Nick Tsichlis
ENVIRON 436
12-1-20

The American Chestnut: Historical Significance, Conservation Efforts, and Reintroduction Implications

Introduction

An icon of eastern North American forests, the American Chestnut (*Castanea Dentata)* is widely revered for its past ecological importance as well as its central role in both the subsistence livelihoods of both European settlers and Indigenous Peoples. Because of its swift excurrent growth, reliable stump regeneration, and consistent seed production, it was the source of a multitude of ecosystem services for those who depended on the land for their sustenance. A foundation species in ecosystems from Maine to Georgia, *C. dentata* was also integral in regulating fluxes of energy and nutrients in forests and influenced their canopy structure and carbon sequestration potential. The demise of *C. dentata* and the ecological, economic, and social reorientations that followed elucidate the consequences of the industrialization and expansion that occurred during that period in American history. Moreover, subsequent efforts to revive *C. dentata* through traditional and new-age techniques of genetic manipulation reflect an evolving understanding of the underlying biological processes which underpin ecosystems as well as shifting cultural attitudes regarding resource conservation and sustainability (Andam et al., 2015). In eastern North America, centuries of rampant deforestation, subsequent land degradation, ubiquitous pollution, and the perennial introduction of foreign species have resulted in periodic, seismic changes in forest composition and structure. Many of these macro-level changes, such as habitat fragmentation and reduced species diversity, have been accepted by a large percentage of populace as inevitable byproducts of the technological maturation of civilization. Additionally, generally low levels of ecological literacy preclude most from grasping the magnitude of these changes as well as visioning what productive, sustainable future relationships with the natural world would look like. Thus, the potential reintroduction of *C. dentata* represents a unique opportunity to facilitate dialogue between ethnobotanists, private landowners, and Indigenous Peoples regarding the impacts of biotechnological innovations on natural processes. *C. dentata*, a ghost of contemporary forests, is an important American cultural icon and, to many, a source of patriotic pride. Now that multiple groups are on the verge or reestablishing genetically altered blight-resistant specimens within the species' natural range, it is more important than ever before to understand its historical ecological niche, it's cultural relevance to the descendants of European immigrants and Indigenous Peoples, and its potential to disrupt the ecosystem functions of previously rebalanced contemporary forests.

Literature survey methods

The data and scientific analysis synthesized in this research paper were examined primarily through Google Scholar and the University of Michigan Library online search tool. Relevant papers were downloaded and saved as .pdf files by signing into the online library database. Papers were then organized within the Mendeley Reference Manager desktop application for ease of access and citation accuracy.

Discussion

Prior to its demise, *C. dentata* was a dominant tree species throughout its 800,000 km^2 native range, and sometimes comprised up to half of the standing biomass in forest ecosystems (Jacobs et al., 2013). While it exhibits the ability to establish itself under a wide range of ecological conditions, it prefers non-calcareous, moderately acidic upland habitats with well drained, sandy soils (Jacobs, 2007). Because of the ecological niche it provided and its regulatory effects over ecosystem functions, it is widely considered to have been a foundation species in the Appalachian Mountains. Unlike keystone predators, which often exist at the top of the trophic pyramid, foundation species tend to occupy low trophic levels and are responsible for the stable conditions that allow for other species to thrive. Because trees can alter microclimates, define forest structure, and influence nutrient fluxes, they are often considered foundation species, and their loss can have irreparable effects on the ecosystems they regulate (Andam et al., 2015). Once co-dominant with oaks throughout its range, the loss of *C. dentata* undoubtedly affected ecosystem function in this way. The American chestnut has a rapid growth rate when exposed to sunlight, quickly establishes root collar sprouts after fires, and grows tall to influence canopy structure. Its leaves have a low C:N ratio and break down quickly in aquatic systems, indicating that they provide a reliable source of nutrients to producers in mountain streams and rivers. *C. dentata* wood also has high tannin content and breaks down considerably more slowly than wood from other species, so the omnipresence of chestnut biomass in forests and streams creates habitats and specialized niches for other animals to exploit (Andam et al., 2015). Considering these attributes, the American chestnut was a major component of forest ecosystems in the eastern United States.

