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Reintroduction of American Chestnut in the National Forest System

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American chestnut restoration depends on a multitude of biological, administrative, and technological factors. Germplasm traditionally bred for resistance to the chestnut blight disease caused by the exotic pathogen *Cryphonectria parasitica* has been deployed on national forests in the Eastern and Southern Regions of the National Forest System (NFS) since 2009. Trees were challenged by biological factors, primarily deer browse and ink disease (caused by *Phytophthora cinnamomi*). Because of these problems, inferences regarding resistance or tolerance to blight are premature. Mitigation to improve success includes improved technology in seedling production for planting and selection of appropriate test sites with limited management restrictions. We suggest that chestnut restoration within the USDA Forest Service be conducted through deployment of a series of long-term multidisciplinary tests. Limitations in resources required for this effort necessitate partnership building both within and outside the agency. Vegetation establishment targets that include chestnut test plantings within the NFS should be developed.

Keywords: backcross breeding, chestnut blight, USDA Forest Service, high-quality seedlings, progeny testing

The restoration of American chestnut (*Castanea dentata* [Marsh.] Borkh.) in eastern North America has been of great interest to the public and an objective of tree breeders for almost a century (Van Fleet 1914, Graves 1942, Clapper 1952, Anagnostakis 2012). The American chestnut was devastated by two exotic diseases from Asia. Ink disease (causal agent *Phytophthora cinnamomi* Rands) first arrived in the early 19th century (Anagnostakis 2012) causing widespread mortality in the southern portion of the species

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range (Hough 1878, p. 470, Baker 1884, p. 232–233, Buttrick 1915). Chestnut blight (causal agent *Cryphonectria parasitica* [Murr.] Barr) was first noted in New York in approximately 1904 and quickly spread throughout the natural range (Ziegler 1920, Anagnostakis 2012). As the 21st century unfolds, fulfilling a chestnut restoration goal may be attainable through an integrated approach using traditional breeding, biotechnology, and forest management (Griffin 2000, Nuss 2005, Anagnostakis 2012). However, the mechanics of achieving restoration goals and the process of instituting management or administrative decisions have yet to be thoroughly discussed.

The USDA Forest Service and partners have implemented research and associated management activities, initiating the first steps toward restoring this treasured species. Public lands offer long-term and sustainable management approaches for restoration of American chestnut owing to stable ownership, laws, and policies that prescribe ecological restoration as a goal (e.g., USDA Forest Service 2011, 2013) and continuous planning to maintain viable populations (e.g., National Forest Management Act). Recent field results and orchard screenings have revealed achievements and challenges to early success in test plantings and durable blight tolerance of material (Hebard 2012, Clark et al. 2014a). The objective of this article is to summarize the current status of American chestnut reintroduced in research plantings on national forests, to discuss challenges in restoration, and to offer suggestions that may accelerate and improve the viability of the current American chestnut reintroduction approach within the Forest Service.

Historical Importance and Strategies to Combat Exotic Pests

American chestnut was a keystone species throughout the eastern deciduous forest from the end of the Wisconsinan glacial period to the early 20th century before the chestnut blight and ink disease relegated the species to a multistemmed understory shrub (Delcourt and Delcourt 1981, Paillet 2002). The full impact of the species on society and ecological systems is not fully understood because the tree was extirpated before empirical research could be conducted. Personal accounts recorded during preblight conditions (Bolgiano and Novak 2007), early plant and forestry reports (Emerson 1846, Pinchot and Graves 1896, Ashe 1911, Frothingham 1924), paleovegetation studies (Delcourt and Delcourt 1981, 1997), and historical reconstructions (Lorimer 1980, Diamond et al. 2000, McEwan et al. 2006) offer selective insights into the historical importance and ecological function of American chestnut throughout the eastern hardwood forest biome. The extirpation of the chestnut probably caused dramatic shifts in forest structure and function (Opler 1979, Stephenson et al. 1991, Rhoades 2007) and human population dynamics (Freinkel 2007). Native Americans valued the tree as a high-quality food source and used the tree for medicinal treatments (Schlarbaum 1990, Freinkel 2007). Chestnut was an extremely versatile tree for forest products. Tannins were extracted from wood to process leather, and the rot-resistant timber was used for a multitude of products (Buttrick 1915, Ziegler 1920). The nuts were highly valued as a commodity source in Appalachian communities (Buttrick 1915).

When the chestnut blight was first introduced, the now defunct USDA Bureau of Plant Industry began crossing American chestnut to Asian species to produce timber-type trees with blight resistance (Graves 1942, Clapper 1954). The work was then transferred to the Connecticut Agricultural Experiment Station (CAES) in the 1940s, but the research was largely unsuccessful (Burnham et al. 1986). The backcross breeding method was not proposed in American chestnut breeding programs until 1986 (Burnham et al. 1986). Three major breeding programs currently exist to combat chestnut blight and ink diseases: the CAES, the American Chestnut Cooperators Foundation (ACCF), and the American Chestnut Foundation (TACF). The CAES program is the oldest in the country and creates complex hybrids using backcross breeding to transfer resistance to chestnut blight, Asian gall wasp (*Dryocosmus kuriphilus* Yasumatsu), and ink disease from the Asian chestnut species, Japanese chestnut (*Castanea crenata* Siebold and Zucc.) and Chinese chestnut (*Castanea mollissima* Blume), while maintaining desired American chestnut characteristics (Burnham et al. 1986, Anagnostakis et al. 2011, Anagnostakis 2012). The CAES program incorporates hypovirulent chestnut blight strains that contain a virus that reduces blight virulence (discussed below). The ACCF, founded in 1980, intercrosses large surviving American chestnuts with partial levels of blight resistance and uses hypovirulence for blight control (Griffin et al. 1983, Griffin 2000, Anagnostakis 2012). The integrated approach currently used by ACCF to achieve durable blight tolerance incorporates the effects and interactions of site conditions, forest management, and genotype over long temporal scales (Griffin et al. 2006). The TACF, founded in 1983, is perhaps the most well-known breeding program. TACF uses primarily two Chinese chestnut sources of resistance (Graves 1942, Clapper 1963, Hebard 2012). Sources of resistance from a new cultivar, "Nanking," are being incorporated into the program (Hebard 1994, 2012). TACF has also incorporated testing for ink disease resistance among breeding lines (Jeffers et al. 2012). The principal TACF orchard facility at Meadowview, Virginia, is producing the most advanced breeding material, commonly referred to as the BC_3F_3,

