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American Chestnut, *Castanea dentata*

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American chestnut (*Castanea dentata*) was once a dominant tree species, historically found throughout eastern North America and comprising nearly 1 of every 4 trees in the central Appalachian region. Valued for its nuts (eaten by people and a key source of wildlife mast), rot resistance and attractive timber, it was a central component of many eastern forests (Fig. 1). However, the invasive chestnut blight fungus (*Cryphonectria parasitica*), introduced to North America from Asia in the early 1900s, wiped out the majority of mature American chestnut throughout its range. While American chestnut is still functionally absent from these areas, continued efforts to return it to its native range, led by several different non-profit and academic research partners and using a variety of different approaches, are underway and provide hope for restoring this species.

Figure 1. Large healthy American chestnuts like this, once valued for timber, are now very rare. Most succumb to chestnut blight when they are much younger.

Figure 4. Larger trunks and branches have deep vertical furrows.

Photos courtesies: Figure 1: USDA Forest Service - Southern Research Station, USDA Forest Service, SRS, Bugwood.org; Figure 4: Megan Buland, University of Kentucky

Species Characteristics

American chestnut is a member of the Fagaceae family, the same family to which oak and beech trees belong. The leaves and branches of American chestnut are alternate in arrangement (Fig. 2). Leaves are simple and lanceolate or oblong in shape, 5-8" long, with a coarsely serrated margin, each serration ending in a bristle tip (Fig. 3). Leaves are dark green above, pale below and are neither waxy nor hairy. The buds are shiny and dark brown in color and resemble tiny footballs held closely against the branches. The bark of younger branches is a deep brown color and is covered in small, pale lenticels. The bark on larger branches and the trunks of larger trees is a dull grey color, with vertical fissures separating the bark into plates and ridges (Fig. 4). Male flowers (catkins) and female flowers appear together on mature trees in the summer (Fig. 5). These develop into fruits, 2-3 nuts held within

Figure 2. The leaves of American chestnut are alternate and serrated.

Photo courtesy: Ellen Crocker, University of Kentucky

Figure 3. The margins of American chestnut leaves are serrated, ending in a bristle tip.

Photo courtesy: Ellen Crocker, University of Kentucky

Figure 5. Spike-like male flowers (catkins) are conspicuous during the summer when in bloom and have a distinctive smell.

Photo courtesy: USDA Forest Service - Southern Research Station, USDA Forest Service, SRS, Bugwood.org

Figure 6. Fruit of the American chestnut, spine covered burs.

Photo courtesy: Paul Wray, Iowa State University, Bugwood.org

Figure 7. The nuts of American chestnut were a highly valued food source by humans and wildlife alike.

Photo courtesy: USDA Forest Service - Southern Research Station, USDA Forest Service, SRS, Bugwood.org

a sharp, spike covered green bur that turns to brown in the fall (Fig. 6 and 7).

Chestnut Blight

Chestnut blight is caused by a non-native fungal pathogen, *Cryphonectria parasitica*, native to Asia, that infects American chestnut trees and, in most cases, ultimately leads to tree death. The pathogen that causes chestnut blight was first found on American chestnut in 1904, in New York City's Zoological Park. In the decades following its initial detection it spread throughout the eastern US, killing American chestnut as it progressed.[1]

American chestnut can still be found in forests throughout the eastern United States, though nearly always in the form of immature trees growing from either a seed or as sprouts from the roots of a chestnut tree previously killed by blight. American chestnut is less susceptible to the blight when young and trees may grow, and thrive, in the forest understory or canopy gaps until reaching heights of up to 15 meters and a trunk diameter of 20 centimeters.[2] At this size, the tree becomes more susceptible to infection by the chestnut blight fungus. Trees growing in the dense forest understory are less likely to become infected by wind dispersed fungal spores and may remain uninfected longer than trees growing in more open conditions. Only the above-ground portion of the tree is impacted by chestnut blight. Following the death of a central trunk by the blight, root systems may send up many shoots that can thrive until they reach a sufficient size to themselves be infected. For this reason, it is not unusual to see small or bush-form American chestnut in forests. However, it is important to note that these trees are still susceptible to the blight and above ground shoots will continue to be killed by the fungus over time.

