

Ecology and Paleoecology of American Chestnut in Eastern North American Forests

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ABSTRACT. Recent surveys of surviving American chestnut populations demonstrate that chestnut sprout clones are an important part of the understory in many eastern woodlands, and may be increasing as a percentage of total stand biomass. Studies in southern New England indicate that most chestnut sprouts originated as seedlings and were never associated with former canopy-dominant trees. The distribution of these sprouts probably reflects the pattern of chestnut seedling establishment in New England at a time when agricultural lands were being abandoned, and forest trees were invading old fields surrounding small woodlots. Woodlands with many logs from former large chestnut trees and few surviving sprouts may indicate that chestnut was not reproducing in some former chestnut stands. These results are used to construct a model for chestnut reproduction as a two-step process, namely seedling establishment followed many years later by the release of suppressed stems. Comparative studies of chestnut and chinquapin indicate that both species possess similar growth forms, but that chestnut exhibits sprouting characteristics suited for survival as a canopy tree, while chinquapin exhibits sprouting characteristics suited for multiple cycles of release and reversion to shrub form. Further insight into the chestnut ecology was obtained by studying the frequency of chestnut pollen in bogs, forest hollows and soils at a site near the modern

range limit of chestnut in northcentral Massachusetts. Pollen data from bogs indicates that chestnut increased to approximately 15 percent of the total forest about 2000yr ago, but may have been present at much lower frequencies as much as 4500 yr ago. Pollen data from soils indicate that the regionally averaged chestnut frequency inferred from bog sediments represents the average of large cyclic variations in chestnut at specific locations, with local increases in chestnut pollen following disturbances such as wind-storm and fire. These results and other data indicate the abrupt increase in chestnut pollen about 2000 yr ago at most sites in southern New England represents a subtle and complex change in disturbance regime, and is not the simple result of climate Change or delayed migration.

American chestnut (*Castanea dentata* (Marsh.) Borkh.) was an important tree in the eastern deciduous forests of North America (3), but was removed from the forest canopy after 1900 by an introduced pathogen (2), the chestnut blight fungus (*Cryphonectria parasitica* Murr. Barr). As a result, relatively little is known about the ecological characteristics of chestnut in preblight forests (20). Renewed interest in the ecology of chestnut has resulted from several factors. These include an interest in reconstructing the role of chestnut in preblight forests (5,

6), the apparent association of chestnut with late-Holocene climate changes inferred from pollen data (12, 22), the unexplained abundance of chestnut sprouts in modern forests (1, 13, 14, 21), and an interest in understanding how chestnut ecology may relate to the control of blight and the establishment of blight-resistant chestnut clones in future forests (8). This paper reviews more than a decade of research on chestnut ecology and discusses how these results may be used to interpret the role of chestnut in prehistoric forests inferred from studies of fossil pollen in New England.

MATERIALS AND METHODS

Mapping and distribution. The locations of chestnut sprout clones and large logs and stumps of former chestnut trees were mapped at several locations in New England (USA). Most of these study sites are in south-central Connecticut, northeastern Massachusetts and southern New Hampshire (12, 13, 14). Chestnut population densities were characterized as absent, low (less than 20 clones per ha), moderate (between 20 and 100 clones per ha) and abundant (more than 100 clones per ha). The precise locations of individual sprouts, logs and stumps were mapped over selected areas of from 0.2 to 1.0 ha, and along 2 m-wide transects extending over distances from 0.3 to 2.0 km. Sites where chestnut clones were found were classified as old fields, former coppiced woodlands, former pastures, etc. according to available land use records and physical inspection of the sites.

Growth form. Chestnut sprouts in mapped areas at the study sites were separated into classes based on number of stems, height, stem shape and estimated age class. Overall clone vigor was given by the average yearly elongation of terminal leaders on primary lateral branches. Dead chestnut wood was identified using the criteria given by Panshin et al. (18). The color, ring structure and absence of rays made chestnut simple to recognize in the field. Dead chestnut was classified according to size, number of stems and type (sawed stump, snag, fallen log, etc. (14)). The size and shape of root collars, and number of pre-formed buds were noted for sprout clones in some of the mapped areas. Similar studies of growth form were conducted in a small, naturalized but unblighted chestnut stand in Wisconsin (16), and in chinquapin (*Castanea pumila* L. [Miller]) stands in Arkansas and Virginia (15) for comparison with blighted chestnut in New England.