In addition to these contributions to the functionality of forests, the chestnut also provided a multitude of ecosystem services for those who worked on and relied upon the land. Indigenous Peoples utilized the nuts as a food source, eating them raw and preparing them either by boiling or grinding them into flour. They used chestnut bark as roofing for their shelters and built canoes from their wood (Lutts, 2004). In Appalachia, where European settlers established homesteads and created communities, the American chestnut often comprised a quarter or more of the forest tree composition. Chestnut timber proved invaluable, as the straight-trunked tree is fast growing and easily coppiced. Its rot-resistant wood proved to be extremely useful for split-rail fences because of structural properties that allowed long sections to be evenly divided with an axe. Additionally, newly settled peoples utilized the chestnut to construct cabins, barns, furniture, musical instruments, coffins, shingles, and a plethora of tools and other household wares (Biermann, 2016). In later years, the straight, rot resistant trunks would be used as telephone poles and, enabled by the production of tannic acid through a process of boiling the chestnut bark, a lucrative tanning industry would emerge in the Southeastern United States (Biermann, 2016). Already familiar with the European Chestnut *Castanea sativa*, settlers in the region quickly discovered the value of American chestnuts, and also boiled them and made them into flour. They used these products to make cakes, breads, pudding, and porridge. Extract from chestnut leaves was also used for medicinal purposes, and was administered for whooping cough, burns, swelling, and snakebites (Lutts, 2004). “Nutting” became a recreational activity for both subsistence farming families and the well-off, as each autumn brought massive, consistent chestnut harvests. In active competition with local fauna, families would enthusiastically collect as many as possible, carefully extracting the hard, smooth nuts from their spherical, spine-covered casings. General stores in local towns operated as exchanges, allowing farmers to trade bushels of nuts for provisions and tools or to pay down debts. School-aged children traded nuts for shoes, clothes, and school supplies. In many areas, chestnuts were the only source of monetary income for subsistence farming families (Lutts, 2004).

Beyond feeding the people who called these areas home, yearly chestnut crops were integral to livestock production in the region. Farmers fattened their hogs by letting them run wild through the forests which encompassed not just their land but also their neighbor’s and the land in between, facilitating a network of “chestnut commons” in which land was communally utilized for the benefit of local residents. Slaves, smallholder farmers, and sharecroppers benefited immeasurably from this, as they often owned too little to support their livestock but had access to vast, unimproved tracts of mountainous land. Each fall the cattle, hogs, and domesticated turkeys feasted on the acorns and chestnuts that coated the landscape, and in the process enriched the livelihoods of local farmers, who salted and stored meat for use throughout the winter months and sold it at local markets as another source of income (Lutts, 2004).

The emergence of chestnut blight (*Cryphonectria parasitica*) destroyed many of these mutualistic relationships. An aggressive diffuse canker disease, it first appeared in 1904 in the Bronx Zoological Park in New York City and quickly infected trees throughout the eastern United States with an extremely high mortality rate (Jacobs, 2007). A necrotrophic pathogen likely introduced on *Castanea* seeds from Asia, *C. parasitica* enters trees through small openings in the bark and rapidly colonizes the cambial zone, resulting in stem dieback and tissue death. Because it often takes multiple years to fully consume chestnut trees, the fungus readily sporulates from ongoing infections, allowing it to spread rapidly to neighboring chestnut populations (Jacobs et al., 2013). By 1950 the blight had spread throughout the entirety of its native range, and by 1060 it had killed an estimated 4 billion trees. This catastrophic loss had profound ecological consequences, including catalyzing a succession in canopy dominance from the American chestnut to several co-occurring species (Jacobs, 2007). Its widespread demise, roughly equivalent to 9 million acres of pure chestnut stand, also led to the collapse of the populations of black bear, turkey, and squirrel species, as well as other consumers within the ecosystem. As consistent mast production steadily declined in the region, the carrying capacity for many wildlife species across multiple trophic levels was reduced, and food webs became stressed and collapsed (Lutts, 2004). While the root systems of some of those original chestnut trees survive and continue to produce root collar sprouts, they rarely survive to a reproductive age, and their cumulative biomass, seed production, and leaf litter have negligible effects on the surrounding forest, rendering the species technically present but functionally extinct (Andam et al., 2015).

Breeding programs to rescue the American chestnut began almost immediately after the fungus was identified, and in 1909 the USDA initiated a breeding program aimed at creating a disease-resistant hybrid between *C. dentata* and the Chinese chestnut *Castanea mollissima*. However, repeated attempts failed to produce a functionally improved American chestnut tree that had had the qualities of the original as well as sufficient blight resistance. A tree with similar structural characteristics, wood of equivalent quality with high tannin content, and consistent seed production to support wildlife and livestock was never produced, and the breeding program was terminated in 1960 (Jacobs et al., 2013). Aided by advances in technology, research in subsequent decades has produced three modernized approaches to address the widespread loss of the chestnut: biocontrol of chestnut blight with a mycovirus (a virus that attacks fungi), improved inter- and intra-species breeding methods, and genetic engineering of *C. dentata* by inserting genes from unrelated species into its genome.

