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Toward development of silvical strategies for forest restoration of American chestnut (*Castanea dentata*) using blight-resistant hybrids

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ABSTRACT

Backcross breeding has provided a viable means to restore American chestnut (*Castanea dentata* (Marsh.) Borkh.) to eastern North American forests, where the foundation species was essentially extirpated by an introduced pathogen. With the prospect of American chestnut reintroduction imminent, it is critical to formulate restoration strategies based on the ecology and silvics of the species, operational confines, social or policy limitations, and ecological implications. American chestnut was apparently adapted to a relatively wide range of site conditions, has evolved a capacity to survive for prolonged periods beneath forest canopies yet respond rapidly to disturbance, and demonstrates extraordinary growth and competitive ability. These characteristics are discussed in reference to operative planting techniques and potential for migration of regeneration from hybrid chestnut plantings into forests of the original American chestnut range. The use of hybrid trees for American chestnut reintroduction may generate social and policy ambiguities that require conciliation. Additionally, potential long-term ecological implications associated with reintroduction of American chestnut to the original species range, or introduction to areas outside its original range, must be realized and integrated into reintroduction strategies. Limitations in genetic fitness, potential for disease mutation, and threats from other exotic insects and pathogens may serve as continual challenges to American chestnut restoration. This paper helps establish preliminary guidelines for restoration plantings and creates awareness of imposing ecological issues and barriers that must be overcome to successfully restore American chestnut to its natural range, while simultaneously maintaining ecological integrity and ensuring conservation benefits to eastern North American forests.

1. Introduction

Globalization of trade during the past century has resulted in importation of multiple exotic insects and pathogens into North America, some of which have severely affected keystone tree species and thereby impacted natural forest ecosystems. Examples include an exotic fungus (*Sirococcus clavigignenti-juglandacearum* Nair, Kostichka and Kuntz) that causes lethal cankers in and has seriously threatened butternut (*Juglans cinerea* L.) (Michler et al., 2006) and Dutch elm disease (*Ophiostoma ulmi* (Buisman) Nannf.), which devastated the important urban and forest tree, American elm (*Ulmus*

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americana L.) (Karnosky, 1979). However, perhaps the most tragic ecological event in the post-glacial history of eastern North American forests was the demise of the ill-fated monarch, American chestnut (*Castanea dentata* (Marsh.) Borkh.) through introduction of the blight-fungus, *Cryphonectria parasitica* (Murr.) Barr.

In the early 1900s, American chestnut was a dominant species in many forests of eastern North America (Russell, 1987), with a natural range exceeding 800000 km^2 (Braun, 1950) (Fig. 1). American chestnut sometimes comprised more than 50% of basal area of standing trees in stands (Braun, 1950), and contributed a unique and important ecological niche to these forests (Ellison et al., 2005). The introduced pathogen *Cryphonectria parasitica*, an aggressive diffuse canker disease (Anagnostakis, 1987), rapidly annihilated American chestnut throughout its range (Roane et al., 1986). This Asian pathogen was believed to have been imported on *Castanea* spp. seedlings from Asia and the disease was first discovered in 1904 at the Bronx Zoological Park in New York City (Roane et al., 1986). By 1950, the disease had spread throughout the range of American chestnut, and by 1960 had killed an estimated 4 billion trees and essentially extirpating the species as a canopy tree from its range (Hepting, 1974; McCormick and Platt, 1980; Anagnostakis, 1987).

American chestnut is still a common component of eastern North American forests, but nearly all individuals currently present are sprouts that originated from blight-killed trees (Russell, 1987; Stephenson et al., 1991). Cycles of sprouting, infection, dieback, and re-infection often persist for decades (Paillet, 1984), with sprouts generally not exceeding small tree size and rarely growing to reproductive maturity (Paillet, 2002). The species is now classified as endangered in its native range in Canada and in several US States.

Loss of American chestnut has had substantial ecological consequences. Prominent effects on canopy dominance have occurred, with shifts in species composition toward a variety of co-occurring species (Keever, 1953; McCormick and Platt, 1980). Replacement of American chestnut by other forest vegetation has likely affected processes such as decomposition, nutrient cycling, and productivity (Ellison et al., 2005). Absence of American chestnut has resulted in less consistent and abundant mast production, which has markedly reduced the carrying capacity for certain wildlife species (Diamond et al., 2000).