Management and Policy Implications

American chestnut was a keystone species throughout eastern North American forests until devastated by two exotic pathogens from Asia. Current restoration efforts have primarily focused on production of trees resistant to one of these pests, the chestnut blight (*Cryphonectria parasitica*), but landscape-level restoration will require much more than a blight-resistant tree for deployment. The USDA Forest Service has provided support to external breeding programs and has begun to deploy a series of tests using advanced breeding material. To date, research has been composed primarily of separately implemented field studies that are not multidisciplinary in nature. Chestnut activities on national forests have been conducted using funds not specifically designed for chestnut work, and this has probably limited planning of operational processes. We suggest that the agency develop short-term goals for installing chestnut test plantings on appropriate sites within the National Forest System. Experiments should incorporate environmental or technological independent variables within the study design and use the most advanced science available. We suggest modifying the current funding mechanism within the National Forest System so that chestnut work can be prioritized for forests with appropriate resources to conduct activities.

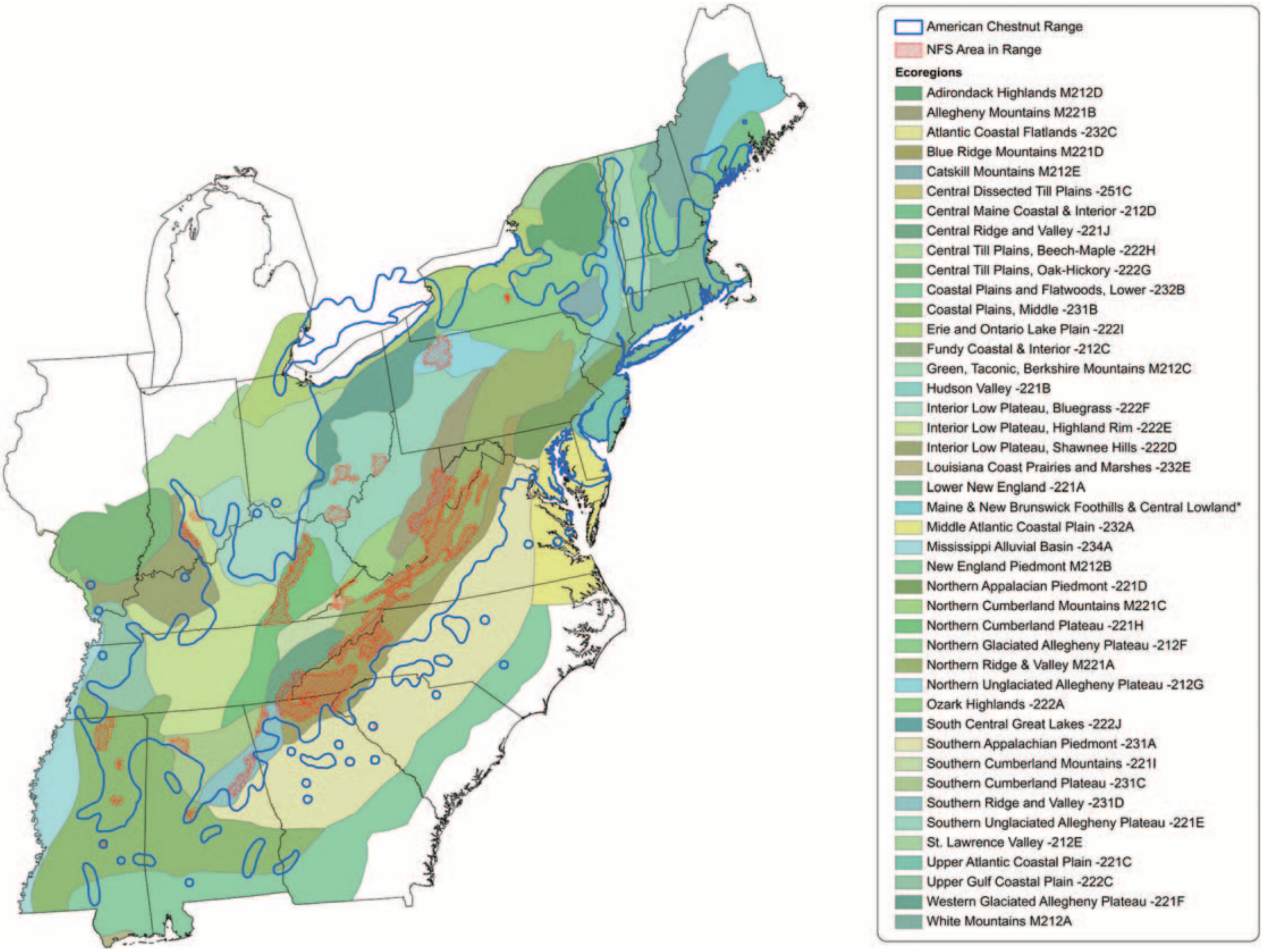

Figure 1. The former range of the American chestnut (adapted from Little 1977), the USDA Forest Service NFS properties, and Bailey's ecoregion sections (Bailey et al. 1994) within the species' former range.

