2	30	7.8
Castanea dentata	0.01	0.1	15	3.8
Acer pennsylvanicum	0.01	0.1	7	2.0
Picea rubens	0.01	0.1	7	2.0
Total	23.20	100.0	378	100.0

Sugar maple, cucumber magnolia (*Magnolia acuminata* L.) hemlock (*Tsuga canadensis* (L.) Carr.) and American ash (*Fraxinus americana* L.) had invaded since the death of chestnut. The stand had a mesic character and seemed to be becoming more so. The former dominance of chestnut was still evident from the numerous large logs and dead snags still present (Figures 1 and 2).

The stand on Scottish Mountain had twelve species with stems one inch or greater, of which red maple, northern red oak and hickories were most numerous (Table 8). The largest specimens in this stand were oaks. Northern red oak was dominant in total basal area, with white oak (*Quercus alba* L.) and red maple also important. Total basal area was 15.3 square meters per hectare.

The site was more xeric than the Mt. Sterling stand because of its southern exposure. Hickories, white pine (*Pinus strobus* L.) and pitch pine were present. Hemlock and striped maple (*Acer pennsylvanicum* L.) had recently become established.

Northern red oak and red maple seedlings were abundant in both stands (Tables 9 and 10). White oak and chestnut oak reproduction was abundant on Scottish Mountain, while chestnut oak seedlings were poorly represented on the more mesic Mt. Sterling site. Some mesic species were reproducing on the drier Scottish Mountain site such as sugar maple, striped maple and silverbell which were not present at the time of the chestnut death.

Composition of these stands was somewhat different from the composite composition of the Coweeta "chestnut plots," few of which were as high



FIGURE 1

Mt. Sterling site in the Great Smoky Mountains National Park, May 1976. Two leaning dead chestnuts and several fallen logs, as well as young maples, silverbells, and oaks are present.



FIGURE 2

Mt. Sterling site in the Great Smoky Mountains National Park, May 1976. Numerous fallen chestnut logs show the former importance of chestnut on this site.

TABLE 8

Woody Stems Over 2.5 Centimeters Diameter Breast Height: Per Hectare: 1976: Scottish Mt. Site, Great Smoky Mountains.

Species	Basal Area		Stems	
	M^2	%	No.	%
Quercus rubra	10.84	71.0	104	17.0
Quercus alba	1.89	12.3	37	6.1
Acer rubrum	1.25	8.2	282	46.8
Robinia pseudo-acacia	0.45	2.8	7	1.2
Quercus prinus	0.41	2.7	22	3.6
Carya sp.	0.29	1.8	89	14.5
Pinus rigida	0.09	0.6	7	1.2
Tsuga canadensis	0.03	0.2	7	1.2
Castanea dentata	0.01	0.1	30	4.8
Pinus strobus	0.01	0.1	7	1.2
Amelanchier arborea	0.01	0.1	7	1.2
Acer pennsylvanicum	0.01	0.1	7	1.2
Total	15.29	100.0	606	100.0

TABLE 9

Woody Seedlings Under 2.5 Centimeters Diameter Breast Height: 1976: Mt. Sterling Site, Great Smoky Mountains.

Species	Stems per Hectare	Percentage
Quercus rubra	19,580	28.6
Acer rubrum	15,831	23.2
Halesia carolina	13,956	20.3
Acer pennsylvanicum	5,416	7.9
Acer saccharum	3,125	4.6
Amelanchier arborea	3,125	4.6
Betula lenta	2,291	3.4
Prunus serotina	2,083	3.0
Magnolia acuminata	1,250	1.6
Quercus prinus	833	1.2
Quercus alba	208	0.4
Carya spp.	208	0.4
Sassafras albidum	208	0.4
Fraxinus americana	208	0.4
Total	68,322	100.0

TABLE 10

Woody Seedlings Under 2.5 Centimeters Diameter Breast Height: 1976: Scottish Mt. Site, Great Smoky Mountains.

Species	Stems per Hectare	Percentage
Acer rubrum	20,205	36.6
Quercus rubra	9,582	17.4
Quercus prinus	8,124	14.8
Sassafras albidum	6,874	12.5
Quercus alba	4,166	7.6
Carya sp.	2,083	3.8
Amelanchier arborea	1,875	3.4
Prunus serotina	833	1.5
Betula lutea	208	0.4
Halesia carolina	208	0.4
Acer saccharum	208	0.4
Acer pennsylvanicum	208	0.4
Pinus strobus	208	0.4
Picea rubens	208	0.4
Total	54,990	100.00

as 1220 meters. Yellow poplar and dogwood, important at Coweeta, were absent from the Smokies stands, most likely because of their high altitude.