In response to this ecological catastrophe, the US Department of Agriculture (USDA) initiated efforts to control chestnut blight and breed or discover blight-resistant chestnut trees as early as 1920 (Bettite and Diller, 1954), but control efforts failed and no tree-like cultivar was discovered. The USDA program was subsequently abandoned in the 1960s. Research into examination of hypovirulent strains of the fungus has also not shown any degree of success at the population level (Milgroom and Cortesi, 2004), largely due to the slow dissemination of the hypovirus to infected trees (Double and Macdonald, 2002).

In the early 1980s, a plan to breed a blight-resistant hybrid chestnut tree through backcross breeding with Asian chestnuts, primarily Chinese chestnut (*Castanea mollissima* Blume),

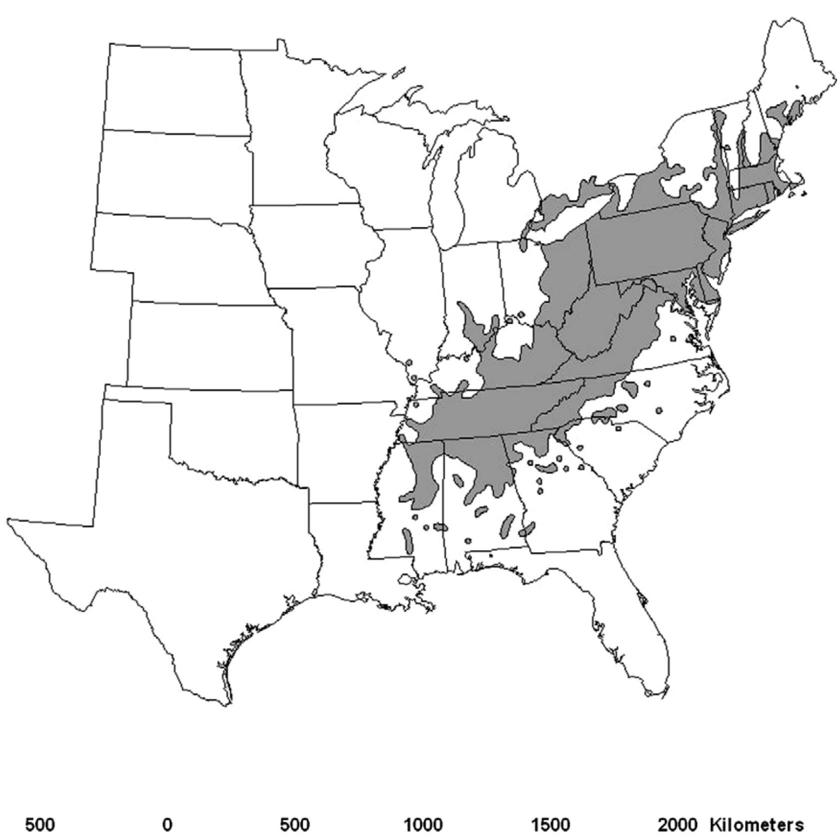

Fig. 1 – Original natural range of American chestnut in eastern North America, as adapted from Little (1977).

was conceived (Burnham, 1981; Burnham et al., 1986). This has been the foundation of the research and breeding efforts of the non-profit group, The American Chestnut Foundation (TACF). The ultimate goal of the program is to breed a hybrid chestnut tree for reintroduction to the native range that is phenotypically indistinguishable from American chestnut (Diskin et al., 2006; Hebard, 2006).

The current format of the breeding program of TACF is outlined in Table 1 and detailed by Hebard (2001, 2006). Briefly, blight-resistance is conferred through initial hybridization of American chestnut with Chinese chestnut (F1 hybrid). A series of three backcrossings with American chestnut help reduce the proportion of Chinese alleles and regain American chestnut phenotypic characteristics (leading to a BC3F1). Selected BC3F1 trees that exhibit blight-resistance are then intercrossed twice, while simultaneously being selected again for resistance character, resulting in the final hybrid cross for reintroduction (BC3F3). Statistically, the BC3F3 trees and their progeny should average 94% American chestnut and 6% Chinese chestnut, though this proportion may be skewed slightly in either direction depending on results of specific genetic crossings (Diskin et al., 2006). Recent research has verified the inheritance of many basic leaf, bud, and twig morphological traits in juvenile BC3 trees from the American parents (Diskin et al., 2006), though longer-term traits such as growth and form have yet to be confirmed. Nevertheless, current data suggests that most BC3 hybrid trees will botanically be classified as American chestnut (Diskin et al., 2006).