from "Graves" and "Clapper" lines (Hebard 2012). The BC_3F_3 seedlings were hypothesized to have blight resistance similar to that of the Chinese parent and morphological traits similar to those of the American parent (Burnham et al. 1986, Hebard 2006).

In North America, the success of blight control using hypovirulence in forest settings is partially dependent on forest management practices that limit stress to young trees, resistance levels in trees, and vegetative compatibility (i.e., ability of the virulent strains to convert to hypovirulent strains) (MacDonald and Fulbright 1991, Griffin 2000, Milgroom and Cortesi 2004). Multiple decades of blight control on pure American chestnut has been achieved in North American plantings and sprout populations within and outside the range of chestnut (MacDonald and Fulbright 1991, Robbins and Griffin 1999, Anagnostakis 2001, 2012), but biological blight control in North America has been largely unsuccessful (Milgroom and Cortesi 2004). Success might be improved by increasing vegetative compatibility (Springer et al. 2013), in conjunction with changes in deployment mechanisms, use of resistant stock, or selection/management of site conditions (Griffin 2000, Milgroom and Cortesi 2004, Nuss 2005).

Genomics could aid in restoration of chestnut, particularly through marker-aided selection for identification of disease-resistant genes from the Chinese chestnut (Kubisiak et al. 2013), which would enhance and accelerate traditional breeding efforts (Wheeler and Sederoff 2009, Hebard 2012). Genetic engineering work is currently being conducted with the hope of deregulation of transgenic American chestnut material by 2020 (Kremer et al. 2012). Public acceptance of deploying transgenic American chestnut trees on public lands is uncertain, because transgenic material could enter human and wildlife food chains (Merkle et al. 2007). Genetically modified blight strains (Choi and Nuss 1992) might be most useful as part of an integrated approach to control chestnut blight through forest management, traditional breeding, or transgenic modification of the tree (Nuss 2005, Root et al. 2005).

Forest Service Investment

The USDA Forest Service National Forest System (NFS) currently owns and manages approximately 15 million acres within the former range of the American chestnut in the Southern (Region 8) and Eastern (Region 9) Regions (Figure 1). The specific areas suitable for American chestnut restoration within NFS boundaries have not yet been determined, but NFS lands will of-

Table 1. Estimates of USDA Forest Service investment in American chestnut restoration and research since 2004.

Branch/station or region	Total agency expenditures	Part of total agency expenditures from TACF grants program	Primary purpose	Deliverables
R&D				
SRS RWU-4157	541,000	12,000	Forest restoration research	Established 11 BC_3F_3 progeny tests to test blight resistance using TACF material in Region 8; incorporated silvicultural, entomology, physiology, and phenology research into progeny tests.
NRS				
NRS RWU-01	9,000	0	Forest restoration research	Established 2 BC_3F_3 progeny tests to test blight resistance using TACF material in Region 9.
NRS RWU-14	110,000	55,000	To produce blight-resistant trees and forest restoration research	Completed 26 BC_3 lines and begun breeding three BC_3F_2 lines. Established 2 BC_3F_2 seed orchards. Established 2 BC_3F_3 progeny tests to test blight resistance using TACF material in Region 9.
NRS RWU-10	15,800	0	Forest restoration research	Established 1 BC_3F_3 progeny test to test blight resistance using TACF material in Region 9. Incorporated silvicultural research into progeny test.
State and Private Forestry	3,062,000	0	To produce blight-resistant trees	Grants to TACF to support efforts to produce blight-resistant trees.
NFS				
Southern Region (Region 8)	79,100	0	Provide land for research plantings	Planning, installation, and maintenance of 17[1] BC_3F_3 progeny tests to test blight resistance using TACF material in Region 8.
Eastern Region (Region 9)	33,500	0	Provide land for research plantings	Planning, installation, and maintenance of 8[2] BC_3F_3 progeny tests to test blight resistance using TACF material in Region 9.
NFS, State and Private Forestry, and R&D	3,000,000	0	To produce blight-resistant trees	Forest Health Initiative to support efforts to produce a genetically engineered chestnut, identify genes for blight resistance, and to create genetic maps.

NFS, National Forest System; NRS, Northern Research Station; RWU, research work unit; SRS, Southern Research Station.
[1]Eleven of these tests were led by the Southern Research Station; 6 were led by TACF.
[2]Three of these plantings were led by the Northern Research Station; 3 were led by TACF.

fer substantial opportunities for test plantings. Results from a scant number of older experiments using American chestnut or various hybrids indicate that restoration will be an adaptive process to integrate NFS management objectives and maintain experimental rigor (Rhoades et al. 2009, Pinchot 2011, Clark et al. 2012a, Clark et al. 2014b). Multidisciplinary research will be required for restoration efforts to be successful (Clark et al. 2014a). The restoration strategy of the Forest Service has primarily been to provide resources to support development of a blight-resistant tree and to use in-kind resources to accomplish experimental plantings on the NFS. For example, the Forest Service has provided grants to and partnered with TACF for breeding work, funded part of the Forest Health Initiative[1] for genomics research, and installed field tests of traditionally bred trees (Clark et al. 2014a).