The fungus infects susceptible trees through wounds or cracks in the bark. Once infected, trees exhibit sunken lesions, called cankers, on trunks and branches as the fungus kills the tree's cambium. Cankers are characterized by cracked, discolored bark (Fig. 8). Bright orange tendrils or pustules may also sometimes be observed in and around these cankers, especially in wet weather.

Figure 8. Chestnut blight cankers, exhibiting orange sporulation and cracked, sunken bark.

Photo courtesy: Ellen Crocker, University of Kentucky

These are the spore-producing structures of the pathogen, which produces these fruiting bodies instead of the more commonly recognized mushroom-type structures produced by many other fungi. However, these spores serve the same purpose and airborne yellow spores from infected tissue can reach new hosts and continue the cycle of infection. Other signs of disease include wilted, yellowing leaves (signs of water stress as the tree's vascular system is compromised), epicormic shoots and root sprouts (Fig. 9).

Figure 9. Branch dieback symptoms caused by chestnut blight.

Photo courtesy: Ignazio Graziosi, University of Kentucky, Bugwood.org

Chemicals produced by the pathogen directly inhibit the formation of callus tissue which trees normally produce to wall off and compartmentalize infections.[3] Secretion of the metabolite oxalic acid by the fungus hampers the tree's ability to combat the infection, allowing the cankers to continue to expand. Ultimately, these cankers often cut off the movement of water and nutrients between the roots and leaves of the chestnut tree, killing the vascular tissue of the tree around the canker. Small stems may be killed within months of infection while cankers on larger trunks and branches may get progressively worse over several years.

While American chestnut is the species most impacted by chestnut blight in North America, other chestnut species are also impacted to varying degrees:

- American chestnut (*C. dentata*): most susceptible, lethal infections

[1] Rigling, D. and Prospero, S. (2018). Cryphonectria parasitica, the causal agent of chestnut blight: invasion history, population biology and disease control. Molecular plant pathology, 19(1), 7–20. https://doi.org/10.1111/mpp.12542

[2] Paillet, F. (2002). Chestnut: History and Ecology of a Trans formed Species. Journal of Biogeography. Vol. 29, No. 10/11. https://www.jstor.org/stable/827566

[3] Havir, E.A. and Anagnostakis, S.L. (1983). Oxalate production by virulent but not by hypovirulent strains of Endothia parasitica. Physiol. Plant Pathol. 23, 369–376

- European chestnut (*C. sativa*): highly susceptible, lethal infections
- Chinese chestnut (*C. mollissima*) and Japanese chestnut (*C. crenata*): low susceptibility, occasional minor branch infections

In addition, many species serve as hosts to the pathogen, including oaks like white oak (*Quercus alba*), scarlet oak *(Q. coccinea*), and post oak (*Q. stellata*), and maples. These species are typically highly resistant to the pathogen and infection is noted to be most common for weakened trees or when disease pressure is very high. These hosts are likely to serve as a long-term source of inoculum and, even if American chestnuts are absent from a site for a long time, the pathogen will persist in the environment ready to infect American chestnut trees in the future.

Phytophthora root rot

Chestnut blight is not the only challenge facing American chestnut trees in North America. Phytophthora root rot (also called ink disease) is a root disease caused by the non-native pathogen *Phytophthora cinnamomi* that has infested American chestnut in its southern range since around 1824[4]. *P. cinnamomi* seems to be most problematic for American chestnut growing in lowland and clay soils throughout its range.

The causal agent of Phytophthora root rot is a soil borne oomycete. Oomycetes are "water-loving" and, while surveys have found *P. cinnamomi* present throughout the landscape in infected regions, it is most commonly associated with disease in moist sites with poor soil drainage. It has proven especially challenging in establishment of new orchards of American chestnut as seedlings are particularly susceptible. *P. cinnamomi* does not survive freezing temperatures well and, therefore, is most impactful to American chestnut in the southern parts of its range where soil temperatures are milder in the winter. However, as the climate changes the northern limit of *P. cinnamomi* may push further north. *P. cinnamomi* has a broad host range extending far beyond American chestnut and includes oak and pine species in the eastern United States. However, in mature trees symptoms of *P. cinnamomi* infection can be difficult to diagnose and its impact in forest settings overall is hard to assess.