Dendrochronology. Increment cores were taken from numerous living chestnut sprouts and canopy trees (oak, pine and birch) adjacent to sprouts and the remains of large, blight-killed chestnut trees. Cross-sections also were taken from various sized chestnut stems to reconstruct growth histories and ages of these stems. Ring increments were measured using a wood microscope by the U.S. Geological Survey Tree Ring Laboratory in Reston, Va. Increment series were processed and analyzed using the techniques described by Fritts (7) and Paillet (13).

Pollen analysis. Pollen samples were recovered from soils and moss polsters within the naturalized chestnut stand in Wisconsin. Samples were treated as described by Paillet et al. (17), Heidi (9) and Winkler (2). All pollen data are given as percentages of total arboreal pollen in a given sample, with percentages based on a minimum of 300 counts per sample.

RESULTS

Mapping and distribution. Mapping of the distribution of chestnut sprouts at various sites in New England indicates that sprouts are abundant in old forests, but are very irregular in distribution. Local areas of dense populations include sites where chestnut sprouts completely dominate the understory (Figure 1). The concentrations of sprouts sometimes coincide with the location of former large chestnut trees, and are separated by areas of very low population densities. In at least some locations there are many large chestnut stumps, yet few or no living sprouts. At other sites, the modern distribution of sprouts indicates a "halo" around the location of former woodlots that were dominated by chestnut, but now are dominated by hemlock (Figure 2). In Connecticut, chestnut sprout densities seem to be related to local terrain features, with concentrations of sprouts around old stone walls, roadsides and on the edges of swamps and streams (14). Only those sprouts clearly arising from the base of former canopy chestnut trees showed a relationship to preblight chestnut trees. Host sprouts (more than 95% in New England) appear completely independent of former trees. This result agrees with similar results given by Keever (10), and documented for preblight forests by Zon (24).

Growth form. Most chestnut sprouts in New England are 1-3 m tall, 2-8 cm in diameter 1 m above ground level, 10-40 yr old and consist of a single main stem. For example, about 60% of the clones mapped in Figure 1 consisted of a single stem or one large stem with one or more much smaller secondary stems in 1983. Shoot elongation on the largest lateral branches varies from 2-10 cm per year. Less than 5% of the clones in undisturbed woodlots indicate the presence of an active blight infection during the previous two years, but nearly 100% of clones in areas where chestnut is released are infected by blight within 5 yr after removal of the overstory.

Comparison of the growth form of chestnut and chinquapin indicates that both have similar growth forms, but that chestnut sprouts are slightly larger and tend to have fewer stems per clone (15). Both species apparently have similar life cycles involving long periods of suppression, seed production after release and generation of a larger stem. The only significant difference between chestnut and chinquapin in addition to overall size is that chestnut sprouts are consistently found with root collars that originated with the current stem, whereas chinquapin stems originate from the same root collar over many generations of sprouts.