Chestnut Stand Understory

Shrubs present on one or both of these Smokies sites included the heaths flame azalea (*Rhododendron calendulaceum* (Michaux.) Torrey), mountain laurel and *Vaccinium* sp. Heaths were common in the understory of chestnut woods. Mapleleaf viburnum (*Viburnum acerifolium* L.), oilnut (*Pyrularia pubera* Michaux.), *Rubus* sp., and leatherwood (*Dirca palustris* L. were also present and were found in chestnut woods (Braun 1942, Barclay 1957).

Melampyrum lineare Desr., *Viola hastata* Michaux., and *Prenanthes* sp. L. were the most typical herbaceous species of the two Great Smoky Mountains stands (Table 11), occurring in dry open woods. Other species important on the Scottish Mountain site included *Chimaphila maculata* (L.) Pursh. and *Potentilla canadensis* L. (Table 11), both typical of dry, open woods.

Stellaria pubera Michaux., *Aster* sp. L., and *Solidago* sp. were other important taxa on the Mt. Sterling site, occurring on sites where chestnut was dominant (Braun 1942). The majority of other species on these sites were found in chestnut woods or dry, open woods.

The north-facing Mt. Sterling site had several mesic species including *Disporum lanuginosum* (Michaux) Nicholson, *Smilacina racemosa* (L.) Desf., *Trillium grandiflorum* (Michaux.) Salisbury, *Anemone quinquefolia* (L.) and *Cardamine diphylla* (Michaux.) Wood (Table 11). Braun (1942)

TABLE 11

Herbaceous Species on Smokies Sites: 1975-76: Number of Stems and Frequency Given for Month of Greatest Abundance (April or October)

Species	Mt. Sterling Site		Scottish Mt. Site	
	Stems No.	Frequency %	Stems No.	Frequency %
Silene stellata	1	8.3	2	8.3
Goodyera pubescens	24	25.0	2	16.7
Conopholis americana	5	25.0	2	16.7
Chimaphila maculata	22	16.7	25	58.3
Pedicularis canadensis	20	16.7	24	16.7
Viola hastata	145	66.7	118	33.3
Viola emarginata	5	16.7	3	16.7
Stellaria pubera	53	58.3	57	16.7
Potentilla canadensis	7	8.3	139	16.7
Prenanthes sp.	2103	100.0	116	50.0
Galium sp.	24	8.3	5	8.3
Panicum sp.	3	16.7	13	25.0
Melampyrum lineare	261	75.0	725	91.7
Houstonia purpurea	8	25.0	11	8.3
Aster sp.	20	50.0	21	6.7
Solidago sp.	50	83.3	25	16.7
Smilacina racemosa	4	16.7	2	8.3
Cardamine diphylla	25	8.3	-	-
Anemone quinquefolia	7	8.3	-	-
Ranunculus sp.	3	8.3	-	-
Disporum lanuginosum	1	8.3	-	-
Trillium grandiflorum	2	8.3	-	-
Epigaea repens	-	-	2	16.7
Zizia trifoliata	-	-	12	16.7
Thaspium trifoliatum	-	-	4	8.3
Lysimachia quadrifolia	-	-	2	8.3

TABLE 11 (continued)

Species	Mt. Sterling Site Stems No.	Mt. Sterling Site Frequency %	Scottish Mt. Site Stems No.	Scottish Mt. Site Frequency %
Gaultheria procumbens	-	-	3	8.3
Galax aphylla	-	-	42	8.3
Eupatorium rugosum	-	-	11	16.7
Gentiana sp.	-	-	4	8.3

found all of these in mixed mesophytic communities of the Cumberland Mountains. All but *Anemone quinquefolia* and *Cardamine diphylla* also occurred in chestnut communities in the Cumberlands.

Thelypteris noveboracensis (L.) Nieuwland was the only fern present in these Smokies stands, occurring on the Mt. Sterling site. *Thelypteris noveboracensis*, *Anemone quinquefolia* and *Cardamine diphylla* are herbaceous species presently found on these former chestnut stands that probably did not occur there when chestnut was dominant. While there did not appear to be dramatic changes in herbaceous vegetation, the data was included in Table 11 to provide a detailed record of herbaceous vegetation of these stands some 40 years after chestnut death.

CHAPTER V

DISCUSSION

American chestnut leaves, wood and bark have been shown to contain several substances of known allelopathic potential including tannins and their derivatives. Several of these substances inhibit nitrification, slow decomposition of organic matter in soil, and inhibit seed germination.