Hypovirulence (the reduction in virulence of *C. parasitica* caused by infecting the fungus with a mycovirus) has been an effective tool in controlling chestnut blight in Europe. Both through natural spread and artificial inoculation, these mycoviruses can help trees fight infections and ultimately result in the healing of cankers. While mycoviruses have been discovered inside cankers of *C. dentata trees* in Michigan, field trials in several other states have failed to produce consistent results. In most cases the mycoviruses did not demonstrate the ability to move between trees, and in some cases, they did not spread to multiple cankers on the individual inoculated trees (Jacobs et al., 2013). More research is necessary to determine the efficacy of mycovirus treatments, and they remain a potential tool to strengthen the resistance of future *C. dentata* hybrids if they are widely reintroduced.

Another widely pursued strategy to confer blight resistance in the American chestnut involved building on previous breeding work performed by the USDA. In the early 1980s The American Chestnut

Foundation (TACF) initiated a backcross breeding program using existing *C. dentata* and *C. mollissima* specimens with the goal of producing a fully blight-resistant hybrid chestnut which is phenotypically identical to *C. dentata*. This experimental breeding program involved several steps. Initially, American and Chinese chestnut trees were crossed, producing offspring with relatively 50 percent of the DNA of each parent, and those F1 hybrids were inoculated with the fungus. The surviving blight-resistant trees were then backcrossed three times with American chestnut trees, each time halving the percentage of Chinese alleles present in their genomes. To ensure that there was adequate biodiversity in the samples, it was necessary to continually use wild type (WT) American chestnut pollen when performing this backcrossing procedure so that a sufficient number of native species alleles were present in the resulting hybrids (Jacobs et al., 2013). Those trees (BC3F1) were then inoculated once again with the fungus, and the survivors which were the most phenotypically indistinguishable from the original American chestnut were selected and crossed with each other twice to create a BC3F3 generation. Averaging 94 percent *C. dentata* and 6 percent *C. mollissima* DNA, these genetically modified trees appear identical to the original American chestnut are now producing seed, although more time is necessary to elucidate long term phenotypical traits such as growth and form (Jacobs, 2007). Aided by a robust network of volunteer groups and supporting institutions, mother trees have been protected and seed orchards have been established in several states to provide consistent sources of WT DNA. Because of the expansive original range of the American chestnut a sufficient gene pool will be necessary to facilitate its adaptation to a multitude of microclimates, and TACF is currently developing breeding lines that involve over 20 *C. dentata* parents in order to provide the necessary genetic diversity to accomplish that task (Jacobs et al., 2013).

Similar in desired outcome but fundamentally different from traditional backcrossing methods, genetic engineering (GE) has also been utilized to develop blight-resistant trees. Recently, transgenic *C. dentata* hybrids have been produced by inserting a gene from wheat that confers blight resistance into the chestnut genome. Trees with this gene, oxalic oxidase (OxO), have high levels of blight resistance because they enable cells to process the toxic oxalic acid produced by the fungus into hydrogen peroxide and carbon dioxide (Westbrook et al., 2020). Once this pathway was confirmed in the first transgenic trees, a series of experiments were performed to find out how similar they were to WT American chestnut trees. The data revealed no discernable differences between the two in leaf litter decomposition rates, root colonization by mycorrhizal fungi, pollen nutrition, or seed germination of other species (Westbrook et al., 2020). Encouraged by these findings, the transgenic hybrids are now being outcrossed with a variety of WT chestnut trees from throughout its native range. This process is far less laborious than the backcrossing program undertaken by TACF because, rather than inoculating every tree with the fungus, it is possible to identify the presence of the OxO gene through laboratory testing alone. With only 1 out of every 150 hybrids conferring sufficient resistance in the backcrossing study, the transgenic approach is more time, labor, and cost efficient. Through outcrossing techniques using WT parent sources, scientists are aiming to produce at least 500 genetically unique transgenic *C. dentata* hybrid trees for reintroduction. This will minimize genetic drift in the population and lower the odds of creating inbreeding depression issues (Westbrook et al., 2020).

