American Chestnuts in the 21st Century

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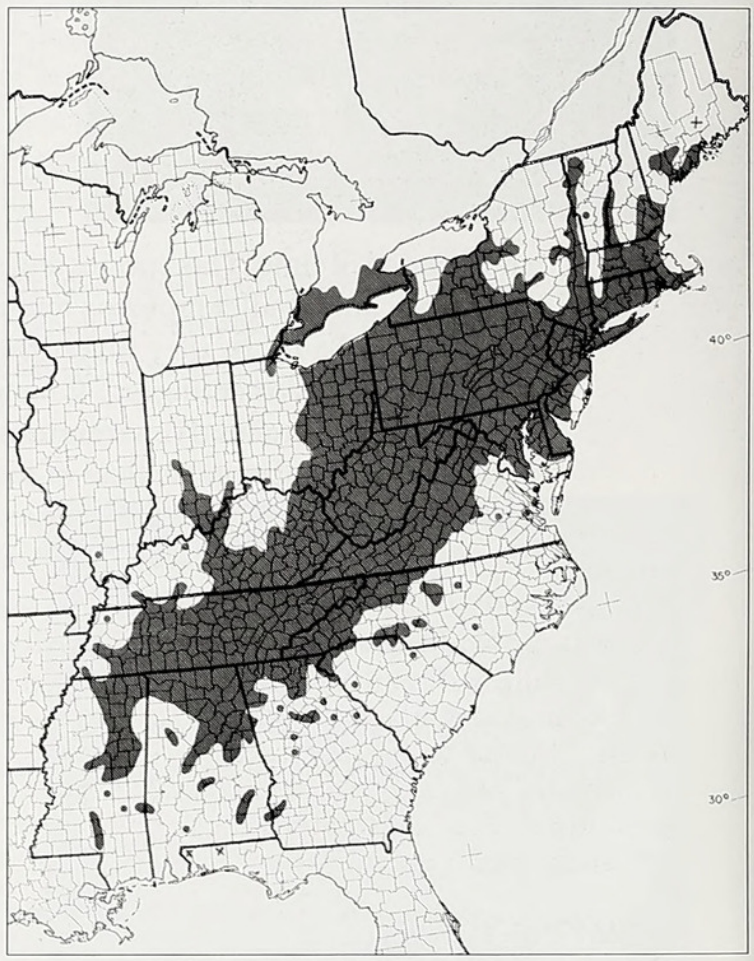
New England was heavily forested in 1600, and American chestnut (*Castanea dentata*) was commonly found in Connecticut and Massachusetts woodlands (Cogbill et al. 2002). At that time, American chestnut was abundant throughout its native range from southern Maine to northern Georgia, all along the Appalachian Mountains (Saucier 1973). In the following centuries, European settlers cleared land for farming and cut trees for fuel, and the forest cover was greatly reduced by 1850. This was followed by the introduction of coal as a fuel, which was brought easily to New England by the railroads. Once wood was no longer being harvested for fuel, and more fields were left fallow as people abandoned farms and moved west or into the cities, the trees started to take back their habitats.

When hardwood forests were harvested and left to resprout, the chestnuts grew faster than the oaks and maples with which they shared the land, and the number of chestnut trees greatly increased. Many woodlots became nearly pure stands of chestnut. A bulletin issued by the Connecticut Experiment Station in 1906 stated that regenerating hardwood forests covered most of the wooded area of Connecticut and "the most important tree of this type is the chestnut which constitutes fully one-half of the timber" (Hawes 1906). Forest surveys done at the turn of the last century show that there were about 130 million mature American chestnut trees in Connecticut alone.

These stands of chestnut trees were valued because chestnut is a strong wood that resists rotting. Chestnut was used extensively for framing and woodwork, and was also essentially the only wood used for telephone poles and most of the railroad ties laid as rail lines pushed westward (Pierson 1913).

The Blight Arrives

The fungal pathogen causing chestnut blight disease (now called *Cryphonectria parasitica*) was introduced into the United States in the late 1800s on Japanese chestnut trees. The disease was spread up and down the east coast by mail-order sales of infected trees (Anagnostakis 2001, http://www.ct.gov/caes/cwp/view.asp?a=2815&q=376754). In 1908 chestnut blight disease started killing American chestnut trees in Connecticut (Clinton 1912), and



SAUCIER 1973

Native range of American chestnut (*Castanea dentata*) in Eastern North America.

