Restoring a Forest Icon

COULD RETURNING THE AMERICAN CHESTNUT REMODEL OUR WILDLIFE LANDSCAPE?

By Stacy L. Clark, Scott E. Schlarbaum and Joseph D. Clark

Credit: The American Chestnut Foundation

▲ **Biologists are closer than ever to restoring the iconic American chestnut to forests of eastern North America.**

Mother Nature was not making it easy. It was Feb. 18, 2009, and winds were gusting, sleet was falling and temperatures were hovering around 40 degrees Fahrenheit. Our nine-person crew, made up of personnel from the U.S. Forest Service Southern Research Station, the Cherokee National Forest and The University of Tennessee's Tree Improvement Program, was attempting to establish the first test planting of American chestnuts (*Castanea dentata*) bred for resistance to the chestnut blight (*Cryphonectria parasitica*), an exotic fungal pathogen that had nearly eliminated the native tree from the North American landscape.

With each hole dug and seedling tamped into the ground, our hope was that we were one step closer to restoring an important wildlife food to eastern hardwood forests.

After a century of research, we are closer than ever to restoring this iconic tree to the forests of eastern North America, but there is still a long way to go. Evaluation of blight resistance and growth of seedlings in our research plantings continue. Seedlings are not yet available for general reforestation. Once established, trees will have to live long enough to flower, bear fruit and regenerate in the face of a changing climate and the progressively increasing presence of invasive pests in American forests.

Given the challenges, is chestnut restoration really worth the time and effort? When we understand the effects of its demise on humans and wildlife and the investments already made towards restoration, the choice seems clear.

Chestnut blight was accidently introduced into New England in the late 19th or early 20th century, probably on imported Japanese chestnut (*Castanea crenata*) nursery stock. The Asian species was originally imported to breed with the native American chestnut and chinquapin (*C. pumila, C. ozarkensis*) species to improve nut production. The American chestnut had little natural resistance. Once infected, trees began to die off rapidly. By the 1940s, they were virtually eliminated.

Ironically, the hybrids — created by breeding American chestnuts with the Asian trees that likely brought the blight — would become a starting point for a breeding solution to this disease.

Breeding a solution

The early decades of breeding for blight resistance resulted in trees that were either too much like the Asian chestnut species in appearance (e.g., poor growth habit, poor adaptability) or had insufficient blight resistance. Not until the 1980s did a crop breeder propose the 'backcross' method to transfer resistance. Hybrid trees commonly referred to as the BC_3F_3 (the third generation of the third backcross) were available for the first time for field testing in 2007 and were predicted to have relatively high levels of blight resistance.

Unlike food crops, hardwood trees take years to sexually mature. A breeding approach would take decades. Luckily, the Connecticut Agricultural Experiment Station had first-generation backcross trees from early breeding efforts. The American Chestnut Foundation (TACF), founded in 1983, was able to use the Connecticut trees to spearhead its breeding program, which received sustained support from partnerships and donations from public and private entities. By 2007, the first BC_3F_3 nuts were produced in numbers sufficient to field test them in research plots.

While TACF continued to evaluate blight resistance in orchard plantings at Meadowview, Virginia, we tested the BC_3F_3 seedlings in real-world forest test plantings in the Blue Ridge Mountains. Cooperating with the oldest hardwood tree improvement program in the country at the University of Tennessee, three national forests and TACF, we embarked on a collaborative journey now in its 11th year.

A keystone species?

Until recent decades, discussions involving the chestnut concentrated on resistance breeding results. Little discussion took place on the effects that chestnut restoration would have on ecosystem processes and functions, including wildlife population dynamics. The initial motivation for breeding programs was largely to recover an important economic resource. It was not until the 1990s and early 2000s that the conversation shifted to include potential impacts on the ecosystem.

The American chestnut is often referred to as a keystone or foundation species in eastern North America. Early forestry records suggest the tree was a prolific mast producer, and its nuts were used by an array of wildlife species, as well as humans. Chestnuts ranked as one of the most important plants in the eastern U.S. to support wildlife food habitat (Martin et al. 1951). The nut itself has relatively low fat content but is high in protein and carbohydrates with a low tannin content, making it more palatable to wildlife than acorns (Minser et al. 1995; Blythe et al. 2015).