We estimate that the Forest Service has invested approximately $6.9 million in American chestnut restoration research from fiscal years 2003 to 2013 to assist in efforts to produce a blight-resistant tree and to establish restoration research tests. Estimates were provided by personnel within the NFS, the Research and Development (R&D) branch, and State and Private Forestry. The majority of this investment has been on development of blight-resistant material (Table 1). Tests that did not incorporate blight resistance as part of the study design objectives or tests that did not include BC_3F_3 material (e.g., Rhoades et al. 2009, Pinchot 2011, Gurney et al. 2011, Clark et al. 2012a) are not part of this estimate. Estimates for establishment costs for the NFS were $500–5,000 per acre. Approximately $500–1,000 per acre per year will be spent on maintaining each planting up to 5 years after establishment. Costs were site specific and vary according to cultural prescriptions used to establish and maintain plantings (e.g., slash removal, herbicide use, and deer fencing) and in-kind support from outside partners.

A funding mechanism specifically targeting chestnut test plantings does not currently exist within the NFS. The majority of resources to date have come from appropriated funds within existing NFS vegetation management programs. On rare occasions, Knutson-Vandenberg (KV)[2] funds were used to install and maintain chestnut plantings, but KV funds are limited in their applicability and have a finite window of availability per test planting site. Available KV dollars are dependent on timber sale funds, and the requirement is that they be used to fund priority reforestation activities leaving little remaining for chestnut test plantings. Test plantings must be prioritized above other approved activities on each KV plan. Because of the uncertainty in availability of planting stock from year to year (Hebard 2012), prioritizing chestnut test plantings above other approved work becomes problematic.

Chestnut research has been integrated into R&D work unit descriptions in both the Southern Research Station (SRS) and

Table 2. American chestnut reintroduction trials established on USDA Forest Service NFS lands.

Year(s) planted	No. of plantings	No. of trees	Bailey's ecoregion section(s) (Bailey et al. 1994) and NFS region	Organization leading research	Method of establishment	Dependent variables studied	Survival rate (%)
2009, 2010, 2011	11	3,940	Northern Cumberland Mountains, Blue Ridge Mountains, Northern Ridge and Valley; Region 8	Forest Service, SRS	1-0 bareroot nursery seedlings	Survival, growth, blight resistance, bud-break phenology, competition assessments, animal damage	63
2011	2	1,750	Allegheny Mountains; Region 9	Forest Service, NRS	1-0 bareroot nursery seedlings	Survival, growth, blight resistance	85
2011, 2012	2	1,100	Interior Plateau; Region 9	Forest Service, NRS	1-0 bareroot nursery seedlings	Survival, growth, blight resistance	30
2012	1	550	Northern Ridge and Valley; Region 9	TACF	Direct-seeded nuts	Survival, growth, blight resistance	50
2012	1	568	Allegheny Mountains; Region 9	TACF	Direct-seeded nuts and containerized stock	Survival, growth, blight resistance	40 for direct seeded; 85 for containers
2013	1	675	Allegheny Mountains; Region 9	TACF	Containerized seedlings	Survival, growth, blight resistance	Not yet available
2013	5	3,054	Blue Ridge Mountains; Region 8	TACF	1-0 bareroot nursery seedlings	Survival, growth, blight resistance	Not yet available
2013	1	120	Blue Ridge Mountains; Region 8	TACF	Containerized stock and 1-0 bareroot nursery seedlings	Survival, growth, blight resistance	Not yet available
2013	1	435	Green, Taconic, and Berkshire Mountains; Region 9	Forest Service, NRS	Direct-seeded nuts	Survival, growth, blight resistance	88

the Northern Research Station (NRS), primarily using appropriated dollars. The current research within R&D consists of several separately implemented test planting programs but relatively little integration or technology transfer among programs has occurred to date. Outside agency partners have greatly contributed to R&D programs. Procurement of the germplasm from TACF's breeding programs in Meadowview, Virginia (Hebard 2012) or Indiana orchards has been the basis for the majority of chestnut research to date. The University of Tennessee's Tree Improvement Program (UT-TIP) invested approximately $100,000 in working with the Forest Service during 2009–2011 in deployment of the initial research plantings of the TACF BC_3F_3 generation seedlings in Region 8 (Clark et al. 2012c). The UT-TIP provided necessary infrastructure and expertise and assistance in labor needed to establish test plantings using the most technologically and scientifically advanced protocols. UT-TIP continues to assist with ongoing measurements. Additional funding was provided by NFS Region 8 to pay for seedling production at a state nursery each year. A similar partnership exists between the NRS and the University of Vermont Rubenstein School of Environment and Natural Resources for test plantings in New England.

Current Status of Test Plantings

From 2009 to 2013, a series of test plantings that incorporated the most advanced breeding material from TACF (BC_3F_3) were established on NFS lands (Table 2). Planting locations are described to the section level using Bailey's ecoregions (Bailey et al. 1994). These experiments were intended to be long term and were led by R&D scientists or by TACF. Plantings differed in terms of study objectives, experimental design, and protocols used for planting establishment and maintenance, but all plantings included "control" species (Chinese and American chestnut) and were established to test blight resistance of various BC_3F_3 progeny through natural infection.