Putatively resistant BC3F3 seed was first attained by TACF in 2005 (Diskin et al., 2006), and it is expected that resistant hybrid chestnut trees will be available for reintroduction within the next decade (Griffin, 2000; Ronderos, 2000). Historically, American chestnut research has focused nearly exclusively on genetics and breeding for blight-resistance. However, accelerated success of American chestnut breeding over the past several years suggests the imminent nature of initiating hybrid chestnut planting programs to restore American chestnut to forests of eastern North America.

American chestnut disappeared from eastern forests decades before the development of modern principles of forest ecology (Paillet, 2002). Thus, our knowledge of basic silvicultural and ecological characteristics of the species is rudimentary compared to associated species (Paillet, 2002; Jacobs and Severeid, 2004; McCament and McCarthy, 2005), and much of our perception regarding establishment and early growth of American chestnut comes from historical observations or growth of stump sprouts (Paillet, 1982, 1984, 2002). Remnant stands of American chestnut exist, but many of these are blight-infested, thereby limiting their potential use for ecological interpretations (Tindall et al., 2004; McEwan et al., 2006). However, with increasing optimism toward initiating a reintroduction program, there has been greater emphasis in recent years on silvicultural studies to examine American chestnut growth and development following planting (McNab, 2003; Jacobs and Severeid, 2004; McCament and McCarthy, 2005) or in natural forests (Paillet and Rutter, 1989; McEwan et al., 2006).

To facilitate success of upcoming American chestnut restoration programs, it is essential to begin to critically formulate silvical guidelines to aid in restoration. These must be crafted in consideration of the ecology and silvics of the species, current planting technologies and operational limitations, potential for migration of regeneration into natural forests, and policy guidelines of federal, state, and local agencies. The long-term ecological implications associated with reintroduction of American chestnut to its native range, or introduction of American chestnut to areas outside its original range must also be integrated into reintroduction strategies. Silvical guidelines for planting should evolve concurrently alongside the blight-resistance breeding program, and each program should adapt with the dissemination of findings from corresponding programs. This paper is designed to synthesize present knowledge of the ecology, biology, and silvical characteristics of American chestnut for consideration in pending deployment. Short- and long-term challenges to be faced in the wake of American chestnut reintroductions are simultaneously discussed with the intent of setting preliminary baseline guidelines for restoration plantings and creating awareness of imposing ecological issues that must be overcome to successfully restore American chestnut, while maintaining ecological integrity and ensuring conservation benefits of eastern North American forests.

2. Ecology and silvics of American chestnut

2.1. *Natural range*

American chestnut frequently dominated upland habitats composed of non-calcareous, acidic to moderately acidic, and moist but well-drained sandy soils (i.e., submesic or

Table 1 – American chestnut characteristics and blight-resistance for each hybrid generation in the breeding strategy, as synthesized from Hebard (2001, 2006)

American character (%)	Hybrid generation	Estimated degree of resistance (%)		
		None	Moderate	Resistant
50.00	F1[a]	0.00	100.00	0.00
75.00	BC1[b]	75.00	25.00	0.00
87.50	BC2	75.00	25.00	0.00
93.75	BC3	75.00	25.00	0.00
93.75	BC3F2	43.75	50.00	6.25
93.75	BC3F3	0.00	0.00	100.00

a F1 is the American chestnut × Chinese chestnut hybrid.
b BC refers to the “backcross” combination back to American chestnut.

subxeric sites) in mixed forests (Abrams and Ruffner, 1995; Russell, 1987; Stephenson et al., 1991; McEwan et al., 2005). American chestnut generally grew poorly in very wet or very dry soils, and its range was notably truncated in areas of high pH, limestone-derived soils (Russell, 1987). A recent survey of surviving trees in Canada found they were most likely to occur in deciduous forest habitats with high canopy cover (>50%), gentle slopes (0–10°) and acidic (pH 4–6), sandy (>75%) soils (Tindall et al., 2004).

It was formerly assumed that American chestnut was seldom found in ravines or valleys, partly due to frost sensitivity (Parker et al., 1993), which was also presumed to limit American chestnut proliferation at higher latitudes in northern forests (Russell, 1987). However, its historical prominence in riparian forests of the southern Appalachians has recently been documented; American chestnut represented 25–40% of basal area in pre-blight stands of sites sampled in riparian zones (Vandermast and Van Lear, 2002). Ashe (1912) reported that American chestnut in Tennessee grew best in rich, deep coves. American chestnut's capacity to proliferate in finer-textured, mesic habitats was further corroborated by recent observations that first-year seedling growth was negatively correlated with proportion of sand in soil (McCament and McCarthy, 2005). This combined evidence implicates American chestnut as a generalist, adapted to a relatively wide range of site conditions.