A pure stand of American chestnut in Connecticut in 1910.

infections were reported in Cape Cod, Wellesley, and Pittsfield, Massachusetts (Metcalf and Collins 1909).

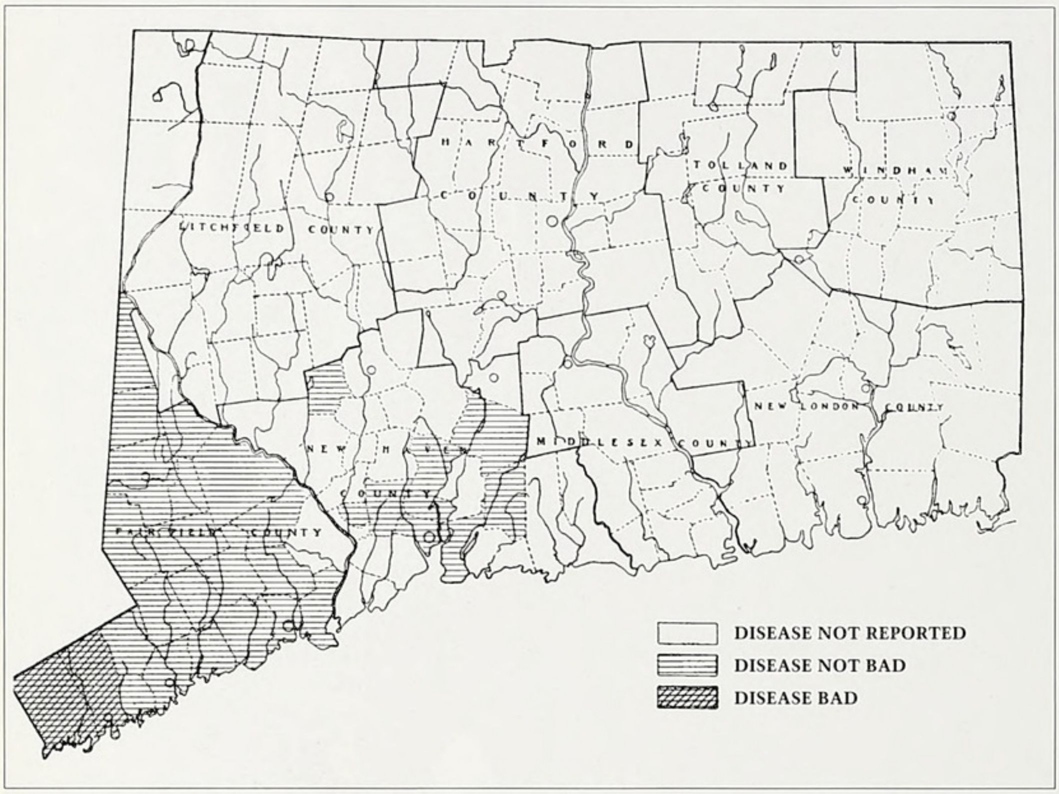
Chestnut blight disease has reduced American chestnuts to understory shrubs, which die back, sprout from the base, die back, and sprout again. This fungus is now present throughout the original range of *C. dentata,* and has spread to many of the Midwestern locations where chestnuts were planted.

Chestnut Breeding

Chestnut trees are monoecious and bear separate male and female flowers on the same tree. As with many fruit trees, they must be cross-pollinated for fully formed nuts to develop. Without cross-pollination, burs with small, flat nuts comprised of all-female tissue are all that form. Although the size of the nuts formed is completely dependent on the female parent, the pollen parent influences the flavor of the nuts (Anagnostakis 1995a, Anagnostakis and Devin 1998).

Growers interested in getting nuts as large as those of Japanese or European chestnut but with the superior flavor of American chestnuts started creating hybrids in the late 1800s. After chestnut blight disease began killing timber

CLINTON 1912



This map shows the presence of chestnut blight disease in Connecticut in 1908.

