One of the worst ecological catastrophes to occur in North America’s forests was the introduction of the fungus, *Cryphonectria parasitica*, which causes chestnut blight. Native to Asia, the fungus was first detected on American chestnut trees, *Castanea dentata*, on the grounds of the New York Zoological Garden (the Bronx Zoo) in 1904. It was subsequently isolated and described by American mycologist William Murrill in 1905.

In its native habitat, the chestnut blight fungus’ host trees include Japanese chestnut, *Castanea crenata* and Chinese chestnut, *C. mollisima*. These are relatively small trees, compared to the American chestnut, and are commonly grown in orchards for their edible nuts. Damage to these trees by the fungus is relatively minor and it was not known to science until its introduction into North America.

The majestic American chestnut, which was native to much of the eastern United States (Fig. 1), is highly susceptible to chestnut blight fungus. The disease results in cankers on the stems and branches that cause tree death or reduces trees to small sprouts that can persist for decades. By 1950, the fungus had spread throughout the range of American chestnut and killed an estimated four billion trees.

Allegheny chinquapin, *C. pumila*, and bush chinquapin, *C. alnifolia*, which are shrubs or small trees, native to the eastern United States, are also highly susceptible to the chestnut blight fungus.
Another chestnut relative, the Ozark chinquapin, *C. ozarkensis*, is a drought-tolerant shrub or tree valued for its nut crops and rot-resistant wood. It was once common in the Ozark and Ouachita Mountains. Chestnut blight reached this area in the 1960s and caused widespread mortality. However there are reported to still be a few trees that have not succumbed to the disease. European chestnut, *C. sativa*, is also damaged by this fungus but not as severely as American chestnut. Today pure or nearly pure stands of this species still occur in the Apennine Mountains of Italy even though the fungus was discovered in Europe ca. 1938. Other North American host trees of the chestnut blight fungus include several species of oaks, *Quercus* spp., shagbark hickory, *Carya ovata*, red maple, *Acer rubrum* and staghorn sumac, *Rhus typhina*. These trees are rarely killed but provide for a ubiquitous and long term persistence of the fungus.

The impact of chestnut blight on eastern hardwood forests was catastrophic. In 1900, American chestnut was the dominant tree in many forests (Fig. 2).

In portions of the Appalachian Mountains up to 25% of trees in a stand were American chestnuts. It was an important commercial species that produced decay resistant lumber and tannin for leather. In western North Carolina, many wooden buildings, especially barns used to cure tobacco, were built from American chestnut lumber and still stand today (Fig. 3). The American chestnut’s sweet, edible nuts were an important food source and commodity for rural Appalachian residents (Fig 4). Native Americans used parts of the tree as a cough syrup and to treat other ailments. Chestnuts were also an important food for wildlife and many rural communities relied on chestnut crops to feed livestock.
By the 1950’s roughly 99.9% of American chestnut trees had been killed by chestnut blight. Yet even in the 1960’s, lumber salvaged from blight-killed trees that had toppled over and remained moist on the forest floor produced sound lumber. It’s only “defect” being galleries and stain caused by ambrosia beetles. These added character to the wood, enhanced its beauty and makes excellent furniture (Fig. 5)

Figure 3- Many buildings in the southern Appalachian Mountains were built from American chestnut lumber. Because of its decay resistance, many still stand today.

Figure 4- This drawing by 19th century American artist Winslow Homer depicts young people gathering American chestnuts for roasting.

Figure 5 – Part of an American chestnut coffee table displays the tree’s attractive grain.
The chestnut blight fungus enters susceptible trees via wounds or bark fissures. The fungus grows in and beneath the bark, eventually killing the cambium. The first symptom of infection is a small orange-brown area on the tree bark. A sunken canker then forms as the fungus mycelium spreads under the bark. As the fungus spreads, it produces several toxic compounds, the most notable of which is oxalic acid. This acid lowers the pH of the infected tissue from the normal 5.5 to approximately 2.8, which is toxic to plant cells. The canker eventually girdles the tree, killing all branches above it. Death can occur in several weeks for young trees and up to four or more years for mature trees. Sprouts often shoot up from the base of dying trees and occasionally American chestnuts survive long enough to produce chestnuts (Fig. 6).