2.2. Light, nutrient, and soil moisture requirements

American chestnut exhibits a strong, positive response to high light conditions as compared with co-occurring hardwood species (Boring et al., 1981; Griffin, 1989; Latham, 1992; King, 2003). Tindall et al. (2004) reported that American chestnut growth was positively correlated with decreasing canopy cover in forests of southern Ontario. Further, McCament and McCarthy (2005) evaluated growth response of direct-seeded American chestnut in forest plots in Ohio that were either undisturbed, thinned (30% basal area reduction), prescribe burned, or thinned and burned. Seedling growth and biomass increased with thinning, and greatest performance was observed in the plots receiving both burning and thinning treatments. Wang et al. (2006), studying potted American chestnut seedling development under a range of irradiance levels in an outdoor rainout shelter, reported linear increases in photosynthesis and growth with increasing light availability.

Despite enhanced growth under high light conditions, however, American chestnut demonstrates an ability to survive for prolonged periods in shaded environments (Paillet and Rutter, 1989; Latham, 1992; Tindall et al., 2004; McCament and McCarthy, 2005). For instance, seed germination, health, and survival did not differ significantly in thinned vs. non-thinned stands (McCament and McCarthy, 2005). American chestnut has apparently evolved a mechanism to survive under forested canopies by increasing specific leaf area to compensate for decreasing light availability (King, 2003; McCament and McCarthy, 2005; Wang et al., 2006). This adaptation presumably provides a means to maintain presence in the understory in anticipation of disturbance events. This theory is further supported through evidence that American chestnut rapidly responds following release (Paillet and Rutter, 1989; Billo, 1998; Paillet, 2002; McEwan et al., 2006), which distinguishes American chestnut from co-occurring oaks (Paillet, 2002) and other associated species. Indeed, evidence suggests that most of the modern population of sprouts still present in the original American chestnut range represent sprouts from blight-killed advance regeneration of former American chestnut forests (Paillet, 2002). This implicates American chestnut as an intermediate shade-tolerant (McCament and McCarthy, 2005) or shade tolerant (Wang et al., 2006) species. This current evidence helps clarify the previous uncertainly regarding the shade tolerance of the species (Russell, 1987) and refutes historical observations that the species cannot thrive for long under shade (see Hawley and Hawes, 1925 in Russell, 1987).

Less information is currently available concerning American chestnut responses under varying nutrient regimes, though Latham (1992) demonstrated improved seedling growth performance with increasing soil nutrient availability. Furthermore, positive growth and/or biomass response has been reported for American chestnut with increasing availability of magnesium (leaf mass and area, root mass), potassium (diameter, specific leaf area) (McCament and McCarthy, 2005), and nitrogen (stem, root, leaf parameters) (Rieske et al., 2003; McCament and McCarthy, 2005). American chestnut resists high pH soils, and a recent survey reported that American chestnut height was negatively correlated with pH (Tindall et al., 2004). The former dominance of American chestnut within upland habitats indicates it was a relatively drought resistant species. American chestnut maintained a higher leaf water potential than several associated species of *Quercus* known for drought tolerance when saplings of each species were subjected to an early-season drought (Abrams et al., 1990). Bauerle et al. (2006) reported high water use efficiency of American chestnut seedlings exposed to drought compared to published reports of co-occurring hardwood species. However, modern investigations related to drought capacity of American chestnut are otherwise limited and presumptions are thus far confined largely to site habitat observations.

2.3. Growth rates and response to competition

Reports from early in the last century indicate that American chestnut is highly competitive and fast-growing during early growth (see citations in Jacobs and Severeid, 2004). These historical observations have been confirmed in recent years, with studies reporting radial growth rates approaching 5 mm $year^{-1}$ in plantation or natural stand settings, with maximum values of 10–12 mm $year^{-1}$ (Paillet and Rutter, 1989; Jacobs and Severeid, 2004; McEwan et al., 2006). Paillet and Rutter (1989) described the ability of introduced American chestnut to rapidly out compete and eventually replace other native tree species (e.g., *Quercus* spp., *Carya* spp.) as the dominant canopy tree in a Wisconsin forest. Studying American chestnut development in this same forest, McEwan et al. (2006) further documented rapid growth of American chestnut trees established under the existing forest canopy following a logging event, which exceeded that of associated species. Jacobs and Severeid (2004) reported that juvenile plantation growth of American chestnut on a blight-free site in Wisconsin greatly exceeded that of interplanted black walnut (*Juglans nigra* L.) or northern red oak (*Quercus rubra* L.).

