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HISTORICAL ECOLOGY OF AMERICAN CHESTNUT (*CASTANEA DENTATA*)

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Abstract: American chestnut (*Castanea dentata*) was a very common species in the forests of eastern North America in the early 20th century when it was decimated by the introduced chestnut blight. The post-glacial migration history of chestnut differed from its most common associates, oak and hickory due most likely to differences in the ecological tolerances of the species. By 1500, both pollen evidence and historical documents indicate that chestnut trees formed 5-15% of oak-dominated forests throughout the northeast, as far north as southern New England. The vigorous sprouting of chestnut after it is cut allowed it to develop widespread "sprout forests," where chestnut trees were 50% or more of the stems in many stands, after 18th-19th century logging. This high concentration of chestnut stems may have allowed the blight to spread very quickly throughout its range. In addition, many other changes have occurred in regional forests over the last century, as they have responded to a variety of human-caused disturbances. Thus, introduction attempts should take into account the time period that is of interest to try to restore and the dynamics of current forests in considering what might be the fate of chestnut trees that they reintroduce into today's forests.

Key Words: historical ecology / sprout forests / pollen / historical documents

INTRODUCTION

Doomed sprouts of American chestnut (*Castanea dentata*) are widely dispersed throughout the hardwood and hemlock/hardwood forests of the eastern United States today. In 1900, mature chestnut trees dominated many of these stands, and were very common in many others. A species valued not only for its majestic beauty, but also for timber and fruit, chestnut trees were planted well beyond their natural range. A deadly chestnut blight from an introduced tree in New York City, however, destroyed all mature trees in the early 20th century, leaving only ghostly stumps and shrubby sprouts as legacies of this once majestic tree.

A brighter future for the American chestnut may now be in the hands of foresters who have developed strains resistant to the blight. In considering the possibility of restoring this native tree to its former habitats, it is important to consider its former range, and its unique history as it developed to its distribution at the time the blight killed the trees. There are two major reasons to consider this history.

- First, we need to establish an appropriate goal for restoration. Is there a specific period in the history of this species that is particularly desirable? History can provide analogues that may be considered as possible goals of restoration. This gives the restoration ecologists clear endpoints to consider.

- Second, history can provide a picture of the changing distribution of the species, and of other species that were associated with it, over time, as they may both facilitate and constrain the likely outcome of restoration. Forests are always dynamic in their composition and structure, and understanding these dynamics can allow restoration ecologists to evaluate potential trends and the future of current changes. (Russell 1997).

I will discuss the history of the changing range of American chestnut and the other species with which it was associated in two time periods: 1. from 10,000 BP to 1500 AD, as it migrated to its pre-Columbian range; 2.   from 1500 AD to 1900 AD, after European settlement of the area. This discussion will be based on the record left by trees in the form of pollen preserved in lake sediments and on the historical documentary record. My analysis will focus mainly on the area from northern New Jersey to northern New England, as that is where the most records of the historical distribution have been compiled.

METHODS

Pollen

Pollen preserved in lake sediments provides a unique record of the history of plants, especially in areas which were covered with glaciers in the most recent (Wisconsinan) ice age, where disrupted drainage has left many sedimentary basins which have accumulated sediments over the millennia. Many tree genera, such as pines (*Pinus*) and oaks (*Quercus*), are pollinated by wind, so produce copious amounts of airborne pollen. Others, such as maples (*Acer*), are pollinated by insects, and produce less pollen, since pollination is more assured when the insect carries pollen from tree to tree. American chestnut seems to fall in an intermediate category of pollen production and dispersal. While insects do visit the male catkins of chestnut trees, the trees produce large amounts of windblown pollen.

Pollen is identifiable under the microscope to varying degrees of specificity. Pollen analysts can distinguish oak and hickory pollen only to genus. Chestnut is also identifiable only to genus. However, only two species are found in eastern North America, and of these only *Castanea dentata* is widespread and exists as a large tree that would distribute pollen any distance from the tree that produced it (Paillet 2000).

After pollen is released by a tree, it is carried by the air before falling to the ground. Even wind-pollinated species drop a large proportion of their pollen within a few hundred meters of the tree.
After pollen grains land on a body of water, they eventually sink to the bottom and are incorporated into the sediments. As sediments build up over the years, they thus contain a record of the trees and other plants that have grown in the vicinity as well as of the openness of the vegetation. Pollen grains are very resistant to decay in such as situation, and can provide a proxy for reconstructing past plant, especially tree, distributions.

Large bodies of water, greater than a hectare or so, collect windblown pollen from large regions, 10's of kilometers from the lake, because there is a large ratio of surface area/shoreline. Smaller ponds and hollows, on the other hand, may collect pollen from mainly local sources, 50 m or so from the sedimentation site. These differences allow us to reconstruct vegetation that has produced the pollen on both a regional and a very local, stand-level, basis.