Figure 6 – Occasionally individual American chestnut trees will survive long enough to produce chestnuts but eventually succumb to chestnut blight.

To date, there are no effective means of managing this disease. Removal of blight-infected trees was ineffective and may have resulted in loss of trees with genes for low to moderate levels of resistance. Attempts were made to introduce a hyperparasitic virus into the chestnut blight fungus to weaken it. Initially trees infected with this ‘hypovirulent’ fungus respond positively and began to heal over cankers. However, the virus does not readily spread from tree to tree as effectively as does the chestnut blight fungus.

One of the primary areas of investigation for managing chestnut blight and restoring American chestnut to its former status has been to develop trees resistant to the fungus through selective breeding. As early as 1894, breeding between Asian, European and North American species of Castanea were underway to improve nut production. In 1921, A.H. Graves, working the Brooklyn Botanical Gardens and later with the Connecticut Agricultural Experiment Station, started crossing American chestnut with Asian chestnuts for blight resistance and produced what became a robust collection of chestnut species and hybrids. This work eventually produced the “Graves” tree, ultimately used in the 1980s in backcross breeding programs that are still underway today.
In 1922, breeding for blight resistance began under the USDA Division of Forest Pathology, with American chestnut and Chinese chestnut hybrids selected for a combination of growth form and blight resistance. This produced several promising first-generation Chinese x American hybrids, including what became known as the “Clapper” tree, developed by Russell B. Clapper, who ultimately was employed by the Northeastern Forest Experiment Station of the U.S. Forest Service. It exhibited good growth and slower progression of chestnut blight, but ultimately succumbed to the blight. Like the Graves tree, the Clapper tree was used as starting material for present day backcross breeding programs. Unfortunately none of these efforts produced a fast growing, timber tree with good blight resistance. Every promising candidate fell short in at least one of these respects. The USDA hybrid breeding program, which was taken over by the Forest Service in 1954, was abandoned in 1960.

The American Chestnut Foundation (TACF) was founded in 1983 by a group of prominent plant scientists and lay persons who recognized the severe impact the demise of the American chestnut tree imposed upon the economies of rural communities, and upon the ecology of forests within the tree’s native range. Building upon century-old work by the Connecticut Agricultural Experiment Station and USDA, researchers at TACF are now in their third decade of developing a backcross breeding program to produce trees with the blight resistance of Chinese chestnut and the favorable growth characteristics of American chestnut. Their hope is that hybrid seedlings would be capable of restoring long-term ecosystem processes and functions.

In 2004, U.S. Forest Service Chief, Dale Bosworth, and TACF President and CEO, Marshall T. Case, signed a memorandum of understanding (MOU) that “establishes a framework for the two organizations to work together to introduce blight-resistant American chestnut trees into the forest ecosystem of the eastern landscape.” The press release for the MOU further stated: “The Forest Service and TACF will use scientific research and a breeding program developed by TACF founders to restore the once dominant tree to its native woodlands.” Since approval of the MOU, the Forest Service has provided annual funding to TACF to support implementation of on-going projects. Since the first MOU, there have been two subsequent renewals, in 2010 and again in 2015, to continue this agreement between TACF, the Forest Service, and the Natural Resources Conservation Service.

