

THE REPLACEMENTS OF AMERICAN CHESTNUT: A RANGE-WIDE ASSESSMENT BASED ON DATA FROM FOREST INVENTORY AND PUBLISHED STUDIES

G. Geoff Wang and Huifeng Hu¹

American chestnut [*Castanea dentata* (Marshall) Borkh.] was a dominant or co-dominant species in the upland forests of much of eastern North America (Braun 1950). It was one of the most widely distributed species in eastern deciduous forest, with its main range from southern Maine all the way to central Mississippi (fig. 1). Stands with American chestnut as a significant canopy tree covered 84 million acres, typically in mixture with oaks (*Quercus* spp.) and other deciduous species, but may have occasionally formed a pure stand (Wang and others 2013). American chestnut was also the largest tree in the eastern deciduous forests. It might have grown up to 130 feet tall and 10 feet in diameter and lived up to 600 years of age. No single species today has achieved its abundance in the eastern deciduous forest.

American chestnut was an economically important tree species. It was a good timber species, with a tall and straight trunk, and provided 25 percent of all harvested hardwood timber at the turn of the 20th century. The wood of American chestnut was of very high quality, with straight grain and high resistance to decay. American chestnut produced tasty nuts, consumed by humans and animals, with a dependable crop every year. Another byproduct was tannin, which was important to leather industry. Recent studies also support that American chestnut was the fastest growing tree species in the eastern deciduous forest. So it is not surprising that American chestnut was regarded as one of the most promising trees for forest management by the Society of American Foresters.

However, the great potential of American chestnut to modern forestry was never realized because of an introduced fungus, known as

chestnut blight (*Cryphonectria parasitica*). The fungus was likely introduced with imported nursery stock from Asia and was first detected in 1904 (Wang and others 2013). The fungus entered the cambium and girdled trees, effectively shutting down the water supply from the roots; it killed almost every tree it infected. After its first detection in 1904, chestnut blight spread quickly. By the 1950s, the infestation covered the entire range of American chestnut, killing nearly all American chestnut trees. However, because of its prolific vegetative regeneration and the fact that blight does not affect small stems, American chestnut did not become extinct. In stands previously supporting American chestnut, small chestnut sprouts persist and manage to survive repeated top kills. In open areas, American chestnut can even produce fruit before it is attacked and killed by blight.

Which species have replaced American chestnut in the canopy 60 to 100 years after the blight? Although there were many local studies (fig. 1), a range-wide assessment has not yet been conducted. In this study, we performed such an assessment based on the most recent data obtained through the Forest Inventory and Analysis (FIA) program of the USDA Forest Service as well as data from published studies. Specifically, we assessed the current status of American chestnut based on FIA data, determined what species have replaced American chestnut based on FIA data and published studies, and compared the results.

We acquired data from the most recent (2001 to 2009) measurements of Phase II FIA plots. Study plots were selected if: (1) one or more subplots have live or dead American chestnut trees, saplings, or seedlings; (2) all subplots are

¹Professor, Clemson University, School of Agricultural, Forest and Environmental Sciences, Clemson, SC 29634; and Associate Professor, Chinese Academy of Sciences, Institute of Botany, Beijing, China.