When pollen is produced before leaves, as in the oaks, the wind currents often carry the pollen many kilometers. Chestnut trees release their pollen after the leaves have expanded, which means that the pollen, though copious, is often caught by leaves, and does not enter the air currents. This allows us to interpret chestnut distribution from pollen preserved in sediments on a finer scale that we can determine for many other species which produce large amounts of pollen. Finally, pollen of plants that grow close to the ground in a forested landscape is not carried far, and mostly falls directly to the ground. If the trees are cut, however, pollen produced below a meter by plants such as grasses (Poaceae) and ragweed (*Ambrosia*) can be carried several kilometers. The recent ecological history of eastern North America, characterized by massive regional deforestation after the arrival of European settlers can be dated by increases in these weedy species, even when looking at areas that were not locally deforested.

The pollen data that I will discuss come from three sources.

- First, for the brief discussion of the millennial record, I will use data compiled by Thompson Webb III, and published in numerous publications for interpreting many aspects of post-glacial vegetation and climate trends. Specific references to the pollen collections can be found in Bernabo and Webb (1977).

- The second set of data are those compiled by Russell and Davis (Russell et al 1993, Russell and Davis 2001), which include more detailed records of species distributions over the last 500 years, focusing on human impact on species distributions. These data only cover the area from northern New Jersey north to north-central Maine – the area covered by Wisconsinan glaciation. The trends detected in these data are, however, most likely similar to trends farther south, though further study may either confirm or refute that speculation.

- Finally, I will discuss data from some very small sites in central Massachusetts, which allow the reconstruction of very detailed stand histories (Foster and Aber 2004).

Historical Documents

After the arrival of European settlers in North America, written documents serve also to trace the history of the distribution of forest species. Early travelers provided qualitative descriptions of forest resources, often with excellent taxonomic accuracy. These almost always, however, lack any quantitative information. The earliest quantitative data come from land surveys, generally what are referred to as "metes and bounds" surveys which delineate properties. Surveyors were trained to recognize local tree species, and often used trees as markers for property boundary corners. The parts of the United States settled after the American Revolution were surveyed according to a very clearly codified rectilinear survey, but the colonial lands were surveyed by a variety of methods, some quite systematic and others much less so. By assembling these data, we can, however, obtain a remarkably consistent record of the species distributions in the precolonial forests, before settlers cleared them for farms (Loeb 1987, Whitney 1994, Russell 1997, Cogbill 2000).

The second set of documents that can provide evidence for the preblight distribution of American chestnut is the plethora of forest surveys around the end of the 19th century by state surveyors. The states had begun to realize that careless logging, grazing and fires had severely damaged their forest resources. To evaluate the problem, they embarked on systematic surveys to provide information that could guide their efforts to protect and improve their forests. These provide a snapshot of the condition, composition and structure of the forests of this period, when most heavy logging had moved away from the original 13 colonies, leaving regenerating, generally young forests in the east, especially the northeast (Russell 1987).

DISCUSSION

From the end of the Wisconsinan glaciation to 1500 AD

When the extreme cold of the Wisconsinan glaciation dominated the northern half of North America, tree species that today characterize forests north of the terminal moraine ranged far to the south, where climates were considerably colder than they are today. They were found in novel assemblages, depending on the local climate and the ecological tolerances of species for these conditions (Webb1988, Delcourt and Delcourt 1987). The sketchy pollen record from this time period indicates that American chestnut was a fairly minor component of forests dominated by oak, along with some other associates such as hemlock (*Tsuga canadensis*)or black gum (*Nyssa sylvatica*) (Barclay 1957, Bender et al. 1979, Craig

1969) in the southeastern Appalachian region. In Horse Cove Bog, western North Carolina, however, it was represented in quantities of pollen almost equal to oak between about 1400-150 BP (H.R.Delcourt and P.A.Delcourt, Pers. Comm, University of Tennessee, 1996). As climate moderated, the range of chestnut expanded slowly northeastward along the Appalachian and Ridge and Valley Provinces, reaching very large concentrations in some places before again declining (Barclay 1957, Davis 1983, Webb 1988).

The spread of chestnut into the northern forests lagged behind the oaks and hickory (*Carya*). For example, in southern New York oak had reached its current importance in the pollen record about 9000 YBP, while chestnut did not appear above 1% or so until about 4000 YBP (Maenza-Gmelch 1997). Likely explanations include different climate tolerances coupled with its more demanding pollination mechanism. Because American chestnut cannot self pollinate, a single tree growing beyond the current range of the species could not produce fertile seeds to spread from this point, while a hickory or oak tree could do so.

It is also possible that this distinct history is an artifact of studying all species of oak at one time, because they cannot be distinguished in the pollen record. The different species of oak represented in the east have quite varied ecological tolerances, while we can assume that we are tracing just one species in the case of chestnut. After about 2500-2000 BP, chestnut reached its current range. There is some recent evidence based on lake levels correlated with pollen data that it spread north as climate became more humid after 2000 BP (Shuman et al. 2004).