In 2007, the Southern Research Station of the U.S. Forest Service partnered with TACF, the University of Tennessee’s Tree Improvement Program and the Southern Region of the National Forest System to test blight resistance and growth performance of a backcross-generation of American chestnut seedlings, known as BC3F3. Between 2009 and 2015, the team planted over 4,000 chestnut seedlings in the Cherokee National Forest, Tennessee, the Jefferson National Forest, Virginia and the Nantahala National Forest in North Carolina. The seedlings were mostly planted in areas of even-aged regeneration harvests similar to areas where the trees would eventually be restored once blight-resistant chestnuts are widely available. These were the first forest field tests of blight resistance of BC3F3, the third generation of a third backcross, the most advanced breeding generation currently available. The primary objective of this project was to quantify blight resistance, survivability and competitive ability of genetic families of the BC3F3 breeding generation planted in over a dozen test sites. The oldest trees are currently in their eleventh growing season.

Researchers also compared BC3F3 with less advanced generations, such as BC1F3 and BC2F3, along with disease-resistant Chinese chestnut and disease-susceptible American chestnut. After eight years, blight had infected between 17 and 54 percent of all trees planted: 40 % of trees in Virginia, 17 % percent of trees in Tennessee and 54 % of trees in North Carolina. The BC3F3 generation exhibited resistance more similar to the Chinese chestnut than the American chestnut. Blight was more likely to infect trees after they grew three to five inches in size at the base. Researchers found that 31 % of the planted seedlings died prior to blight detection. This non-pathogen-related mortality was probably due to factors typical of hardwood plantings, including repeated deer browsing and pest damage.
“To my knowledge, our research represents the oldest study examining blight resistance of the BC3F3 generation planted in forest reintroduction trials,” says Stacy Clark, Research Forester with the Southern Research Station (Fig. 7). “We found that blight resistance of the BC3F3 trees was not as good as Chinese chestnut but was better than the American chestnut. Eight years of data is a remarkable research accomplishment, but it’s not sufficient to determine if seedlings have enough blight resistance for restoration plantings.” Clark has also found that hybrid trees appear to be growing competitively in these highly diverse environments where they must contend with fast-growing species like yellow poplar, Liriodendron tulipifera. Some of the hybrids have exceeded 11 meters in height in 10 years.

Research on American chestnut is also underway at the Forest Service’s Northern Research Station. Research Forester Melissa Thomas-Van Grundy and three co-authors (Jane Bard, Jeff Kochenderfer and Paul Berrang) published results of a study in West Virginia that compared mortality, early growth and blight occurrence in hybrid chestnuts with pure Chinese and American chestnut seedlings. Under the leadership of Research Forester Cornelia Pinchot (a great granddaughter of Gifford Pinchot) studies are underway on the Allegheny National Forest and adjacent state and private lands in Pennsylvania, on growth, survival and competitive ability of backcross American chestnuts planted in stands of varying site quality and silvicultural treatments that create different light levels. In the colder reaches of American chestnut’s native range, Research Plant Physiologist Paul Schaberg is investigating the development of American chestnuts that need to be both blight resistant and cold tolerant for restoration at higher altitudes and elevations.

Figure 7 – U.S. Forest Service Research Forester Stacy Clark with some hopefully blight resistant American chestnuts.
In 1989, two members of the newly formed New York chapter of TACF, Herb Darling and Stan Wirsig, met with Doctors Charles Maynard and William Powell of the faculty of the State University of New York, College of Environmental Science and Forestry at Syracuse University (SUNY-ESF). The TACF members represented laypeople seeking researchers who could use the latest tools of genetic engineering (GE) to complement the ongoing TACF backcross breeding program. As a result, blight-tolerant American chestnut trees have been developed using an oxalate oxidase-encoding gene from wheat. This enzyme breaks down oxalate, the chemical produced by the chestnut blight fungus, which forms tree-killing cankers. This results in blight tolerance, where the tree and the fungus can coexist. This is theorized to be more evolutionarily stable relationship than direct pathogen resistance.