American chestnuts had an extensive range and comprised 20 percent or more of tree density in certain upland forests, growing most rapidly in the southern Blue Ridge Mountains. After the blight, oaks (*Quercus* spp.) and hickories (*Carya* spp.) replaced the chestnut in many landscape positions across the Blue Ridge (Elliott and Swank 2008). Acorn and hickory nut production varies annually over a widespread area, which may be a mechanism to thwart predation (Clark 2004). Replacement by oak and hickory did not make up for the loss of American chestnut, which can produce around 230 pounds per acre annually (Gilland et al. 2012), resulting in an overall reduction in carrying capacity for many wildlife species, particularly in the southern Appalachians (Diamond et al. 2000). Moreover, chestnuts are not as episodic in mast production as oaks and hickories, resulting in a more stable annual food resource. Such annual fluctuations in acorn production results in reduced fecundity and increased mortality in white-tailed deer (*Odocoileus virginianus*), black bear (*Ursus americanus*) and gray squirrel (*Sciurus carolinensis*), among others.

Credit: Stacy Clark, USDA Forest Service

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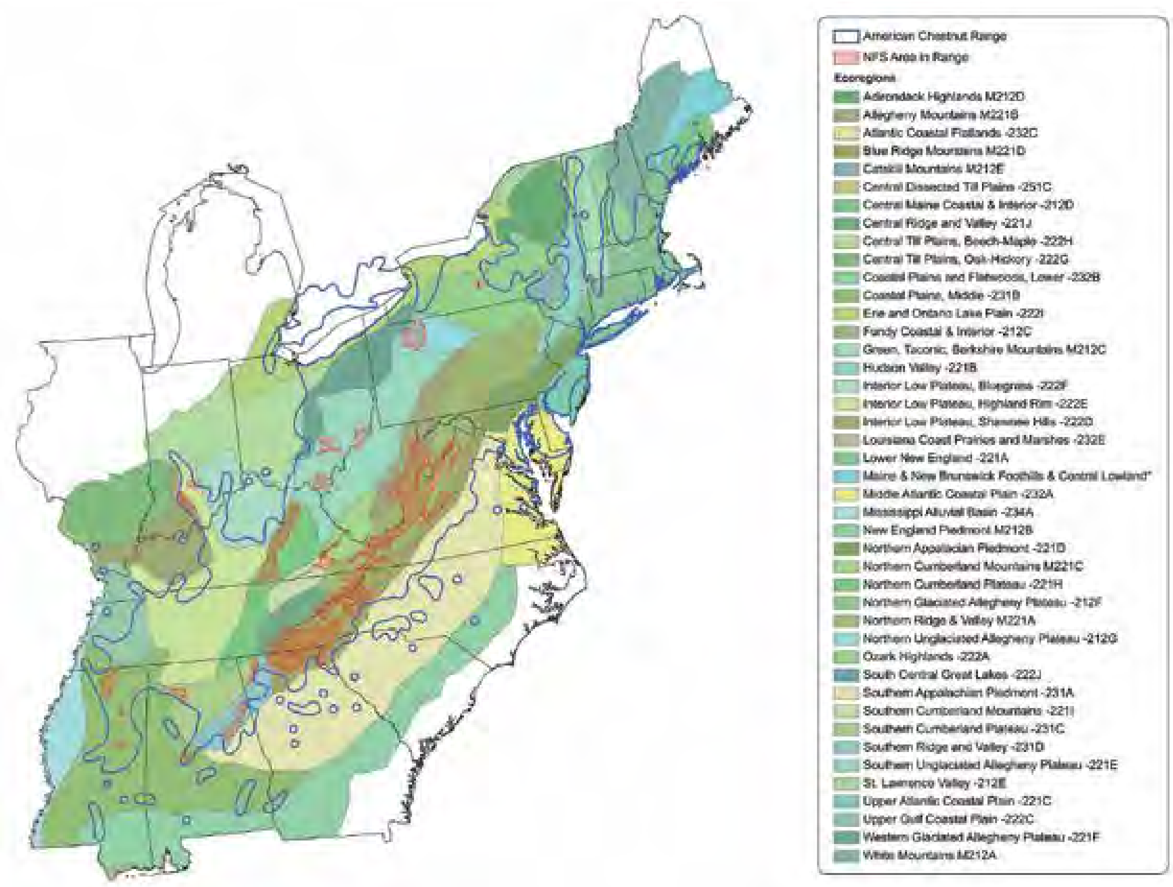
▲ A chestnut sapling (left) planted on the Nantahala National Forest in western North Carolina shows little resistance to chestnut blight infection, as indicated by lack of swelling and callous formation and abundant fruiting bodies (orange stroma protruding from the bark). A chestnut sapling (right) shows some resistance to chestnut blight infection, as indicated by slight swelling and callous formation and lack of fruiting bodies.