<u>1500 AD to the present</u>

By 1500 AD, chestnut was a consistent member of the oak-dominated forests of many eastern forests, according to the pollen record (Russell et al 1993, Davis 1983, Webb 1988). It has a much more restricted range than oak or hickory throughout its postglacial history, being restricted to a fairly narrow band along the Appalachian physiographic province (Davis 1983). Again, this may in part be due to comparing all the species in one genus to one species. By 1500 AD, chestnut contributed 4-9% of the pollen in lake sediments south of northern Massachusetts, where oak and hickory were the dominant taxa in the forests. North of about 43^{o}N, where spruce (*Picea*), pine, birch (*Betula*), hemlock and beech (*Fagus grandifolia*) dominated the forests, chestnut was generally less than one percent of the pollen indicating that it was at most a minor component of the forests (Russell and Davis 2001).
Historical records confirm and expand upon these pollen data. According to data compiled by G. Gordon Whitney, American chestnut trees were generally 5-15% of the trees listed in early land surveys in Pennsylvania, eastern Ohio, northern New Jersey, extreme southeastern New York, Long Island, Connecticut, Rhode Island and the Connecticut River valley in Massachusetts. White oak (*Quercus alba*) dominated these forests, with 25-65% of the stems, along with 5-15% hickory. These data have not yet been compiled from farther south in the range of the species.

A breakdown of the data from the area from northern New Jersey and to western Massachusetts shows some details of this distribution (Table 1). Chestnut was most common in forests dominated by oak, with little hemlock or beech, while it was less common (though occasionally present) in areas where beech and hemlock dominated the forests. In eastern West Virginia, chestnut was most common on ridgetops, where it formed 15% of witness trees, compared with 2-5% in other topographic positions (Abrams and McCay 1996). In Pennsylvania, chestnut was most common in the Allegheny Mountain physiographic province, though present throughout the state. Here, too, it was most common on hilltops (Abrams and Ruffner 1995).

Table 1. Percent of trees in precolonial land surveys in northern New Jersey, eastern Pennsylvania, eastern New York and western Massachusetts (data from Russell 1981, Bürgi et al. 2000, McIntosh 1962 and unpublished data for the Shawangunk Mts. and Rensselaerville, NY)

	n.e. NJ (Morris Co.)	n.e. PA (Pike Co.)	n.e. PA (Wayne Co.)	e. NY (Shawangunk Mts.)	e. NY (Catskill Mts.)	e. NY (Rensselaerville)	w. MA (Berkshire Co.)
Chestnut	15	7	1	7	0	0	6
Oak	64	40	6	41	0	4	16
Beech	1	3	36	1	50	48	23
Hemlock	0	5	22	4	20	14	19
Maple	4	7	16	6	14	14	11
Pine	0	27	3	6	0	1	7
Total number of trees	199	1921	939	342	3744	114	1730

Some details of local distributions and response to disturbances have been found in studies in central Massachusetts (Foster and Aber 2004). In these studies, pollen from small hollows or mor humus soils reflects the proportion of trees growing within 50 meters or so of the sampling point. Chestnut importance appears to have alternated with oak where oak was dominant. In another site, it appears that chestnut responded quickly to disturbance, but was supplanted by hemlock after the chestnut blight.

Whatever further study may reveal, however, it appears that on a broad scale, of a county or more, chestnut was a consistent but fairly minor associate of oak, especially white oak in the precolonial forests. How can we reconcile this with evidence of forests dominated by chestnut at the turn of the 19th century (Russell 1987)? The answer lies in the physiology of the species, in particular, its tendency to sprout vigorously from the root crown when it is cut (Paillet 2000).

Between the first settlement of the eastern United States by European settlers and 1900, the new inhabitants cleared all but the most remote and difficult to reach forests. Some land was turned into farms, but much that was not good agricultural land was repeatedly cut over for fuel and timber, especially for making charcoal to feed iron forges and furnaces. The forests of the first half of the 20th century were designated by E. Lucy Braun as "sprout hardwoods" referring to this tendency to sprout (Braun 1950). There is evidence in the pollen record for this change in the importance of chestnut in the forests of the northeast (Russell et al 1993, Russell and Davis 2001). Chestnut is one of the species that consistently increases in proportion of the tree pollen after the increase in agricultural indicators in the pollen record. It is not a major pollen producer like birch, which also increased, so the apparently small increase recorded in the pollen most likely translates into a much greater increase in the proportion of trees in the forest.

It is likely, therefore, that the forests that the blight decimated were primed to spread a pest like this. While not forming a monoculture, the species was very common by this time, and thus allowed the blight to spread quickly throughout its range (Russell et al. 1993). The distribution and abundance of sprouts in forests today reflect a forest greatly modified by the impact of European settlers. That these sprouts represent seedling trees, not the forest giants, is even more suggestive of the dynamic position of chestnut in these early 20th century forests (Paillet 2000).

Today's forests reflect this complex history. Chestnut sprouts abound, and their distribution indicates the sites that are most appropriate for chestnut to succeed. Disturbance is a positive force for chestnut growth. The current forests of the United States have changed significantly in species composition in the last 500 years, with a general decrease in the amounts of hemlock and beech and an increase in birch. Given the associates of chestnut in the historical record and its responses to disturbance, it seems likely that it would respond well to current conditions.

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