Session 5 Moderator's Report

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The papers presented at the International Chestnut Conference on July 14 review a number of important areas in the study of the ecology of three chestnut species: American chestnut *(Castanea dentata* [Marsh.] Borkh.), Allegheny chinquapin (C. *pumila* [L.] Mill.) and Italian chestnut *(C. sativa* Mill.). Understanding the natural ecology of chestnut is important for a number of reasons, including the management of chestnut forests for timber and wildlife, maintenance of natural and historic landscapes, and understanding of the interaction between blight and chestnut populations. The papers presented at the meeting serve to highlight the number of important questions that remain about the role of chestnut in the prehistoric forests of North America, Europe and Asia, and about the natural reproductive cycle of *Castanea* species. The issues relating to chestnut ecology discussed at the meeting can be divided into a number of general topics as follows:

THE OAK—CHESTNUT FOREST ASSOCIATION

Although not explicitly stated by any one author, several presentations (Hebard, Griffin, Hill and Paillet) touched upon fundamental questions related to the status of chestnut in the former chestnut-oak forest association defined by Braun (1). The ecology of relatively intolerant oaks and especially their establishment as a result of various disturbance cycles continues to be an area of active research. However, reconstructing the natural life cycle of chestnut is made much more difficult because no extensive natural stands of chestnut now exist, and blight destroyed most natural stands before they could be studied. Some limited information is available from the early silvicultural literature (see the review by Russell, (11), and papers by Zon (12), Frothingham (4) and Matoon (5)).

The papers presented by Griffin and Paillet describe a few case histories where intensive studies of chestnut remains and the distribution and character of chestnut sprouts can be used to reconstruct the history of chestnut on a specific site. In new England, where these studies have been performed most intensively (7), a consistent pattern is emerging. In these landscapes, land use history clearly exerted an important control over the distribution of chestnut. Paillet (8) shows that the modern distribution of chestnut in New England often indicates a halo of chestnut reproduction surrounding cores of forest located on the small part of the landscape least suited for agriculture.

The preliminary results presented by Hebard and Griffin at the meeting indicate that detailed studies of the distribution of chestnut in Appalachian woodlands may be as useful in understanding chestnut ecology in those more southern forests as similar studies have been in New England. The locations of former chestnut trees still can be determined from the persistence of chestnut stumps, and "old seedlings" can be identified from the locations of living sprouts that are unassociated with the root collars of former large trees. The most difficult aspect of the study is inferring if there were more old seedlings that have succumbed to competition, blight, or the effects of overstory shading. On at least some locations, long-dead chestnut sprouts probably can be identified. From the limited information provided about the distribution of chestnut wood and sprouts on middle and southern Appalachian sites, it appears that there is significant potential for increased understanding of chestnut populations on these sites. Similar sites with relatively natural chestnut populations may exist at locations in Europe and Asia, but almost all foreign research seems to have focused on cultivated or managed chestnut stands.

CHESTNUT IN PREHISTORIC FORESTS

One of the established methods for studying the natural ecology of forest trees such as *Castanea* is the analysis of fossil pollen. This method has been used intensively by ecologists, and seems especially suited for studies of American and Italian chestnut where a single species can be associated with chestnut pollen in most locations. Several conditions combine to complicate the interpretation of chestnut pollen. First, chestnut is not well represented in the "regional" pollen influx to lakes and ponds. Paillet et al. (10) show that the percent of chestnut pollen recorded in such sediments greatly under-represents the population of chestnut in the forest. Second, chestnut grows on uplands that are often at some distance from lowlands surrounding pollen catchments. The practical issue in palynology is calibrating chestnut tree populations on a scale ranging from 1-2% (possible long-distance transport) to 10-15% (chestnut a co-dominant forest tree in the pollen source area).

One means for circumventing the chestnut pollen representation problem is to seek pollen deposited in forest soils or small "hollows" in upland forests where the pollen catchment is located directly beneath the forest canopy. Chestnut is much better represented in such pollen deposits, and the pollen source can be related to a small area directly adjacent to the catchment, rather than to a large area that includes sites topographically unsuited for *Castanea*. The results of Foster and Zebryk (3) give a clear example of the potential of such studies for the reconstruction of the ecology of chestnut in prehistoric forests.