Other issues

In addition to *Cryphonectria parasitica* and *Phytophthora cinnamomi,* American chestnut may also be affected by a number of other native and non-native insects and pathogens, particularly in the orchard or nursery setting, such as:

- Anthracnose and powdery mildew – native; foliar fungal pathogens
- Asian chestnut gall wasp, *Dryocosmus kuriphilus* – non-native; insect pest making galls in flower and leaf buds, larvae may lead to branch dieback and, in some cases of severe infestations, tree mortality
- Japanese beetles – non-native; foliar feeding beetles
- Periodical cicadas – native, insects lay eggs in branches after feeding, wounding from oviposition (egg laying) may injure tree branches; neither larvae nor adults feed on the foliage or branches
- Ambrosia beetles – a mixture of native and non-native species. Beetles burrow into trees, where they breed and rear their young, it is the mutualistic fungi carried with them that may harm the host tree
- Weevils - a mixture of native species; larvae burrow and feed inside the chestnut fruits, destroying both its culinary and economic value as well as its viability to germinate and grow.

Distribution

American chestnut has a historic range that extends throughout the eastern United States, with the highest densities located in the forests of the Appalachian Mountains (and its foothills). Today, American chestnut remains on the landscape and can still be found as stump sprouts and understory trees. Dry, south and east facing slopes with well-drained acidic soils are ideal site conditions for American chestnut. While it can be found growing in dense understory vegetation, it is more common near roads and forest edges, and other areas with more sun exposure, which it can exploit to grow rapidly, outcompeting other plants under ideal conditions. Throughout Appalachia it is often found growing alongside American beech (*Fagus grandifolia*), chestnut oak (*Quercus montana*), mountain laurel (*Kalmia latifolia*), black cherry (*Prunus serotina*), sourwood (*Oxydendrum arboreum*), and other plant species that prefer similar site conditions.

Research to bring back the American chestnut

Hypovirulence:

Hypovirulence, the infection of a pathogen by another infectious organism, has given scientists some hope for reducing the severity of the chestnut blight due to a loss of virulence of the pathogen. Fungal viruses were discovered infecting the chestnut blight pathogen in Europe, effectively weakening the blight and reducing its ability to infect and kill European chestnut trees. Scientists here in the U.S. have experimented with hypovirulent strains of the chestnut blight fungus that contains these viruses, in an attempt to inhibit the ability of the fungus to kill American chestnuts, though such research has yielded mixed results.[5] Some aspects of the relationship between the virus that causes hypovirulence in chestnut blight, and the pathogen itself, are not well understood and work in the

[4]Crandall, R. S., Gravatt, G.F., and Ryan, M.M. (1945). Rot disease of Castanea species and some coniferous and broadleaf nursery stocks caused by *Phytophthora cinnamomi. Phytopath*. 35:162.:.180.

[5]Milgroom, M.G. and Cortesi, P. (2004). Biological Control of Chestnut Blight with Hypovirulence: A Critical Analysis. *Annual Review of Phytopathology*. 42:1, 311-338. https://www.annualreviews.org/doi/full/10.1146/annurev.phyto.42.040803.140325

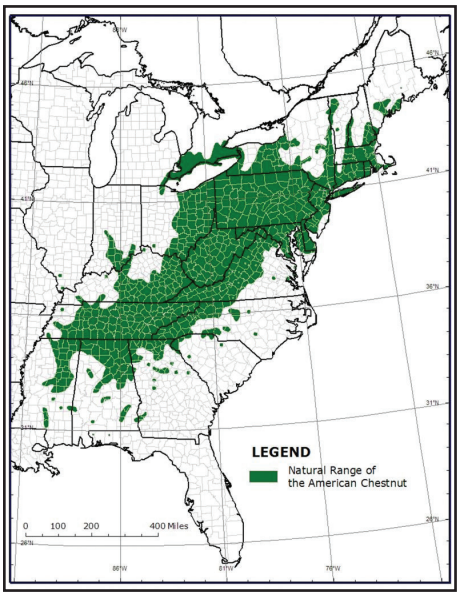

Figure 10. Native range of the American chestnut tree (*Castanea dentata*). Little, E.L., Jr., 1977, Atlas of United States trees, volume 4, Minor Eastern Hardwoods: U.S. Department of Agriculture Miscellaneous Publication 1342, 17 p

lab has not easily been transferred to field trials. Scientists have shown that it is transmissible as a therapeutic treatment of individual cankers. But, success of hypovirulence at a forest population level depends on the natural spread of the virus. Studies suggest that environmental factors and vegetative incompatibility of the chestnut blight fungus restricts virus transmission.[6] However, if researchers can better understand the epidemiological dynamics of this system to determine crucial factors that limit establishment of hypovirulence in forest systems in North America, hypovirulence may prove to be a valuable strategy for restoring American chestnut long-term.