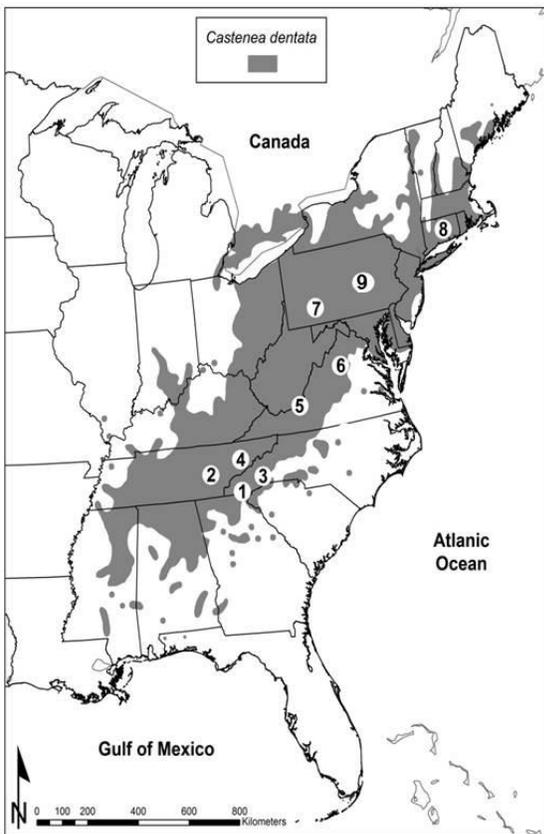


Figure 1--Data from the following published studies are used in the our analysis: (1) Nelson 1955, Elliot and Swank 2008; (2) Myers and others 2004; (3) Keever 1953; (4) Woods and Shanks 1959; (5) Stephenson 1974, McCormick and Platt 1980, Stephenson 1986; (6) Karban 1978; (7) Mackey and Sivec 1973; (8) Korstian and Stickel. 1927; (9) Aughanbaugh 1935.

forested; and (3) subplots are located within the contiguous part of the native range of American chestnut distribution. As a result, we selected 512 plots from 16 states. Importance value of each species was calculated separately for trees (≥ 12.7 cm d.b.h.) and saplings (2.54 to 12.7 cm d.b.h.) on each plot. Diameter distributions of living American chestnut stems (fig. 2) reveal that the majority of American chestnut live stems are seedlings and saplings, with only 5 percent of the plots having any stems ≥ 12.7 cm d.b.h. (4 inches) which is defined as a tree in our study. American chestnut was primarily replaced by oaks [predominantly chestnut oak (*Q. prinus* L.) and northern red oak (*Q. rubra* L.)], followed by red maple (*Acer rubrum* L.), hickories (*Carya* spp.), and other mesophytic species [e.g., yellow poplar (*Liriodendron tulipifera* L.)] (table 1).

Pines (*Pinus* spp.) rarely replaced American chestnut although some replacements by eastern white pine (*P. strobus* L.) were observed. Based on the current population structure, the dominance of oaks is not likely sustainable while the dominance of red maple and other mesophytic species will increase in the future (table 1). This result confirms that oaks are not regenerating well relative to their dominance in the canopy as widely reported in eastern deciduous forests (e.g., Nowaki and Abrams 2008).

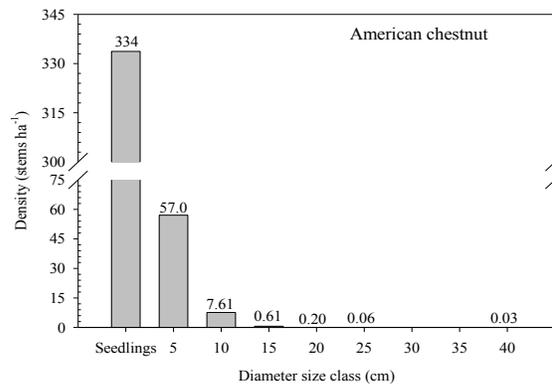


Figure 2--Diameter size-class distribution of living American chestnut stems based on the most recent FIA phase II plot data from 16 states.

We compiled data derived from 13 published studies on composition change after blight in nine different locations (fig. 1). Among them, five studies had both pre- and post-measurements. Importance value was either obtained directly or calculated from reported data. Results on the replacements of American chestnut based on the analysis of these published studies are given in table 1. These results collaborate well with results from the analysis of FIA data (table 1).

In conclusion, American chestnut is rarely found in the overstory but remains abundant in the understory. Oaks are the predominant replacement species for American chestnut, followed by maples. Maples and other shade-tolerant species are currently replacing oaks in the canopy. Results from the analysis of published studies support findings based on FIA data, giving confidence to our range-wide assessment.