The most intensive and largest experiments to date were established in 2009, 2010, and 2011 as part of the research led by the SRS (Clark et al. 2012c, 2014b) (Table 2). These plantings encompassed three ecoregion sections within the southern portion of the species' former range. Ongoing data collection is intensive and has incorporated tests for nursery seedling quality on dependent variables (Clark et al. 2012b, 2014b). Silviculture, *Phytophthora* pathology, physiology, and entomology research was also integrated on a subset of plantings (Case et al. 2013, Knapp et al. 2014). Survival ranged from 38 to 82% across planting sites, and mortality was primarily related to the ink disease pathogen. Blight incidence was <10% across all plantings. Protection from deer browse was used at most SRS-led plantings with tree protectors or frequent application of repellant sprays.

The NRS led establishment of two plantings in 2011 in the Allegheny Mountain section of Region 9 using bareroot nursery seedlings (Table 2). Survival rates were relatively high and soil compaction was hypothesized to be the primary cause of mortality. The NRS also led establishment in 2011 and 2012 of two plantings in the Interior Plateau section using bareroot nursery trees. Survival was approximately 30%, and mortality was hypothesized to be related to root rot disease caused by a *Pythium* species or by a severe drought. The NRS established one planting in 2013 in the Green, Taconic, and Berkshire Mountain section using direct-seeded nuts. Early survival was 88%, and mortality was related primarily to lack of germination. Fencing was necessary at all NRS-led planting sites to control deer browse. Blight incidence was nearly zero at all NRS-led planting sites. State and Private Forestry (Northeastern Area and Forest Health Protection), CAES, and Clemson University partnered with R&D and NFS for disease testing of *Phytophthora* spp. at SRS and NRS planting sites.

In 2012 and 2013, nine additional

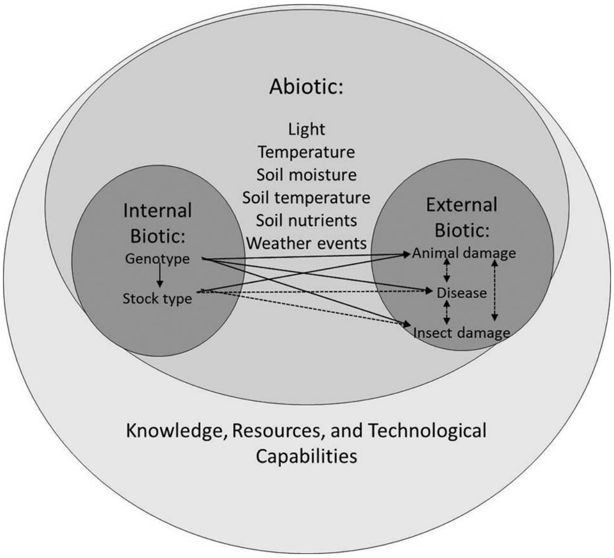

Figure 2. A hierarchal model of abiotic and external and internal biological factors affecting American chestnut restoration. Arrows indicate the direction of interactions between internal biotic factors. Solid lines indicate relationships that have been well documented and/or tested. Dashed lines indicate relationship that are not well documented or not well tested but postulated to exist.

plantings of approximately 5,000 seedlings were established in Regions 8 and 9 of the NFS using a variety of methods that included nondormant container stock, bareroot nursery seedlings, and direct-seeded nuts. These research plantings were implemented by TACF without direct involvement from SRS or NRS. Forest Service decisions on installing TACF-led test plantings were made on an individual forest basis, using guidelines for site selection and preparation developed from their own expertise, R&D scientists, and TACF personnel. Forest personnel ensured that proper administrative approvals were completed (e.g., National Environmental Policy Act approval for activities associated with the planting). TACF provided the experimental designs and assistance in labor for plantings and manages data collection. TACF provided seedling production costs and deer fencing costs on some planting sites. Forest personnel provided labor for all plantings and some labor for the first year of data collection. Preliminary field reports indicate direct seeding was less successful than other methods and that ink disease negatively affected some plantings.

The Forest Service has assisted ACCF by making land available for planting over the last decade (Gary and Lucille Griffin, ACCF, pers. comm., Dec. 3, 2013). ACCF has been responsible for seedling production, experimental design, planting establishment, maintenance, and data collection, and the NFS provides necessary administrative approvals and appropriate sites for planting establishment. R&D has not been directly involved with the ACCF plantings.

Challenges to Restoration of American Chestnut

The results from the plantings described above and from previous studies that used less advanced breeding material (e.g., Griffin et al. 1991, McCament and McCarthy 2005, Clark et al. 2012a) exposed challenges to the successful establishment of American chestnut. Multiple ecological factors present barriers to restoration activities. Factors are hierarchal with internal biotic factors affected by external biotic factors, and both are affected by the abiotic ecological system (Figure 2). Mitigation to improve success will always be limited by available technology, financial resources, and infrastructure (Figure 2). The interactions among this suite of biological factors will influence establishment success of any planting (Dey et al. 2008), but only empirically designed experiments of American chestnut will begin to elucidate their combined effects.

Genotype is an internal biotic factor that interacts with the environment to affect physiological and morphological expression of traits. The research plantings described above tested a relatively small number of genotypes across relatively few sites. Local adaptation is part of TACF's program facilitated by using local American chestnut parents in the second or third backcross (Hebard 2006), and genotypes at each planting were from relatively restricted provenances or the same ecological seed zones (i.e., areas with similar temperature or elevation gradients). Provenance or seed zone testing has received only limited attention in chestnut (Schaberg et al. 2013), but could identify superior genotypes that have broad tolerance to abiotic factors, a trait that could help mitigate the effects of climate change (Erickson et al. 2012). The availability of germplasm is currently too restricting to conduct large-scale provenance or seed zone tests. Advanced breeding material will soon be available from several state TACF chapters (Hebard 2006) and from CAES seed orchards (Anagnostakis 2012).