The high levels of blight resistance from both backcrossed and transgenic hybrids make them excellent candidates for reintroduction, however questions remain about the impact that this species may have on existing forest ecosystems. Because the chestnut blight introduction occurred approximately 120 years ago, very little is known about the forest structure prior to the event, although it is accepted that *C. dentata* was the most important canopy dominant species. Complicating matters further, widespread deforestation occurred throughout the eastern United States from the late 1800’s to the 1930’s, degrading ecosystems and obscuring their traditional dynamics, so it is difficult to build a conceptual model of the landscape before that time (Elliott and Swank, 2008). What the data available does provide are observations as to what occurred after the loss of the American chestnut in Appalachia. In the decades following its demise several other species experienced increased recruitment. Most notably, eastern hemlock (*Tsuga canadensis*) increased both in abundance and distribution, particularly in moist areas near streams. Tulip tree (*Liriodendron tulipifera*) and black locust (*Robinia pseudoacacia*), both light-tolerant pioneer species, increased in size and basal area during this time, although *L. tulipifera* was more successful in maintaining its newfound niche. Both *L. tulipifera* and *T. canadensis* are now the dominant canopy species in the region. Additionally, chestnut oak (*Quercus prinus*), red maple (*Acer rubrum*), and sourwood (*Oxydendrum arboretum*) experienced increases in frequency and abundance throughout the former range of *C. dentata* and are now major components of today's forests (Elliott and Swank, 2008). In addition to these species, many other shade-tolerant trees and shrubs have increased their species richness and evenness as well, filling out a dense forest which no longer resembles the land occupied by generations of native peoples and European settlers.

While some recruitment successes are the direct result of openings in the canopy caused by the loss of *C. dentata*, there is evidence that the leaves of the tree also contained allelopathic chemicals, and upon breakdown in the soil their leachate prevented the germination of the seeds of other species. Few studies have investigated this, however it has been demonstrated that American chestnut leaves have the ability to inhibit the germination of *T. canadensis* as well as rosebay rhododendron (*Rhododendron maximum*), an invasive ericaceous shrub in the region (Vandermast et al., 2002). There are also other causes for concern with respect to reintroduction. Multiple oak species are experiencing regeneration issues, and reintroduction of *C. dentata* could potentially result in more competition in germination sites and exacerbate oak recruitment. Furthermore, *C. dentata* has demonstrated the ability to thrive well outside of its native range in places like Wisconsin, which could be problematic for the native vegetation in those areas (Jacobs et al., 2013).

Conversely, there are several potential benefits of reintroducing *C. dentata* to its native range. The bountiful, predictable production of chestnuts may stabilize a vital food resource for consumers, resulting in population increases of small mammals. This could have several downstream effects, both positive and negative, such as increased pressure on songbird populations, increased risk of Lyme disease to humans, and a decrease in the frequency and severity of gypsy moth outbreaks (Jacobs et al., 2013). The leaves of *C. dentata* have a low C:N ratio and break down more quickly than oak leaves, thus increasing potential nutrient fluxes in mountain streams and supporting higher populations of macroinvertebrates (Jacobs et al., 2013). Chestnut wood, which is produced quickly through fast vegetative growth and is moderately resistant to decomposition, creates micro niches on land and in aquatic settings, and has massive carbon sequestration potential as well. *C. dentata* has a long average lifespan, and the summation of its physical properties could make newly formed American chestnut stands excellent carbon sinks (De Bruijn et al., 2014). There is also afforestation potential: the possibility of planting stands of chestnut trees in fields and other areas that were not historically forested. Mine reclamation sites are an excellent example of prime afforestation locations, and planting *C. dentata* in those situations may be ideal to both reestablish the species in its native range and also quickly sequester atmospheric carbon (Jacobs, 2007).

Finally, when considering reintroduction of the American chestnut it is necessary to seek out and listen to the concerns voiced by Indigenous communities, whose worldviews are fundamentally different from the dominant western perspective articulated by the media and scientific community. For hundreds of years their input has been almost completely ignored, and they have experienced a multitude of environmental injustices as a result. Because the transgenic *C. dentata* would be the first GE species to be reintroduced back into nature after functional extinction and would have the capability to breed with existing WT trees and expand throughout the landscape, it is important to value the opinions of all who may be affected by it. If reintroduced, this tree will cross borders and undoubtedly enter Indigenous communities, where reliance on direct ecosystem services is still an integral component of daily life (Barnhill-Dilling et al., 2020). Currently multiple outreach and consulting efforts are underway, both by the federal government as well as by groups of academic researchers, with the goal of engaging with Indigenous Peoples and establishing channels of dialogue between the two parties. This collaborative approach must continue through the ensuing years as the genetics of the backcrossed and transgenic trees are fine-tuned, so that all parties may reach a level of consensus prior to the onset of reintroduction.