Table 1--Importance values of major tree species currently occurring in the stands with American chestnut as a significant component before blight. Species are separated into trees (d.b.h. \geq 12.7 cm) and saplings ($2.54 \leq$ d.b.h. $<$ 12.7 cm)

Species	-----Tree-----		---Sapling---	
	FIA ^a	LIT ^b	FIA	LIT
<i>Quercus</i> spp.	48.7	46.9	14.4	16.9
<i>Acer</i> spp.	15.5	13.9	28.6	26.9
<i>Pinus</i> spp.	7.3	1.4	4.7	0.7
<i>Liriodendron tulipifera</i>	4.8	2.7	3.0	0.1
<i>Oxydendrum arboreum</i>	3.9	1.3	5.9	1.2
<i>Carya</i> spp.	3.7	6.8	2.8	1.8
<i>Betula</i> spp.	3.5	3.9	4.3	2.7
<i>Nyssa sylvatica</i>	2.0	1.7	9.7	4.5
<i>Tsuga canadensis</i>	1.5	2.0	2.1	0.5
<i>Fagus grandifolia</i>	1.1	0.2	2.3	0.8
<i>Magnolia</i> spp.	1.0	0.4	1.3	0.8
<i>Castanea dentata</i>	0.2	1.8	4.6	3.6
<i>Sassafras albidum</i>	0.6	0.6	2.8	7.0
<i>Amelanchier</i> spp.	0.4	0.5	2.5	2.4
<i>Prunus</i> spp.	0.6	2.5	2.0	1.6
<i>Cornus florida</i>	0.1	2.2	1.7	1.5

^aFIA = analyses based on forest inventory and analyses program.

^bLIT = analyses based on published studies.

LITERATURE CITED

Aughanbaugh, J.E. 1935. Replacement of the chestnut in Pennsylvania. Bull. 54. Harrisburg, PA: Commonwealth of Pennsylvania, Department of Forests and Waters. 38 p.

Braun, E.L. 1950. Deciduous forests of eastern North America. Philadelphia, PA: Blakiston. 596 p. Elliott, K.J.; Swank, W.T. 2008. Long-term changes in forest composition and diversity following early logging (1919-1923) and the decline of American chestnut (*Castanea dentata*). Plant Ecology. 197: 155-172

Karban, R. 1978. Changes in an oak-chestnut forest since the chestnut blight. Castanea. 43: 221-228.

Keever, C. 1953. Present composition of some stands of former oak-chestnut forest in the southern Blue Ridge Mountains. Ecology. 34: 44-54.

Korstian, C.F.; Stickel, P.W. 1927. The natural replacement of blight-killed chestnut in the hardwood forests of the northeast. Journal of Agricultural Research. 34: 631-648.

Mackey, H.E.; Sivec, N. 1973. The present composition of a former oak-chestnut forest in the Allegheny Mountains of western Pennsylvania. Ecology. 54: 915-919.

McCormick, J.F.; Platt, R.B. 1980. Recovery of an Appalachian forest following the chestnut blight or Catherine Keever-you were right! American Midland Naturalist. 104: 264-273.

Myers, B.R.; Walck, J.L.; Blum, K.E. 2004. Vegetation change in a former chestnut stand on the Cumberland Plateau of Tennessee during an 80-year period (1921-2000). Castanea. 69: 81-91.

Nelson, T.C. 1955. Chestnut replacement in the southern highlands. Ecology. 36: 352-353

Nowacki, G.J.; Abrams, M.D. 2008. The demise of fire and "mesophication" of forests in the eastern United States. BioScience. 58: 123-138.

Stephenson S.L. 1974. Ecological composition of some former oak-chestnut communities in western Virginia. Castanea. 39: 278-286.

Stephenson, S.L. 1986. Changes in a former chestnut-dominated forest after a half century of succession. American Midland Naturalist. 116: 173-179

Wang, G.G.; Knapp, B.O.; Clark, S.L.; Mudder, B.T. 2013. The silvics of *Castanea dentata* (Marsh.) Borkh., American chestnut, Fagaceae (beech family). Gen. Tech. Rep. SRS-GTR-173. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 18 p.

Woods, F.W.; Shanks, R.E. 1959. Natural replacement of chestnut by other species in the Great Smoky Mountains National Park. Ecology. 40: 349-361.