Testing of the different sources of resistance is in the early stages on Forest Service plantings, and the oldest plantings contain only the Clapper source of resistance (Clark et al. 2014b). Similarities of TACF BC_3F_3 progeny to the American parent are currently being evaluated. Slight deviations in growth and bud-break phenology were detected in the SRS-led plantings between the American and BC_3F_3 seedlings (Clark et al. 2014b), but the BC_3F_3 progeny performed similarly to the American chestnut in physiological responses to light availability (Knapp et al. 2014). Within-generation differences in progeny with Clapper sources of resistance have been detected in nursery tests and in early field trials (Clark et al. 2012b, 2014b), but inferences regarding these differences were limited because of the relatively low number of families tested (Clark et al. 2014b).

In addition to genotype, the production type (i.e., stock type) and quality of material being planted is an internal biotic factor affecting chestnut response. We propose that the most efficacious mitigation method to combat multiple abiotic and biotic challenges is to improve seedling quality. Planting of high-quality seedlings, defined as trees with identifiable morphological traits (e.g., large root collar diameters, tall stem heights, and large root systems) with superior outplanting performance (Clark et al. 2000, Kormanik et al. 2002, Davis and Jacobs 2005), will help mitigate a number of external biotic factors including animal damage and ink disease and abiotic factors such as light competition or recovery from drought (Dey et al. 2008, 2010, Clark et al. 2014b).

The SRS-led plantings incorporated seedling size as part of the study design, and early results show that large-size seedlings had less deer browse and taller heights than small-size seedlings after four growing seasons (Clark et al. 2014b).

The various seedling production methods each have unique advantages and disadvantages and should be considered with site conditions, financial resources available, and objectives of planting (Dey et al. 2008). For example, seedling quality can be lower if site productivity is lower. Paying for seedlings with the highest quality appropriate for the planting site may be offset by seedlings having faster growth or needing less protection from animals or competition (Spetich et al. 2002, Oswalt et al. 2006, Dey et al. 2010, Clark et al. 2014b). The effect of planting shock (a period of stunted growth or mortality due to recovery of biological functions after planting [Struve et al. 2000]) was partially mitigated when American chestnut seedlings had a relatively large number of roots (Clark et al. 2014b).

The relatively high variation in seedling quality within and among genotypes resulting from production methods (Clark et al. 2012b) can be partially mitigated by grading seedlings before planting (Clark et al. 2000), by discarding nuts with weevil damage (Dalgleish et al. 2012), or by matching seedling quality to site conditions. The technological constraints of producing large seedlings have been overcome in southern commercial nurseries (Kormanik et al. 1994, Clark et al. 2000, 2012b), but ink disease in many nurseries (Crandall et al. 1945, Clark et al. 2012b) requires new technologies to obtain disease-free seedlings of sufficient quality for planting. The patented Root Production Method is a containerized system that has been successfully used in bottomland hardwood species (Grossman et al. 2003, Dey et al. 2010). The Root Production Method is currently being evaluated on chestnut by the CAES and the SRS. Bareroot nursery seedlings grown in northern nurseries (i.e., above 40 degrees latitude) that are less likely to harbor ink disease (Balci et al. 2007) can offer a more economical alternative to containerized systems but pose logistical challenges in coordination of sowing and lifting schedules when used in southern planting sites.

The primary external biotic factors affecting the success of American chestnut restoration efforts, identified from the plantings described above and from the literature, were animal damage, insect damage, and the presence of the exotic pathogen, ink disease (Griffin 2000, Clark et al. 2009, 2014). Animal damage to American chestnut is primarily deer browse to seedlings and predation to direct-seeded nuts (Selig et al. 2005, Clark et al. 2014a). Deer fencing was used on most Region 9 plantings and, although effective, was expensive to install and maintain. Tree shelters and repellants were used with success on some Region 8 plantings (Clark et al. 2014b) and were less expensive than fencing. The benefits of deer protection in artificial regeneration of hardwoods have been well documented (Ponder 1995, Ward et al. 2000), and it will be necessary on sites with large deer populations. Invasive exotic insects, including the Asian gall wasp and the Asiatic oak weevil (*Cyrtepistomus castaneus* Roelofs), affected seedlings at nearly all of the SRS-led plantings (Clark et al. 2014a). Gypsy moth (*Lymantria dispar* L.) was not observed at any research plantings, but this species does feed on American chestnut (Mosher 1915) and could have negative impacts on restoration. Mitigation strategies for controlling invasive exotic insects are in the early stages of development and have not been thoroughly tested for American chestnut (Cooper and Rieske 2008).

Direct seeding of American chestnut seems inadvisable as part of a large-scale testing program, because desiccation or animal predation can reduce germination and seedling establishment by 29–50% (McCament and McCarthy 2005, Selig et al. 2005). Direct seeding has been unsuccessful in artificial regeneration of *Fagaceae* species on upland sites (Dey et al. 2008), and results from the studies discussed here are also not encouraging. Although treating seed with chemical deterrents (e.g., capsaicin and thiram) can deter predation in controlled settings (Willoughby et al. 2011), seed coating carriers have not been shown to persistently hold deterrents on the seed surface in saturated soil and prevent desiccation. Direct seeding may be feasible on small scales in controlled environments (i.e., seed orchards) where nut protection measures can be implemented to protect high-value germplasm (e.g., clonally propagated material). Extremely rocky sites in northern glaciated areas may necessitate direct seeding, but protection from nut predation will still be required.