Conclusion

Due to the tireless efforts of numerous academics, government officials, and citizen scientists, the return of the American chestnut to forests of the eastern United States is on the verge of becoming a reality. Through swift advances in scientific technology and understanding, multiple genetic hybrid chestnut trees have been created utilizing two distinct breeding methods and are currently being evaluated for reintroduction to the landscape. However, questions remain regarding the ecological impacts of reintroducing this foundation species, and the ethics underpinning its reintroduction have yet to be fully debated. The successful creation of a blight-resistant American chestnut represents a massive achievement for those involved and has the potential to radically alter the landscape of the eastern United States, setting the stage for the potential rescue of other threatened tree species. For centuries humans have caused dramatic changes in natural environments across the globe, and in the future the reestablishment of a previously vanquished forest giant may remembered as a victory for both the planet and humanity.

References

Andam, K., Al-hassan, R. M., Asante, S. B., Diao, X., Frohlich, E. D., Ré, R. N., et al. (2015). Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *J. Chem. Inf. Model.* 53, 1689–1699. Available at: http://www.statsghana.gov.gh/docfiles/glss6/GLSS6_Main Report.pdf%0Ahttps://resources.saylor.org/wwwresources/archived/site/wp-content/uploads/2015/07/ENVS203-7.3.1-ShawnMackenzie-ABriefHistoryOfAgricultureandFoodProduction-CCBYNCSA.pdf.

Barnhill-Dilling, S. K., Rivers, L., and Delborne, J. A. (2020). Rooted in Recognition: Indigenous Environmental Justice and the Genetically Engineered American Chestnut Tree. *Soc. Nat. Resour.* 33, 83–100. doi:10.1080/08941920.2019.1685145.

Biermann, C. (2016). Securing forests from the scourge of chestnut blight: The biopolitics of nature and nation. *Geoforum* 75, 210–219. doi:10.1016/j.geoforum.2016.07.007.

De Bruijn, A., Gustafson, E. J., Kashian, D. M., Dalgleish, H. J., Sturtevant, B. R., and Jacobs, D. F. (2014). Decomposition rates of American chestnut (Castanea dentata) wood and implications for coarse woody debris pools. *Can. J. For. Res.* 44, 1575–1585. doi:10.1139/cjfr-2014-0270.

Elliott, K. J., and Swank, W. T. (2008). Long-term changes in forest composition and diversity following early logging (1919-1923) and the decline of American chestnut (Castanea dentata). *Plant Ecol.* 197, 155–172. doi:10.1007/s11258-007-9352-3.

Jacobs, D. F. (2007). Toward development of silvical strategies for forest restoration of American chestnut (Castanea dentata) using blight-resistant hybrids. *Biol. Conserv.* 137, 497–506. doi:10.1016/j.biocon.2007.03.013.

Jacobs, D. F., Dalgleish, H. J., and Nelson, C. D. (2013). A conceptual framework for restoration of threatened plants: The effective model of American chestnut (Castanea dentata) reintroduction. *New Phytol.* 197, 378–393. doi:10.1111/nph.12020.

Lutts, R. H. (2004). Like manna from God: The American chestnut trade in southwestern Virginia. *Environ. Hist. Durh. N. C.* 9, 497–525. doi:10.2307/3985770.

Vandermast, D. B., Van Lear, D. H., and Clinton, B. D. (2002). American chestnut as an allelopath in the southern Appalachians. *For. Ecol. Manage.* 165, 173–181. doi:10.1016/S0378-1127(01)00615-6.

Westbrook, J. W., Holliday, J. A., Newhouse, A. E., and Powell, W. A. (2020). A plan to diversify a transgenic blight-tolerant American chestnut population using citizen science. *Plants, People, Planet* 2, 84–95. doi:10.1002/ppp3.10061.

Acknowledgements

The conceptualization, research, and presentation of this paper would not have been possible without the support and guidance of Professor Christopher Dick as well as the GSI instructors of ENVIRON 436, particularly Jacqueline Edinger. Regarding the research, thank you to the University of Michigan for operating the university library website, which is an excellent research tool and allowed me to locate useful information with ease. I would also like to thank the two reviewers of this paper, Allen Gibson and Pixy Rajpankaja, for their thoughtful advice and critique. Their edits and constructive comments improved the overall design of the paper and I was fortunate to have their input.