Many metabolites are leached from leaves in nature (Tukey 1966). A toxin that can be leached from leaves has the potential to cause changes in surrounding vegetation by inhibiting germination of seeds or by having phytotoxic or phytostatic effects on existing plants.

A water extract of chestnut leaves caused a reduction in germination of radish seeds. Although radish is not a native component of the forest, it was used because the seeds are easily obtained and germinate rapidly. The tests demonstrated the presence of a significant amount of a toxin in chestnut leaves.

Present status and trends in reproduction at Coweeta indicate that both former chestnut and non-chestnut plots are, and will likely remain, mixed oak communities with hickories, red maple, yellow poplar, and sourwood as dominant components. Both oaks and hickories are important in chestnut replacement (Korstian and Stickel 1927, Keever 1953, Nelson 1955). The forest type replacing the oak-chestnut forest on the Coweeta plots seems to be the oak-association complex discussed by Aughanbaugh (1935) and Woods and Shanks (1959). While hickories are abundant, oaks are clearly the dominant taxa.

The former chestnut stands in Great Smoky Mountains National Park are now mixed oak stands, with sugar maple, silverbell and cherry birch as associates. Both areas have shown an increase in the abundance of mesic species since the time of the chestnut blight.

Chestnut sometimes formed almost pure stands after disturbances such as clearcutting and fire (Baker 1925, West 1970). It had a rapid growth rate that permitted it to overtop such species as yellow poplar on dry sites (Ayres and Ashe 1905). Even so, this does not explain its almost complete dominance on certain sites where more mesic species are now able to thrive.

Herbaceous and shrub species on former chestnut sites are similar to those that occurred under chestnut, with additional mesic species which apparently were able to invade following death of chestnut. Mesic, herbaceous plants are often sparce in forests where oaks and chestnut are dominant. The lack of shade in early spring, caused by the normal late leafing out of oaks and chestnut, is partly responsible (Braun 1940).

Leaf litter is more persistent in oak-chestnut forests than in more mesic deciduous forests. This may in part be due to the inhibition of decomposition by leaf tannins of oaks and chestnut (Benoit and Starkey 1968b). Water-soluble substances contained in hardwood and pine leaf litter have been shown to inhibit mycorrhizal fungi (Melin 1948). Toxins are known to be released from leaf litter of sycamore (*Platanus occidentalis* L.) (Al-Naib and Rice 1971) which affect species growing under its canopy.

Whittaker (1970), in discussing allelopathy, said "most effects

will be effects of degree - relative effects on population level and on extent of a population's distribution in a given direction - rather than obvious exclusions and complete incompatibilities of species." This is probably the case with chestnut. Braun (1940) states that, "the boundary between the mixed mesophytic communities and the oak-chestnut communities is placed where the influence of the (oak-chestnut) canopy is reflected in inferior layers." There was not a complete exclusion of other species, as with eucalyptis (*Eucalyptis globulus* Lab.)(del Moral and Muller 1969), where bare areas occur under the canopy. Rather chestnut was able to reduce the numbers of its competitors and perhaps delay invasion of more mesic species.

Toxins produced by chestnut seem to have had an additive effect with its superior growth rate which made it exceptionally successful as a forest species. The release by American chestnut of one or more toxins that affected other vegetation through changes in rate of litter decomposition, inhibition of nitrification, inhibition of mycorrizae formation, or direct inhibition seems likely.

American chestnut is no longer present as a canopy tree in areas where it may have dominated partly through allelopathy, so that understanding the role it played in certain communities is therefore difficult. More extensive research should be conducted to identify the specific toxins involved and their method of release into the environment.

Germination tests should be conducted using seeds of native trees and herbs, both species that commonly occurred with chestnut and those found in mixed mesophytic communities. Tests of germination of native

seeds, such as white oak in chestnut leaf litter might reveal whether toxins are released from decaying leaves. These should be conducted with ecotypes of American chestnut from other areas, as well as in the southern Appalachians.

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VITA

David Flora was born in Winston-Salem, North Carolina on April 26, 1952. His family relocated in Westminster, Maryland in 1952. He attended public primary and secondary schools in Carroll County, Maryland and was graduated from South Carroll High School in June, 1970. He attended Bridgewater College, Bridgewater, Virginia from September, 1970 to June, 1974 when he received a Bachelor of Arts degree in Biology. He began graduate study at The University of Tennessee, Knoxville in September, 1974.