Cryphonectria parasitica is the most intensively studied biotic factor affecting chestnut (Anagnostakis 2012), but field tests using putatively blight-resistant material are only in the early stages. After 4 years, seedlings from the BC_3F_3 generation had the same level of blight incidence as Chinese chestnuts, which was lower than that of American chestnuts (Clark et al. 2014b), but plantings are currently too young to make definitive inferences regarding blight resistance. Hebard (2012) reported that none of the BC_3F_3 families and that 16.2% of BC_3F_3 trees within all families had blight canker sizes similar to those of the Chinese chestnut after inoculations in an orchard. These tests were short-term evaluations of very young trees (<4 years old) in a relatively uniform environment. Juvenile resistance may be affecting results (Clapper 1952, Anagnostakis 2012), and blight tolerance may be expressed according to site conditions or cultural prescriptions (Griffin et al. 2006). Blight resistance is expected to improve when TACF orchards are further rogued (Hebard 2012).

The primary exogenous abiotic factors affecting chestnut that can be controlled or manipulated include light resources and soil characteristics such as texture or pH that affect moisture and nutrient availability. Intense competition for light and poor soil drainage was observed at some Region 8 plantings and could be inciting factors predisposing trees to decline (Griffin et al. 1991, Clark et al. 2014b). Mitigation could include the use of proper silvicultural systems and site preparatory treatments (Jacobs 2007). Chestnut grew better on sites where a commercial regeneration harvest was conducted compared to fully stocked stands, but control of competition is generally required when overstory is removed (Griffin 2000, Rhoades et al. 2009, Clark et al. 2012a). Underplanting in fully stocked stands with or without treatment of the midstory will retard growth of planted chestnut until the overstory is removed, but seedlings can survive many years in reduced light conditions (McCament and McCarthy 2005, Clark et al. 2012a, Belair et al. 2014). Competition control may be needed after overstory removal in underplantings. Alternatively, chestnut may benefit from prescribed burning before planting to further control germinant seedlings (McCament and McCarthy 2005).

Abiotic factors that are not easily controlled include weather events and climate change over the long term. Late-season frost affected some plantings in Region 8. Cold winter temperature was found to contribute to a decline in northern test plantings (Gurney et al. 2011, Schaberg et al. 2013), and limitations in cold tolerance could predispose trees in the northern range and at high elevations to disease pressure from blight (Griffin 2000). Blight tolerance interactions with elevation gradients and forest management treatments are part of the integrated approach used by ACCF (Griffin 2000). Until breeding programs are refined to match genotypes to specific ecological conditions, abiotic challenges may be partially mitigated by establishing test plantings in areas with intermediate thermal and moisture conditions on acidic sites (pH <6). American chestnut was most abundant and had optimal growth on intermediate sites and was rarely found on limestone-derived soils (Frothingham 1924, Russell 1987, Wang et al. 2013). Alternatively, if resources allow, studies should specifically test durable blight tolerance across environmental gradients.

Suggestions for Refining the American Chestnut Restoration Program in the National Forest System

The USDA Forest Service has not developed a comprehensive plan or priorities for future test plantings or for large-scale species restoration for American chestnut for several reasons:

1. Available germplasm from breeding programs is currently not genetically diverse enough to cover all ecological zones or provenances.
2. The durability of blight resistance in advanced breeding material is still under evaluation.
3. Test plantings currently in place are too limited in scope, too young, or too few to provide sufficient information for development of large-scale restoration goals.
4. A formalized funding mechanism to support R&D, NFS, or State and Private Forestry American chestnut activities is not in place.

We propose that the Forest Service develop goals for American chestnut restoration using a long-term, science-based, multidisciplinary approach. Prior efforts, such as the test plantings described here were all established with long-term objectives, but not all were designed from a multidimensional perspective. As with any disease, chestnut blight interacts with genotype and environment. Only localized information can be gathered from plantings that are designed solely to test blight resistance and that have inadequate replication to separate confounding biological factors. Poor seedling quality impedes success, and the usefulness of the data will be limited if data collection does not directly measure important biological factors that affect survival or growth.

American chestnut restoration is theoretically possible, but success will be limited if resources allocated to research and operational processes are not in place. The most advanced technology and science resources should be applied in test plantings, and partnership building within and outside the agency will garner support for important technologies, such as seedling production methods and disease testing. A multidisciplinary research approach for test plantings within the Forest Service is largely lacking because of limitations in available resources and infrastructure. Long-term federal support for breeding programs has been essential for the achievements described here, but these achievements may not be realized without continuing to establish and monitor a series of state-of-the-art reintroduction trials.