SANDRA ANAGNOSTAKIS

Blight canker on an American chestnut tree; note the dead, sunken bark and lumps of fungal tissue that have broken through the surface where they will form spores.

chestnut trees—and Asian chestnut trees were seen to be resistant to the disease—it was hoped that new hybrids could be developed that combined the upright, timber-producing form of American chestnut with the Asian species' resistance to blight.

Arthur Graves, a plant pathologist in Connecticut, began crossing blight-resistant Asian trees and susceptible American trees in 1930. He then tested these hybrids for resistance to chestnut blight disease (Graves 1937). He was soon joined by Donald Jones of the Connecticut Agricultural Experiment Station (CAES), who was a renowned geneticist with a great interest in chestnut. Many of those original hybrids are still alive, and CAES now has what is probably the finest collection of species and hybrids of chestnut in the world. These were planted on land left to the State of Connecticut by Graves, and at the CAES farm, both located in Hamden, Connecticut.

Trees with two forms are being chosen from our continuing breeding efforts at CAES: tall, straight trees with limited energy put into forming nuts but very well-suited for timber production, and short, spreading trees with maximum energy put into forming large, good-tasting nuts, making the trees suitable for commercial or backyard nut orchards. Both kinds of

COURTESY OF BRAD SMITH

American chestnut flowers on a tree near Quabban Reservoir in Massachusetts.

trees must have resistance to chestnut blight disease and be well adapted to the New England climate (Anagnostakis 1992). There is now interest in developing DNA tests for genetic maps of chestnut trees (http://www.fagaceae.org/web/db/index), and we are using specific crosses to study the genetics of resistance to diseases as well as to develop timber and orchard chestnut trees.

To make these crosses, we put waxed paper bags over female flowers in late June before they are fertile, then put selected pollen on the flowers in July and cover them up again. This allows us to know the parents of the nuts that form. During our breeding program we have found that many hybrids that are the result of crosses between two different species do not form functional pollen. These male-sterile trees produce male catkins with flowers that never bloom. Although this lack of pollen is a nuisance in the breeding program, it is a feature valued by commercial nut growers—they can plant orchards of male-sterile trees with a few pollen-producing trees and have yields of nuts that are very uniform.

When it became clear that at least two genes were responsible for resistance to chestnut blight, we began a back-cross breeding program based on the plan of Charles Burnham (Burnham 1988). Asian trees are crossed with American trees, and the hybrids (partially blight resistant) are crossed to American trees again. If there are two resistance genes, one out of four of the progeny from these back-crosses has one copy of both resistance genes, giving it partial resistance. If there are three genes for resistance, one

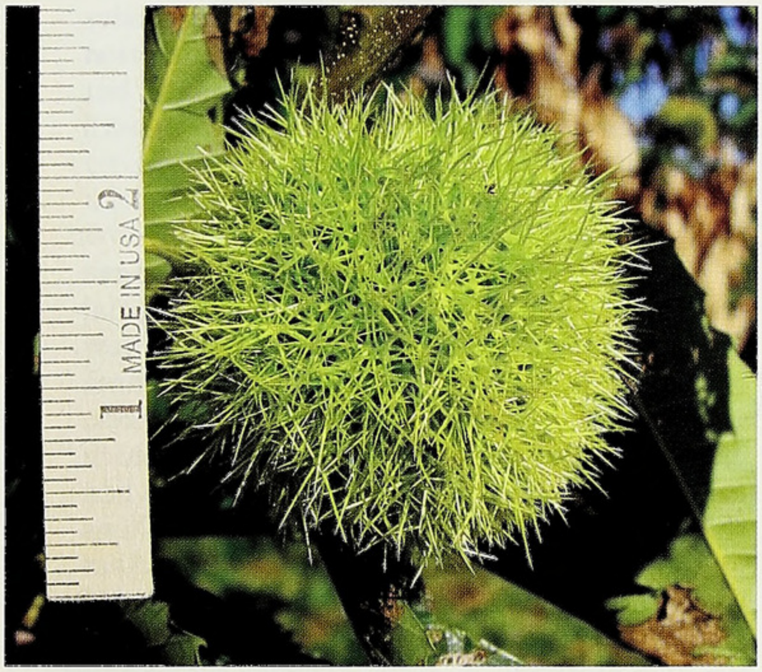
SANDRA ANAGNOSTAKIS

A row of twelve-year-old chestnut hybrids selected for timber qualities.

out of eight of the progeny will have one copy of all three resistance genes. Trees with partial blight resistance are crossed again to American chestnut trees. This repeated back-crossing increases the percentage of American genes in the hybrids, and selecting for partial resistance insures passage of the resistance genes. A final cross of two trees with partial resistance should result in one of sixteen trees having two copies of two resistance genes (or one of sixty four trees having two copies of three resistance genes), which will make them fully resistant to the chestnut blight fungus.