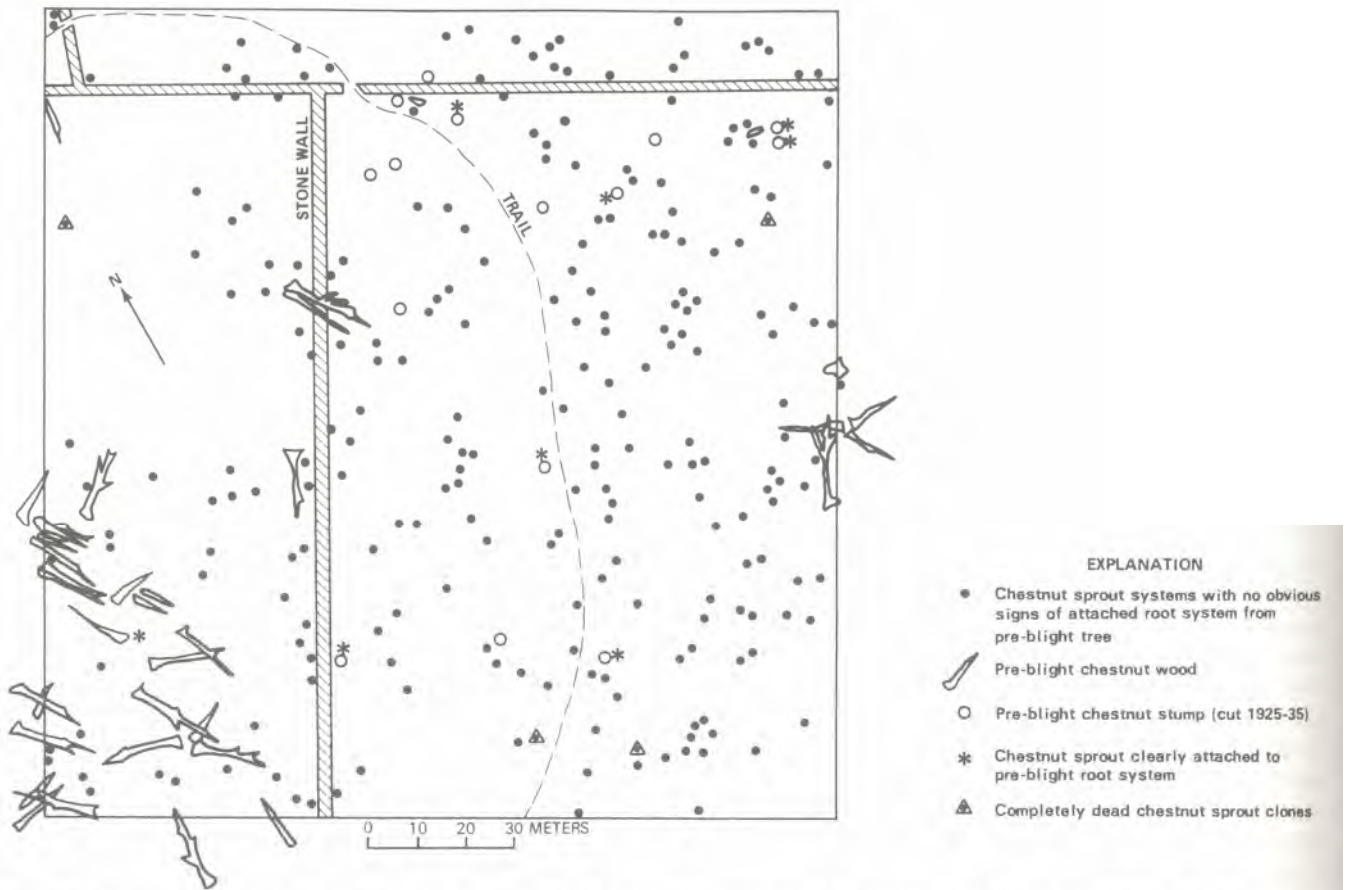


Figure 1. Distribution of chestnut sprout clones on a 1-ha site near Andover, Massachusetts, illustrating typical distribution on sites with dense clone populations and showing location of sprouts with respect to the remains of preblight chestnut trees (13).