Currently, NFS resources used for chestnut plantings come primarily from funds not specifically designed to support chestnut work and have been stable or shrinking for the last several years (USDA Forest Service 2014). This funding mechanism probably limits tactical planning and operational processes. Within R&D, decisions to conduct chestnut research have come from individual work units with missions that fall within the scope of American chestnut restoration research. We offer the following suggestions for advancing American chestnut restoration within the Forest Service for the next 5 years:

1. Develop short-term (i.e., 5-year) goals and objectives for American chestnut restoration based on current technology and previous research. Long-term goals can be developed when sufficient information is gathered on how germplasm performs in various tests and when the Forest Service can commit the necessary resources. Short-term objectives could include establishing and maintaining a series of long-term multidisciplinary experiments, using already established plantings as a guide for future experiments, or maintaining test plantings for mast production for wildlife and establishment of natural regeneration. Objectives could be incorporated into planning documents for the NFS or into R&D work unit problem description areas.
2. Establish a national-level funding mechanism for testing of chestnut. Investments can only be realized with resources dedicated to internal research and management activities. Currently, funds used to establish chestnut test plantings on NFS lands are typically associated with "targets" designed for vegetation establishment or improvement or rarely with KV funds. Chestnut test plantings are more expensive to implement and usually less successful compared with other vegetation work (e.g., planting oaks or pine [*Pinus*] species). A new target for establishment of chestnut test plantings would allow managers to prioritize chestnut work without compromising other targets. This system could be forest specific based on availability of appropriate lands and resources to complete the work.
3. Centralize information on current and future plantings at a regional level and potentially at a national level. Updates on the status of existing plantings and plans for establishment of new plantings would ease information transfer and improve identification of areas where test plantings are most needed.
4. Maintain or move responsibility for germplasm requests made to breeding programs and responsibility of decisions regarding seedling production technologies to the region. Requests to the breeding programs should be made well in advance of planting (at least 1.5–2 years). High-quality seedlings would ensure the best success for test plantings. Bareroot nurseries should be tested for *Phytophthora* spp. before sowing if they are near or below 40° latitude, or seedlings should be grown in nurseries above 40° latitude. Increasing temperatures due to climate change could increase the 40° latitudinal boundary (Bergot et al. 2004), so nurseries should be tested each year. Container-grown seedlings will prevent spread and infestation of ink disease, but container technology has not been extensively tested for chestnut.
5. At the forest level, select sites for testing that have few management restrictions

and administrative approval (as per the requirements in the National Environmental Policy Act for regeneration harvests, herbicide use, and, potentially, prescribed burning). The forests should establish tactical direction for site selection, site preparation, and planting protocols based on the best available science and administrative or logistical constraints of each district. If possible, the planting should be where residual native chestnuts are currently growing.
6. Involve R&D scientists at the forest and regional levels. R&D scientists and their partners should lead test plantings established on NFS lands to confirm that the most technologically and scientifically advanced knowledge is used and that plantings are evaluated over time. Research activities and research work unit descriptions within R&D should continue to include American chestnut research. Funding limitations can be partially overcome by partnership building within and outside the Forest Service. Research should cross station boundaries to examine responses to breeding or silvicultural treatments at broad spatial scales (Dey et al. 2012). Partnership building outside the agency will improve access to resources, technology, and infrastructure (e.g., hypovirulent strains of the chestnut blight pathogen).
7. State and Private Forestry, Northeastern Area and Forest Health Protection, and other university or state agencies should continue to partner with R&D and NFS for disease testing and site selection, as is already being conducted. Disease testing for *Phytophthora* spp. should be conducted on all potential planting areas near or below 40° latitude.
8. Continue to integrate germplasm and approaches from breeding and research programs such as the TACF, CAES, and ACCF into the Forest Service chestnut restoration program. This will help broaden the genetic base, increase genetic diversity, and improve stability in access to germplasm.
9. Maintain and improve communication between the Forest Service, American chestnut breeding programs, and other partners. Goals, expectations, and commitment or sharing of resources of each partner should be refined and discussed. Communication between partners will improve the planning and efficiency of tactical procedures required to install and monitor test plantings.
10. Refine the use of terminology within the agency. "Blight resistance" should be used to refer specifically to the host's ability to express genes that control resistance to infection or reaction to the blight. "Blight tolerance" should be used to refer to the host's ability to thrive in the presence of blight, given interacting environmental factors. No *Castanea* species are immune from the blight.

Restoration of this mighty giant will require long-term commitments and imaginative use of resources. As early as 1924, Frothingham (1924, p. 863) recognized the resources required for American chestnut restoration:

> Because of the large areas involved and the costliness of planting, [sic] artificial reproduction can hardly be seriously considered.

Today restoration is more difficult than in any previous time, because the American chestnut continues to be plagued by multiple exotic and native pests. A significant investment will be required to resolve these problems (Campbell and Schlarbaum 2014). Why is restoration even being considered, given the resources required and the challenges chestnut must face? Perhaps the iconic nature of the species (Bolgiano and Novak 2007, Freinkel 2007), its ecological value as a wildlife species (Diamond et al. 2000), and the long history of investment in breeding for blight resistance (Anagnostakis 2012) demand continuation of restoration efforts. Results for other tree species provide hope and insight into successful programs to combat pests (e.g., five-needle pines and white pine blister rust). We must guard against rushed attempts and overly optimistic expectations that could lead to significant ecological damage and a public that loses faith in the effort. Knowledge is needed to develop realistic goals for large-scale restoration targets (Jacobs et al. 2013). Federal agencies, such as the Forest Service, along with partners are advancing American chestnut restoration, and with patience and continued investment of resources, the species may return as a dominant canopy tree that provides multiple utilitarian and ecological services.

Endnotes

1. For more information, see www.foresthealthinitiative.org.
2. The Knutson-Vandenberg Act (1930) requires purchasers of national forest timber sales to deposit funds to cover activities on the timber sale site including site preparation, planting, or other improvements to the site.

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