Biological Control of Chestnut Blight Disease

In a 1992 *Arnoldia* article we described viruses, called "hypoviruses," that infect *C. parasitica* and keep the fungus from killing trees by reducing its virulence (Anagnostakis and Hillman 1992). Since 1972, when CAES imported



KEITH KANOTI, MAINE FOREST SERVICE, BUGWOOD.ORG

The densely spiny chestnut bur encloses several nuts, typically three.

SANDRA ANAGNOSTAKIS

American chestnut trees in this Hamden, Connecticut, orchard were treated with biocontrol strains from 1978 to 1981, and 15% of the 71 trees survive as the original trunks in spite of the presence of many cankers. Half of the trees continue to be in a repeating cycle of dying back and resprouting. About one third of the trees died back once, resprouted, and the sprouts are still surviving.

Percentage of American genes in back-crossed (BC) hybrid chestnut trees.

PARENTS	AMERICAN GENES			HYBRID
1. American x Japanese	100% American genes 0% American genes	egg + pollen	=	50% A F1
2. American x F1	100% American genes 50% American genes	egg + pollen	=	75% A BC1
3. American x BC1	100% American genes 75% American genes	egg + pollen	=	87.5% A BC2
4. American x BC2	100% American genes 87.5% American genes	egg + pollen	=	93.8% A BC3
5. BC3 x BC3	93.8% American genes 93.8% American genes	egg + pollen	=	93.8% A BC3-F2

virus-containing strains of the chestnut blight fungus from Europe, great strides have been made in understanding how these viruses can keep the fungus from killing trees. The genes of three kinds of these (dsRNA) viruses have been sequenced, and the viruses placed in the genus *Hypovirus* by Bradley Hillman and his collaborators (Hillman et al. 1994). We have studied the movement of both killing and curing strains of the fungus by birds and insects of several kinds (Anagnostakis 1990; Anagnostakis 1995b; Anagnostakis 2001). Although we have introduced hypovirulent strains of the fungus into forest plots, this biological control has not brought about a general recovery of forest chestnuts in Connecticut. However, it has been successful in an orchard of American chestnut trees at the CAES farm in Hamden, Connecticut, where we introduced hypovirulent strains into every canker that we could reach for four years from1978 to 1981. Now, although half of the trees continue to die back from chestnut blight (and sprout, and die back, etc.), about a third that died back once and sprouted now survive and flower even though they are covered with cankers, and about 15% of the trees are the surviving original stems.

Synthesis of Breeding and Biological Control

The crosses that have produced blight-resistant trees for timber have, by necessity, used a rather narrow genetic base, even though different trees were used as parents in each generation. At CAES, this has involved crossing and back-crossing both Japanese and Chinese chestnut trees (*C. crenata* and *C. mollissima*) with locally adapted American chestnut trees. Our strategy has been to keep native chestnuts alive and flowering by using our biological control agent. This eliminates the need to search for American trees that have survived long enough to flower. It also lets us use populations in specific forest clearings. By planting resistant trees in the forests and treating the native trees with our biocontrol, native trees will survive to naturally cross with the resistant trees and will incorporate blight resistance and all of the native genetic diversity into the future generations. The first generation offspring will be intermediate in resistance, but subsequent generations will produce trees with full resistance.

Chestnut Trees for the Orchard

In addition to selecting timber trees, we have continued to evaluate trees for their potential for orchard production in New England. A few acres of chestnut trees can produce enough nuts to sell at farmer's markets or to local stores. The only serious pest is chestnut weevil, which can be controlled by spraying insecticide when the nuts are ripening, or by allowing chickens or guinea fowl to range under the trees and eat the weevils and their grubs. Squirrel control is also essential and every nut farmer has his or her own method.