Credit: Scott Schlarbaum, University of Tennessee

▲ University of Tennessee Senior Research Technician David Griffin, left, and U.S. Forest Service Research Forester Stacy Clark process bare-root nursery seedlings for planting in research plots on national forests in the southern Appalachians. Each tree is tagged and genetic identity as well as tree attributes such as root count and stem height are maintained throughout the study.



Credit: USDA Forest Service

The former range of the American chestnut (blue lines) spanned multiple ecoregions across the eastern United States just prior to the blight, around 1904. The USDA Forest Service currently manages approximately 15 million acres within the former range (shaded red), offering substantial opportunities for research and restoration.

Chestnut flowers are very attractive to pollinators because of their fragrant white flowers, but it is not clear if insect pollination is a requirement for chestnut reproduction. Over 60 species of moths have been recorded feeding on chestnuts, some of which may now be extinct due to the chestnut's disappearance. Loss of chestnut-obligate species may even have negatively impacted other tree species whose defoliators are now more prevalent because their insect competitors disappeared. In addition to moths, defoliating insects — like the appropriately named chestnut sawfly (*Craesus castaneae*) — may have also largely disappeared; although we recently recorded this rare insect at multiple chestnut planting sites. The function of these obligate insects as a food source for birds or other wildlife is virtually unknown.

American chestnuts grow quickly, with good timber form, producing attractive, light and strong lumber with good rot resistance. The

Credit: Stacy Clark, USDA Forest Service

University of Tennessee Research Technician John Johnson observes the appropriately named chestnut sawfly at a chestnut planting on the Jefferson National Forest in southwestern Virginia. This rare native insect species is a late-season defoliator that mimics the teeth of the chestnut leaf, perhaps to avoid predation.

Credit: Stacy Clark, USDA Forest Service

An American green tree frog (*Hyla cinerea*) sits on a leaf of an American chestnut hybrid planted on the Cherokee National Forest. The relationship between chestnut, insects and insectivores like the tree frog are not well understood.

Credit: Stacy Clark, USDA Forest Service

Credit: C. Turnage, The University of Tennessee

▲ Black bears, like this sow and cubs perched in a white oak (*Quercus alba*) tree, historically fed on the American chestnut, which were high in protein and carbohydrates and a relatively stable annual food source.

◀ Scratch marks, suspected to be from a black bear, were found on several hybrid American chestnut trees planted on the Jefferson National Forest in southwestern Virginia.

demand for the nuts was also high. Chestnuts from mountain communities ended up in national and global market places, ultimately "roasting on an open fire," as the popular Christmas carol goes. An entire economy was built around trading chestnuts for goods and services in rural Appalachia. Chestnuts also provided sustenance farmers with free feed for their cattle and pigs, and they attracted bears, deer and turkey for their dinner table.

Challenges to restoration

Challenges to chestnut restoration are real and measurable. The crux of chestnut restoration is to produce hybrid seedlings with growth rates similar to the American chestnut while maintaining high levels of blight resistance from the Chinese chestnut over time. Four-year height and diameter growth of BC_3F_3 hybrid seedlings in our plantings was slightly less than the American chestnut (Clark et al. 2016), and blight resistance after eight growing seasons was not as high as the Chinese chestnut (Clark et al., 2019). Additional breeding work coupled with genotyping is underway to improve outcomes and efficiency of the breeding program (Steiner et al. 2017).

One of the most important challenges to restoration, once blight-resistant seedlings are available, is identifying the appropriate forest management prescriptions for restoration, but this is difficult when experimental material is so limited. Our early research using pure American chestnut and early hybrids shows that seedlings do best in silvicultural treatments that opened the forest canopy through partial thinning or commercial harvests like clearcutting (Clark et al. 2012). There is a balance between providing sunlight to newly planted chestnut seedlings and restricting light to their competitors, and we are only just now beginning to study these relationships.