CHESTNUT REPRODUCTION IN NATURAL FORESTS

Although our understanding of the natural ecology of American chestnut is limited, two specific questions appear to be emerging: 1) What are the adaptive and reproductive advantages of the root collar sprouting mechanism that seems so highly developed as a form of vegetative reproduction in American species of *Castanea?;* and, 2) How well does chestnut reproduce in chestnut dominated woodlands? The first question has received surprisingly little study, but may be of more interest to the cell biologist than to the forest ecologist. However, the highly specialized nature of this mechanism suggests that sprouting is an important part of the natural life cycle of the species. This in turn indicates that understanding the reproductive cycle of chestnut may be difficult, because there can be a long gap between the original establishment of chestnut seedlings and the generation of a specific stand of large chestnut stems. One important concern in the study of American chestnut is that the absence of chestnut sprouts (except for those sprouts clearly arising from the root collars of former canopy dominant trees) could be interpreted as either a lack of sexual reproduction in former chestnut forests, or the inability of such seedling sprouts to survive in poor light conditions under closed canopies of the forests that developed after blight removed the chestnut seed source from the canopy. At present there seem to be several facts emerging from studies conducted so far:

1. The survival of the root systems of former canopy-dominant trees seems to have been highly variable, probably depending upon age of the original root system, site conditions, site history and regional differentiation of chestnut ecotypes.
2. There are many locations where chestnut was a major part of the forest when blight first appeared, but where there are now few if any living chestnut seedling sprouts. In at least some locations, this can be explained by assuming that overstory shading has affected chestnut seedling survival. On some New England locations, site history indicates that overstory shading was never an important factor, and chestnut seedlings were not being established under mature chestnut trees. All of our experience indicates that chestnut produced regular seed crops in North American forests in the years before blight appeared, so repeated failure of the nut crop probably cannot be cited as the cause of the local absence of reproduction. It is assumed that sexual reproduction of chestnut was inhibited by some combination of factors influencing seedling establishment such as drought, browsing and seed predation on these sites.
3. There are many locations where chestnut seedling sprouts are abundant, but where chestnut was apparently not an importunate part of the forest canopy in pre-blight years. Some combination of ecological factors is assumed to be responsible for the successful establishment of chestnut seedlings on these sites.

CHESTNUT AND THE FREQUENCY AND INTENSITY OF DISTURBANCE

All information available at present seems to link chestnut in forests with disturbance. For example, chestnut sprouting and growth rates appear to be adapted for rapid response to release. Tolerance levels assigned to chestnut seedlings also suggest that chestnut cannot compete with more tolerant species such as beech and maple in poor light conditions under dense canopies. However, the former natural range of chestnut shows that the species was never abundant in areas such as the coastal plains of New England where the forest was composed of pine and oak species associated with frequent fires. At the same time, historical data indicates that the disturbance to woodlots during and after settlement in New England resulted in an increase in the amount of chestnut in the forest. The exact relationship between chestnut populations and disturbance in the pre-settlement forests of North America remains poorly defined in spite of the level of interest in characterizing the role of disturbance in forest ecology expressed in the recent literature.

BLIGHT AND CHESTNUT ECOLOGY

Several recent studies, including those presented by Griffin et al., Hebard and Griffin at this conference indicate the complexity of the interaction between blight and chestnut populations. A number of researchers note the relatively low activity of blight in otherwise dense populations of chestnut sprouts. This low blight activity usually is associated with heavily suppressed chestnut populations where the surface area of cambium available for blight colonization is low in spite of the large density of chestnut clones. The specific mechanisms for blight dissemination and their relationship to such factors as genetic variability of blight strains, character and density of possible blight colonization sites, and the role of alternate hosts such as leaf litter and scarlet oak cankers need to be studied in more detail. The evaluation of stand treatment with hypovirulent blight strains will be difficult if the interaction between natural chestnut populations and blight is not well understood.

POSSIBLE ECOLOGICAL EFFECTS OF BLIGHT RESISTANCE

A lot of circumstantial evidence presented in the literature and at the 1992 Chestnut Conference suggests that the characteristics of blight infection in natural populations of chestnut will be affected by the introduction of blight-resistant chestnut strains. The long-term persistence of active cankers on numerous resistant trees probably will have a great impact on the interaction between blight and chestnut trees. In many locations lack of blight resistance means that chestnut stems die quickly, limiting the impact of blight on new sprouts from the infected tree, and on adjacent uninfected trees (9).