Under controlled environmental conditions, Latham (1992) evaluated competitive ability of American chestnut seedlings relative to six co-occurring species across a broad range of light and nutrient levels. American chestnut outranked all other species in traits associated with competitive ability over the range of resource level combinations, implicating American chestnut as both a broad generalist and strong competitor (Latham, 1992). Recent evidence also suggests that leachate from American chestnut litter may have allelopathic properties that constrains the development of some common competitors in the southern Appalachians, such as eastern hemlock (*Tsuga canadensis* (L.) Carr.) and rhododendron (*Rhododendron maximum* L.) (Vandermast et al., 2002). Further insight into the competitive nature of American chestnut can be traced back to historical pollen records. American chestnut's range expansion during the Holocene from glacial refugia was the most recent of wind-pollinated trees (Paillet, 1982, 2002; Russell, 1987), and its rapid expanse to canopy dominance implicates American chestnut as an exceptionally competitive species (Latham, 1992).

3. Strategies to guide restoration plantings

3.1. Reforestation vs. afforestation plantings

Availability of blight-resistant hybrid chestnut seedlings for restoration will provide a new resource for integration into existing hardwood planting programs. Compared to production conifer plantations, most of which are monocultures for timber production, hardwood plantings are generally established as mixed species plantings with multiple management goals, including timber production, creation of wildlife habitat, soil or water conservation, and recreation (Jacobs et al., 2004; Ross-Davis et al., 2005). Recent observations of American chestnut growth and competitiveness (Paillet and Rutter, 1989; Jacobs and Severeid, 2004; McCament and McCarthy, 2005; McEwan et al., 2006) are encouraging for the successful reestablishment of hybrid chestnut within mixed species plantings.

Hybrid chestnut may be established using either reforestation (i.e., plantings on sites currently or recently in forest) or afforestation (i.e., plantings in fields not previously forested) techniques. Potential limitation in suitable sites for reforestation suggests that afforestation plantings might provide a greater quantity of land to facilitate restoration. For instance, it has been estimated that a maximum of about 160 ha $year^{-1}$ of National Forest Service land within the original American chestnut range could be harvested to facilitate hybrid chestnut plantings (personal communication, Safiya Samman, USDA Forest Service). In contrast, afforestation plantings of mine reclamation sites (Jacobs et al., 2006) and marginal agricultural lands would provide abundant planting sites for American chestnut restoration. For instance, mine reclamation plantings represent a substantial proportion of total hardwood plantings in eastern North America; in 2004, around 40% of coal mining operations in the US occurred within the Appalachian Coal Basin (USDI Office of Surface Mining, 2006), a region all-inclusive of the original range of American chestnut. Thus, targeting reintroduction to afforestation plantings may represent a logical means to help rapidly repopulate American chestnut into its natural range.

Careful attention to species selection and planting densities may be necessary when designing mixed hardwood planting prescriptions involving hybrid chestnut. For instance, Jacobs and Severeid (2004) suggested that without silvicultural intervention, even other fast-growing hardwood species may be overtopped and suppressed by the rapid, competitive initial growth of American chestnut. Despite the aggressive early development of American chestnut, effective silvicultural management will be necessary to ensure vigorous seedling establishment in reforestation or afforestation plantings. For instance, intense sprouting of other species was reported to out compete American chestnut seedlings in clearcuts (McNab, 2003). This suggests that burning might reduce competition and facilitate hybrid chestnut establishment (McCament and McCarthy, 2005), though there are specific practical and policy limitations to implementing burning programs. Alternatively, herbicide application has been demonstrated as an effective means to control competition and improve American chestnut growth in field plantations (Selig et al., 2005).

3.2. Dissemination of regeneration

Because the ultimate goal of American chestnut reintroduction is to restore American chestnut to the forests of its original range, it is important to ensure that hybrid chestnut maintains itself in areas of restoration plantings and successfully migrates to neighboring forest stands. Historically, regeneration success of American chestnut may have largely been dependent upon its ability to sprout vigorously from the root collar following disturbance; regeneration from seed may have contributed only nominally due to tendency for seed consumption (Russell, 1987; Paillet, 2002) and susceptibility of seed to frost or desiccation damage (Paillet, 2002). American chestnut can maintain itself and even increase in volume and density from sprouting (Paillet, 1982, 1984) so thinning and burning in natural forests may further encourage regeneration (Russell, 1987; McCament and McCarthy, 2005).