Fortunately, the rapid growth rate of chestnut seedlings facilitates restoration. We have documented seedlings averaging two feet in height growth a year, with some seedlings growing more than six feet in a single season. This gives chestnuts a leg up on oak seedlings, which become easily suppressed by faster growing species. Vegetation competition from fast-growing trees like yellow poplar (*Liriodendron tulipifera*) will be a problem on productive sites, but with proper management and site selection, chestnuts can keep up with the poplars. This is important because poplars create deep shade. Chestnuts may be able to live under this shade for a while, but they will not grow sufficiently to become a part of the next stand.

For trees to even have the chance to compete for sunlight, they must first escape browsing by white-tailed deer, which can keep trees near ground level for years, as first noted by Henry Thoreau. The largest seedlings at the time of planting had a much lower probability of browse, but planting only large seedlings would mean discarding the small seedlings, which is difficult to justify given the resources that have gone into producing these trees. Erecting deer shelters or deer repellent sprays are also options, but they can be expensive and labor intensive.

A challenge to restoration will be the ability of chestnuts to naturally spread. The relatively large size of the nut prohibits dissemination by wind or by attachment to animal fur or bird feathers. Small mammals like tree squirrels can assist by caching seed away from planting areas. Hybrid nuts were cached at farther distances than pure American chestnut (Blythe et al. 2015), which might actually assist in restoration efforts.

The continuing parade of invasive exotic species into the United States will impede restoration. The chestnut is negatively impacted by a host of other exotic species, most notably root rot, caused by *Phytophthora cinnamomi,* which arrived in the

Credit: Stacy Clark, USDA Forest Service

Credit: Joe Clark, USGS

▲ A newly planted American chestnut seedling was browsed by deer. Repeated browsing will stunt tree growth and may eventually lead to mortality.

▶ White-tailed deer would benefit from chestnut restoration, but they also represent a challenge to restoration as they browse on newly planted seedlings. The use of large seedlings, tree shelters or deer repellant spray have all been tested to mitigate browse.

early 19th century. This organism has been the most detrimental deterrent to chestnut restoration in the southern United States, causing die-off in a number of new test plantings (Clark et al. 2014), and a breeding program for its resistance has only just begun. In our plantings, we have also noted impacts from the Asiatic oak weevil (*Cyrtepistomus castaneus*), which defoliates leaves and feeds on roots, and the Asian gall wasp (*Dryocosmus kuriphilus*), which hinders growth and flowering for nut production. The European gypsy moth (*Lymantria dispar*) is within sight of our most northern planting in Virginia, and chestnut is a preferred host. Exotic plant species such as tree-of-heaven (*Ailanthus altissima*) and Japanese honeysuckle (*Lonicera japonica*) will outcompete seedlings for sunlight and water.

One of the most difficult challenges to restoration will not be biological but is related to the lack of existing resources, knowledge and infrastructure to implement large-scale restoration in a successful manner (Clark et al. 2014). The current effort relies on public and private partnerships and collaboration, but a large portion of the planned restoration effort has not been formalized.

Potential impacts of restoration on wildlife species

Will wildlife response to chestnut recovery be the same as during its heyday? Probably not.

Many species that historically fed on chestnut such as the Carolina parakeet (*Conuropsis carolinensis*) and the passenger pigeon (*Ectopistes migratorius*) are long gone (Schorger 1955). Nevertheless, the species that remain stand to benefit tremendously. This is especially true given the alternative consequences of our aging oak forests and widespread problems with oak recruitment.

Our expectation is that carrying capacity for many wildlife species that depend on hard mast (e.g., deer, bears, turkeys (*Meleagris gallopavo*), small mammals and their predators) would be raised and the annual booms and busts due to sporadic acorn production would be lessened if chestnut restoration is successful. As diets and resulting fecundity improve, however, bear- and deer-human conflicts may increase, necessitating additional resources be devoted to already strained systems (Clark 2016).

Given the over 100 years of effort, the importance of the species, and potential positive impacts, chestnut restoration efforts should proceed optimistically but with caution. Since that cold and rainy day in February 2009, we have planted an additional 4,000 trees in research test plots on three national forests. Some of the BC_3F_3 chestnuts in our first test plantings are now over 30 feet tall and survival rates are relatively high (70 percent), but nearly 20 percent were succumbing to blight after eight growing seasons.

We remain optimistic, however, that trees with high levels of blight resistance will be forthcoming. After just over a decade of research, we realize a lot more remains for us to learn, but we anticipate that a restored American chestnut will be a boon to many wildlife species in the East. ■

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