GENETIC DIVERSITY AND REGIONAL ECOTYPES

The natural range of American chestnut extends from the southern coastal plains and Gulf coast to New England and southern Canada. This range includes a number of different climates and geological substrates. There also are several localized outliers in the chestnut distribution such as the sandstone and shale hills of southern Illinois, the loess bluffs of western Mississippi and the outwash sands of southern Ontario. There are probably a number of different genotypes of chestnut within the natural range. Very little, if any, effort has been made in characterizing the differences in these species. This information would be important in both reintroducing blight-resistance varieties of American chestnut into the wild, and in developing varieties for various economic purposes. The survival of chestnut sprouts throughout the range of the species indicates that most of this natural genetic diversity is available for study. There also is the possibility that some of this diversity may begin to be lost as the introduction of blight-resistant chestnut changes the "rules" of the game relating to the interaction of blight and sprout populations.

SUGGESTIONS FOR FUTURE RESEARCH

1. Site studies. The primary tool for understanding chestnut ecology will remain intensive investigation of chestnut sprouts and dead chestnut trees on specific sites. The relative decay-resistance of chestnut wood and the survivability of chestnut seedling sprouts make such studies feasible. More of these studies need to be completed at sites where there is at least some information on forest conditions and land use history in pre-blight years.

2. Natural chestnut stands. Some naturalized American chestnut stands can be found, and relatively undisturbed chestnut populations probably exist in remote parts of Asia (Caucus mountains, forest relicts in China). Some insight into the natural ecology of chestnut (especially for the effective reintroduction of blight-resistant chestnut) can be obtained by locating and studying these limited stands.

3. Early forest literature search. Chestnut was a valuable forest resource before the appearance of blight in North America, and chestnut is discussed in some of the old forest literature. Some additional effort could be made to survey the known chestnut bibliography, and to seek out records pertaining to chestnut that are now "lost" in the archives of institutions (Harvard and Yale Forestry Departments, for example) that were active in forest research before 1920.

4. Blight interactions. The interaction between natural stands of chestnut and blight needs to be studied in more detail, both to understand the possible emergence of blight resistance in recent years, and to address the effect of introduced blight-resistance on the large populations of chestnut sprouts now present in eastern forests. Blight resistance probably will have a great effect on both the dissemination of blight infection among chestnut populations, and in the dynamics of the competitive balance between chestnut sprout clones and other tree and shrub species.

5. Paleoecological studies. The interesting results emerging from high-resolution pollen studies coupling regional pollen data from bogs and lakes with local pollen from soils and hollows demonstrate the great potential of such studies. The results now obtained by Foster and Zebryk (3) in New England need to be compared to similar results obtained from carefully selected sites further south and west within the natural range of chestnut.

6. Historic chestnut studies in New England. The early forest records from locations in New England offer one particular example where known results can be combined with pollen and ecological studies to infer useful silvicultural information about chestnut. Early records (6) indicate that chestnut had increased to more than half of the timber resource in New England as a result of land use practices and timber management. Pollen studies similarly indicate a measurable increase in regional chestnut pollen production associated with European settlement after 1700 (for example, from about 8 to 11% at sites near New Haven, Connecticut (2)). Enough information exists from pollen in sediments and early records of agricultural and forestry practicers to use this particular situation to construct models of chestnut interaction with other species in New England woodlots.

SUMMARY

An improved understanding of the natural ecology of American chestnut is a challenging and interesting subject. The topic is of interest because it relates to a species that was once a major forest tree in eastern North America; understanding chestnut ecology is just another piece in the immense puzzle of forest ecology in general. Recent research has just begun to uncover the complicated story of climate change, disturbance frequency and ecological interaction of species. This information is of interest in its own right, and also has important practical application in managing ecological reserves, national parks and other biological reserves. What we learn from the study of chestnut ecology may have important implications for the management of these areas in the future.

At the same time, chestnut ecology has important applications in the biotechnology of blight. The ecological characteristics of chestnut clearly influence the interaction of the species with blight. Very little consideration has been given to how the introduction of blight resistance may affect the natural population of chestnut. It is possible that introducing changes in the way blight interacts with chestnut may influence the ability of chestnut to compete with other shrub and tree species in undisturbed woodlands, and in woodlands subjected to various types and intensity of disturbance.

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