Hybridization:
Hybridization of susceptible American chestnut with resistant species has long been pursued as a possible means of developing a disease-resistant trees. Such attempts have been conducted by crossing American chestnut with a resistant Asian chestnut species and then backcrossing (crossing this hybrid tree back to another American chestnut) and selecting for resistance to the blight. The goal of this approach is that over time a tree will be achieved that exhibits some level of the disease resistance of the Asian chestnut ancestor but the other growth traits of the American chestnut.[7] To do this, typically American chestnut flowers are pollinated by Chinese chestnut (*Castanea mollissima*). Chinese chestnut is mostly resistant to the effects of the pathogen; however, it has a smaller form and is not able to become a dominant forest tree. This hybridization approach has been spearheaded by The American Chestnut Foundation, in collaboration with a wide range of researchers, citizen scientists, and volunteers. Currently their program has seedlings that have been backcrossed for several generations, with a genetic make-up that is roughly 80-90% American chestnut and 10-20% Chinese chestnut in their composition. While results are mixed in terms of resistance to chestnut blight, these hybrid trees do appear to have higher resistance than pure American chestnuts.[8]

Biotechnology:
Another means of obtaining blight resistance in American chestnut through breeding may lie in the use of biotechnology to develop an American chestnut with the ability to tolerate the chestnut blight. Scientists at SUNY's College of Environmental Science and Forestry (ESF) are using a genetic modification approach as a way to bring back the American Chestnut. The chestnut blight pathogen *Cryphonectria parasitica*, produces oxalic acid (OA) among other chemicals to produce cankers and eventually kill the cambium of the tree. But scientists involved in The American Chestnut Research and Restoration Project at ESF and collaborators at the American Chestnut Foundation, have identified a gene from bread wheat which potentially could enhance blight resistance by detoxifying OA.[9] This defense gene produces an enzyme called oxalate oxidase (OxO) which blocks OA production by the fungus. By transferring the OxO gene from wheat (and a marker gene to help ensure the resistance gene is present), into the chestnut genome, the enzyme then protects the tree, allowing the fungus and tree to coexist. These blight tolerant trees can then be outcrossed to surviving mother trees and continued outcrossing may produce diverse and blight-tolerant trees over time.

[6]Kolp, M., Double, M., Fulbright, D., MacDonald, W. and Jarosz, M. (2020). Spatial and temporal dynamics of the fungal community of chestnut blight cankers on American chestnut (*Castanea dentata*) in Michigan and Wisconsin. *Elsevier, Fungal Ecology*, Vol 45, 100925.

[7] Diskin, M., Steiner, K.C. and Hebard, F.V. (2006). Recovery of American chestnut characteristics following hybridization and backcross breeding to restore blight-ravaged Castanea dentata. *Forest Ecology and Management*. Volume 223, Issues 1–3; Pages 439-447. https://www.acf.org/wp-content/uploads/2016/09/RecoveryofAmericanChestnutCharacteristics-3.pdf

[8]Westbrook, J.W., Zhang, Q., Mandal, M.K., Jenkins, E.V., Barth, L.E., Jenkins, J.W., Grimwood, J., Schmutz, J. and Holliday, J.A. (2019). Genomic selection analyses reveal tradeoff between chestnut blight tolerance and genome inheritance from American chestnut (*Castanea dentata*) in (*C. dentata x C. mollissima*) x C. dentata backcross populations. BioRxiv 690693. doi: https://doi.org/10.1101/690693; https://www.biorxiv.org/content/10.1101/690693v1.abstract

[9]Powell, W. and Newhouse. A. (2019) Developing Blight-Tolerant American Chestnut Trees. Cold Spring Harbor, Perspectives in Biology. 12 (7).

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