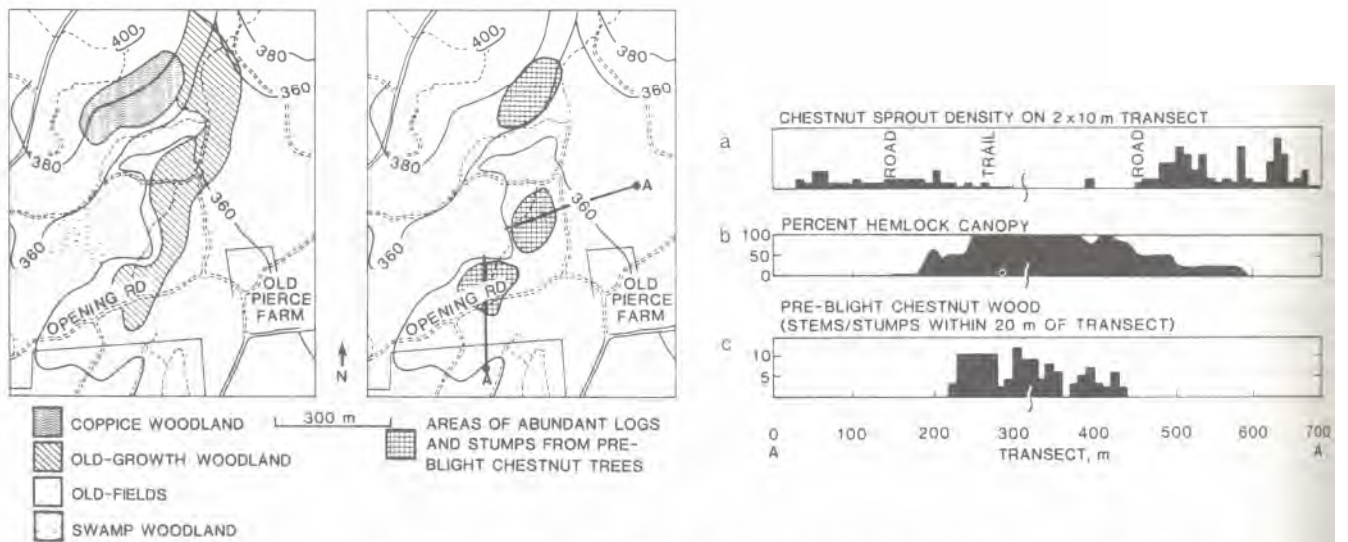


Figure 2. Distribution of chestnut clones along a transect through a core of old-growth woodland surrounded by old fields near Petersham, Massachusetts (14).

Po Dendrochronology. Increment borings indicate that most chestnut sprouts have stems that increase in diameter by about 0.20 cm per year. However, chestnut sprouts were found growing less than 0.05 cm per year where they were heavily suppressed, and at rates of more than 1.5 cm per year when they were released. Increment borings on oaks and chestnut trees released by the blight destruction of chestnut indicate that blight reached southern Connecticut by 1910, and extreme northeastern Massachusetts before 1925 (13). The oldest chestnut sprout stems found in New England are now about 40 yr old, and hence originated long after blight killed the canopy chestnut trees in New England. Analysis of variations in ring widths otherwise indicate that chestnut was unusually insensitive to short-term variations in climate (R.L. Phipps, personal communication).

Pollen analysis. Analysis of pollen obtained from soil and moss polsters in a naturalized American chestnut stand in Wisconsin indicate that chestnut is slightly over-represented in pollen deposits located directly under the source trees. Paillet et al. (17) conclude that measured

percentages of chestnut pollen need to be multiplied by a factor of 0.8 to estimate the local percentage of chestnut in the pollen-producing canopy (Figure 3). In contrast, chestnut pollen is poorly dispersed above the canopy, so that chestnut is severely under-represented in the sediments of lakes and bogs. Paillet et al. (17) conclude that the percentage of chestnut pollen counted in such sediments needs to be multiplied by a factor of 3.0 to approximate the percentage of chestnut in the forest canopy contributing pollen to the bog catchment (Figure 4). However, it is important to note that a large area (many sq km) contributes to the pollen influx into lakes and bogs, while a small area (probably a few ha at most) contributes to the soil pollen. The correlation between chestnut pollen and chestnut bundance in prehistoric forests (17) can be applied to pollen studies published by researchers at the Harvard Forest (5, 6).