With the development of GE American chestnuts underway, scientists at SUNY ESF have begun a three-phase program:

1. Establishing new American chestnut seed production orchards with GE trees.
2. Establishing a diversity orchard with trees from throughout the American chestnut’s natural range.
3. Communicating regularly with three U.S. regulatory agencies (EPA, USDA, and FDA) and Canadian regulatory agencies to determine protocols for a successful regulatory review of GE blight resistant American chestnuts. The regulatory review for genetically engineered plants is rigorous and thorough. It is especially complicated for American chestnut because it was established based on laws and regulations for crop plants, some of which are not necessarily applicable to trees. Dr. Powell and his team have recently submitted a petition for regulatory approval of the transgenic tree to USDA-APHIS for review and eventual public comment.

The immediate objective is to produce 10,000 GE American chestnuts for evaluation under the wide range of conditions throughout the natural range of American chestnut.

While work continues to restore the viability of American chestnut as an integral component of eastern hardwood forests, numerous other introduced pest species have appeared in our forests, the direct result of increased international trade and travel and ineffective programs to control their spread. For example Dutch elm disease (DED), caused by fungi of the genus Ophiostoma and its insect vector, the European elm bark beetle, Scolytus multistriatus, was discovered in North America in 1928. Another native of Asia, DED arrived in North America via logs imported from Europe and killed millions of American elm, Ulmus americana, and other elms throughout the eastern and Midwestern United States before disease-tolerant varieties were developed by the U.S. Forest Service. Emerald ash borer, Agrilus planipennis, native to China, Japan, Mongolia and the Russian Far East was discovered in Detroit, Michigan in 2002. This insect has since spread to 35 states and has killed hundreds of millions of ash trees.

Footnote
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The American chestnut was in deep trouble prior to the introduction of the chestnut blight fungus. Large numbers of American chestnuts were killed in the southern parts of its natural range by a root disease caused by Phytophthora cinnamomi.

Phytophthora is a genus of oomycetes or water molds. They can cause disease of a wide range of plants important in forestry and agriculture. P. cinnamomi was first described from the island of Sumatra (Indonesia) in 1922 where it was established as the cause of a canker of the cinnamon tree. It has been introduced into Australia, the Mediterranean countries of Europe and Africa, and the southeastern United States. It was probably introduced into North America by European colonists during the 1700’s and is believed to have eradicated American chestnut from forests in portions of the southeastern United States prior to the introduction of chestnut blight. Today, P. cinnamomi is known primarily as the cause of littleleaf disease of shortleaf pine in the southern United States.

Several species of Phytophthora are important forest pests in the United States. P. lateralis causes a root disease of Port Orford cedar in the Pacific Northwest. More recently, P. ramorum has been identified as the cause of sudden oak death in California and Oregon. This pathogen is also known to occur in many parts of Europe. P. infestans was the causal agent of the Irish potato famine of 1845-1849. This caused over 1 million deaths from starvation and resulted in the emigration of another million people from Ireland.

The U.S. Forest Service (USFS), The American Chestnut Foundation (TACF) and their partners recognize that to restore American chestnut as a viable component of eastern hardwood forests, it will be necessary to develop genetic strains that are resistant to both chestnut blight and P. cinnamomi. In addition, American chestnut has several non-native insect pests that may plague its reintroduction including the Asian gall wasp, Dryocosmus kuriphilus, which impacts flowering and growth, the Asiatic oak weevil, Cryptepistomas castaneus, which defoliates trees and feeds on roots and the gypsy moth, Lymantria dispar, a defoliator of many broadleaf trees.

A collaborative project between the USFS, TACF, and Clemson University is in its third year of screening advanced-generation backcross hybrid American chestnut seedlings for resistance to P. cinnamomi at the U.S. Forest Service’s Resistance Screening Center in Asheville, NC. Survivors from these greenhouse screenings will help identify resistant parents that could be employed in breeding programs to produce selections with combined resistance to both pathogens.

Watch CBS This Morning story that features Rex Mann sharing the story of the American Chestnut
https://youtu.be/-4yHysNph5U