The most productive chestnut orchards are planted with named cultivars, which are vegetatively propagated clones of the original named trees selected for efficient nut production. Since cuttings of chestnut trees will not form roots, chestnut orchard cultivars must be grafted onto suitable rootstock for propagation. Although this increases the cost of the plants, the value in having proven clones makes the purchase price well worth it.

Another challenge faced by growers is that some splendid cultivars that do well in one part of the country do not do well in other places. For example, cultivars suited to the far south or to the far west may not do well in New England. Selections from Ohio have generally proven

SANDRA ANAGNOSTAKIS

A basketful of nuts from a hybrid chestnut orchard.

reliable in southern New England, as have the few cultivars released from CAES. Since I am the International Registrar for Cultivars of Chestnut, information on new trees usually crosses my desk, and I keep a list of the names used and some of their characteristics on our website (http://www.ct.gov/caes/cwp/view.asp?a=2815&q=376864).

The biggest challenge to development of a nut industry in New England is the lack of an established market—many people have never eaten chestnuts and are hesitant even to try them. Also, many who have bought chestnuts and then had weevil larvae crawl out of them will never buy them again. Efforts to develop markets and grower awareness in Michigan and Missouri are making some progress and can serve as examples for New England.

The Next Problem

Even as progress was being made toward blight resistance, another serious chestnut pest arrived. The oriental chestnut gall wasp, *Dryocosmus kuriphilus,* was introduced into the United States in 1974 by a grower who evaded plant quarantine (Payne et al. 1976). The insect lays its eggs in leaf and flower buds, resulting in defoliated trees with no flowers. Entomologist Jerry Payne chronicled the devastation of orchards of Chinese chestnut trees planted in the state of Georgia. We have reports of infestations throughout Alabama, North Carolina, and Tennessee, and most recently in Columbus, Ohio.

As a consequence, breeding work must now include selection for resistance to this pest. Jerry Payne has observed that American and Chinese chinquapins (*Castanea pumila, C. ozarkensis,* and *C. henryi*) are resistant to infestation, as are some cultivars of *C. crenata.* Once again, the CAES collection of species and hybrids is being used for making new crosses, and progeny from these crosses are being tested in North Carolina where the insect is now endemic. These trees were examined by Stacy Clark of the United States Forest Service in 2006 and the preliminary results were encouraging. Of 93 trees planted in 1995, there were 53 that survived the droughts, deer, rabbits, and weed competition for 12 years. Among the survivors, 11 had no wasp galls and 25 had few galls. We hope to understand how resistance is inherited and will incorporate this resistance into our trees as quickly as possible.