DISCUSSION

Distribution of chestnut in New England. The distribution of chestnut clones in New England forests indicates

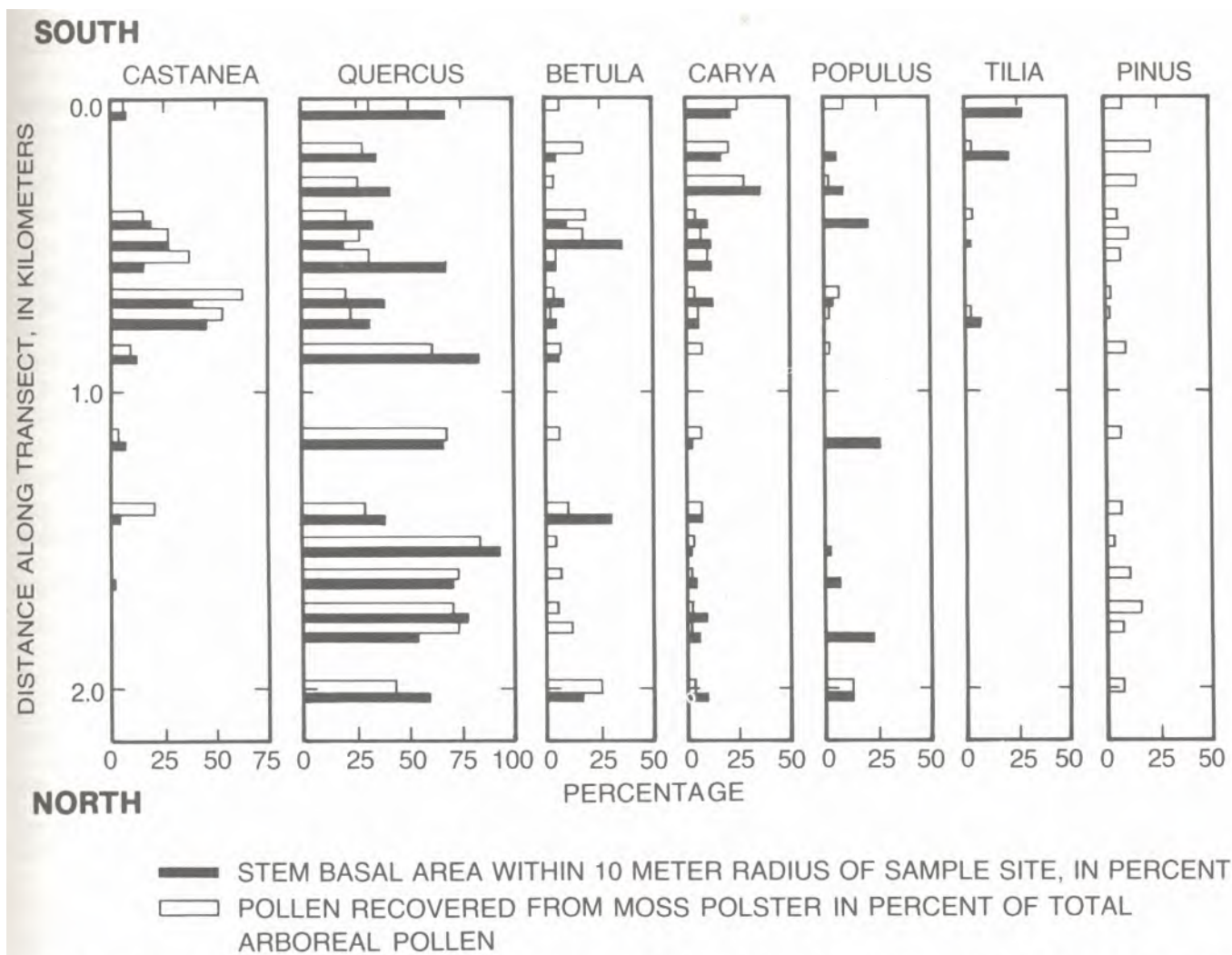


Figure 3. Comparison of the percent chestnut pollen in soils and moss polsters with percent chestnut in the canopy within a 10-m radius of the sample site in a naturalized stand of chestnut located near West Salem, Wisconsin (17).

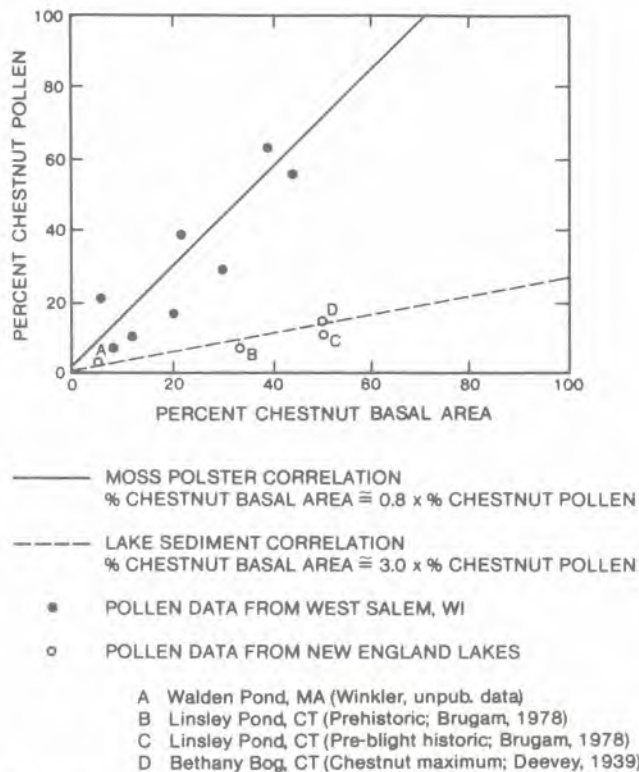


Figure 4. Relationship between chestnut pollen frequency in soils and lake and bog sediments with percent of chestnut in the surrounding forest (17).

that most of these clones originated as seedlings established in the years before blight removed the seed source. Chestnut sprouts only from the root collar, so that sprouts arising from former canopy trees are always closely associated with the stump of the former tree. These results suggest that the modern distribution of chestnut sprouts effectively represents the distribution of chestnut seedlings in New England at a time when most agricultural land was being abandoned, and old fields were being invaded by chestnut and many other tree species.

Growth form and reproduction. Chestnut is a tree suited for long-term survival in the understory of relatively open, oak-dominated forests. Chestnut and chinquapin exhibit similar growth forms, involving adaptations for surviving long-term suppression, and mechanisms for rapid response to release. In addition to the obvious size difference between the two species, there is a significant difference in root collar structure that affects sprouting. Chestnut actively walls off new sprout tissue from the old root collar, and generates a new root collar and root system in each cycle of sprouting. Chinquapin retains the entire root collar and old root system as a locus for continued sprouting throughout the lifetime of individual stems. These differences probably reflect adaptations for maintaining a defect-free stem for a long-lived canopy tree (chestnut) and for efficient reversion to shrub form for a sub-canopy tree or shrub (chinquapin).

The high density of chestnut sprouts originating as seedlings and the long period since a chestnut seed source

was present in New England demonstrate the ability of chestnut to "store" reproduction in the understory. It is proposed that the life cycle of chestnut is a two-step process: seedlings first are established in the understory, later attaining a position in the canopy only after disturbance. Many other temperate and tropical tree species have a similar ecological life cycle (11,19), but chestnut appears to use this strategy more effectively than any other deciduous tree in eastern North America.

Paleoecology of chestnut in New England. The correlation between chestnut pollen and chestnut tree populations in prehistoric forests (17) can be used to interpret pollen data from sites in New England. Analysis of pollen in bog sediments, forest hollows and soils at a site in north central Massachusetts indicates an abrupt increase in the percentage of chestnut pollen about 2000 yr ago, which is similar to increases at about the same time found at most other locations in southern New England (4, 22). However, forest hollow sediments where chestnut is better represented in the total pollen influx have some chestnut pollen in sediments as old as 4500 yr (5). The regional chestnut pollen influx of about 5% in bog sediments indicates a relatively steady population of chestnut in the regional forest in the last 2000 yr. In contrast, the pollen records from soil and small catchments directly under the forest canopy indicates that local chestnut populations were variable, and that large increases in chestnut pollen followed such disturbances as fire and windfall (5, 6). These results suggest that although the regional average chestnut population was stable, this average was composed of a continuously shifting mosaic of local chestnut-dominated stands. The abrupt increase in chestnut about 2000 yr ago was apparently related to a subtle change in disturbance regime (prehistoric human activity, fire and windstorm frequency, etc.) and other environmental effects rather than the direct result of a simple change in climate, or delayed migration from glacial refuge as hypothesized by Davis (4).

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