JERRY A. PAYNE, USDA AGRICULTURAL RESEARCH SERVICE, BUGWOOD.ORG

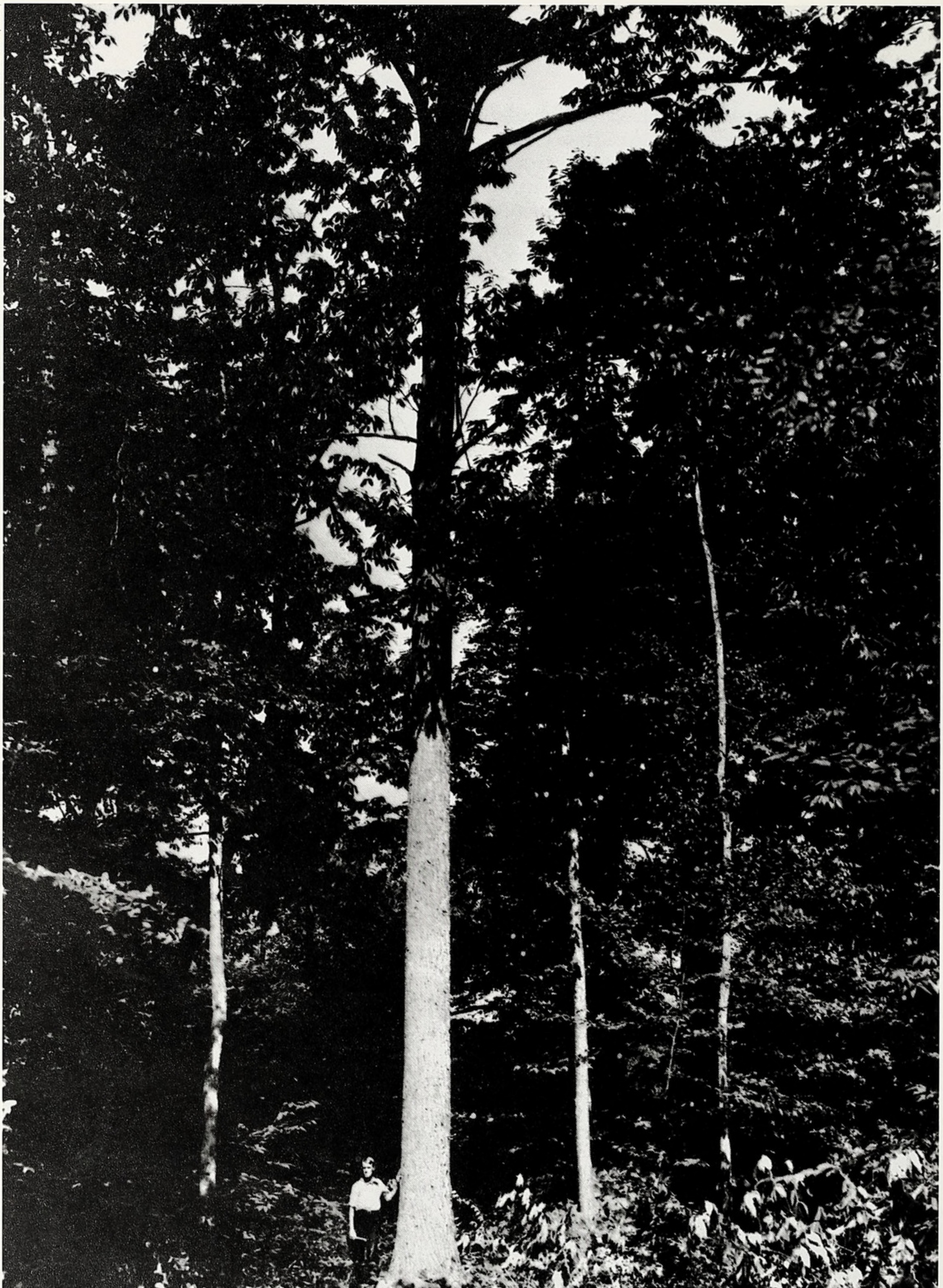
Developing gall and damaged chestnut shoot caused by the Oriental chestnut gall wasp.

The other ray of hope for dealing with gall wasp is that Asian parasites released by Jerry Payne seem to be moving with the wasp (Payne et al. 1976). Lynne Rieske recently reported that parasites were now in the Ohio population (Rieske 2007). If these parasites continue to improve as control agents for gall wasp, it is possible that only stressed trees will be seriously damaged by wasp infestation.

What's Next?

We will soon have timber chestnut trees that can survive in New England. These trees will provide another source of lumber and will also increase the diversity of tree species in forests. We are learning about growing chestnuts in orchards in New England and selecting better

FROM CONNECTICUT EXPERIMENT STATION BULLETIN 154 (1906)



This 1905 photograph shows the tall, straight trunk of a then 103-year-old American chestnut in Scotland, Connecticut.

nut-producing cultivars to make a new niche crop for farmers.

The work goes slowly, but is very satisfying. When I talk to scientists who conduct laboratory research, and expect results within months, they are often astonished that I have been working at this research for more than 40 years. There are no quick solutions to the complicated problems in the environment, and trees take a long time to grow. When many factors are interacting they must all be considered. We can make crosses of our trees, wait 10 years for the seedlings to mature, select them, make more crosses, wait 10 years, and still miss some crucial clue in the soil or the weather or animals or insects that will affect our hoped-for outcome. When talking with students I try to emphasize the need for patience, keeping an open mind, and noticing everything. "Publish or Perish" and "More Grant Funding for Survival" are still driving forces that tempt scientists to focus on small things that can be examined in isolation and written up quickly for scientific journals or granting agencies, but it is important to keep looking at the big picture.

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Sandra L. Anagnostakis continues her research at the Connecticut Agricultural Experiment Station in New Haven. She is still having too much fun to consider retiring.