Migration into adjacent natural forests from hybrid chestnut restoration plantings will depend upon successful dispersal and establishment of reproduction. Blue jays, squirrels, and other rodents have been noted as significant historical consumers and dispersers (Russell, 1987). Paillet and Rutter (1989) reported on the migration of American chestnut into natural forests on a site in southwestern Wisconsin. In 70 years, nine planted American chestnut trees provided sufficient regeneration to spread the species over 1 km from the original source. On an adjacent hillside and along the woodland edge for approximately 0.5 km from the original plantation, American chestnut comprised at least 25% of total canopy basal area and pre-dominated among advanced saplings entering the canopy. Paillet and Rutter (1989) hypothesized that migration of American chestnut regeneration involved a multi-step process (Fig. 2). Individuals or groups of pioneer trees established following seed dissemination in areas of light gaps. Over time, large pools of advanced regeneration developed in the understory of these pioneer trees. These seedlings persisted underneath the established

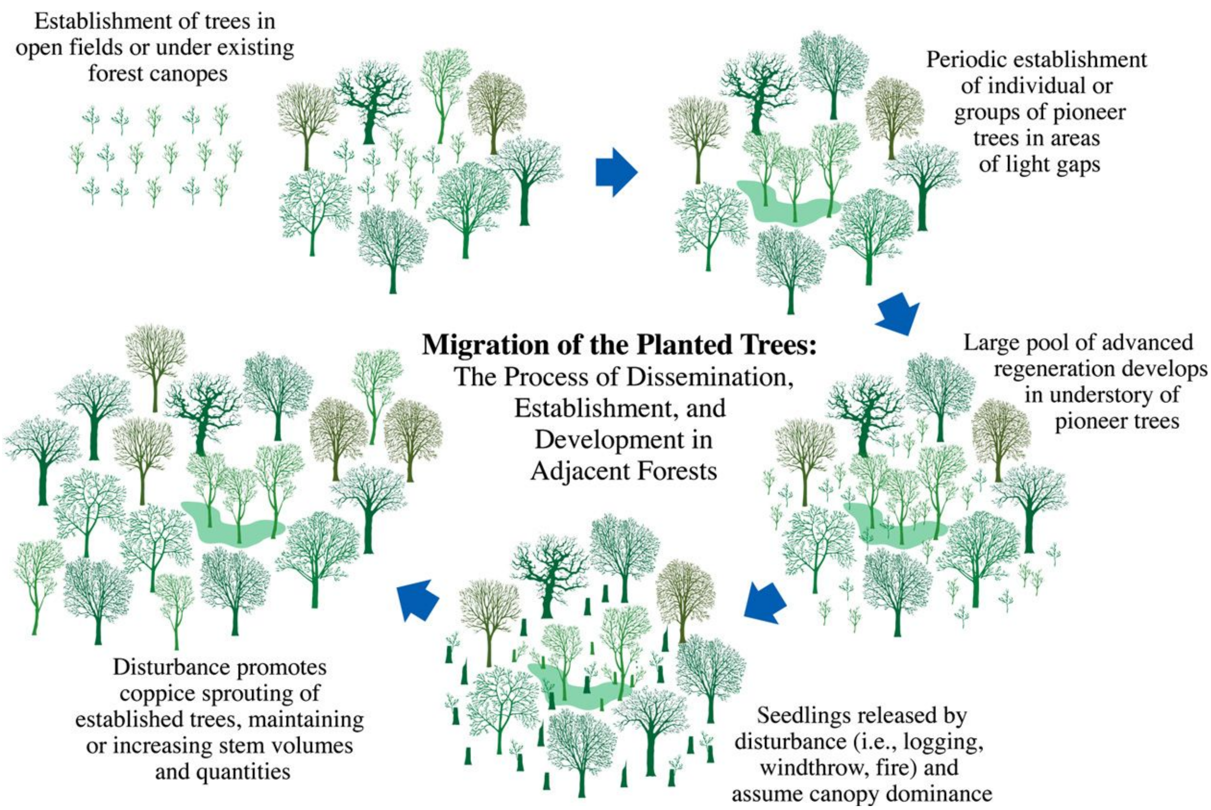

Fig. 2 – Illustrative diagram of multi-step processes to promote dissemination of American chestnut regeneration into natural forest stands from field-planted trees (Paillet and Rutter, 1989), and maintenance of or increasing abundance of established American chestnut trees resulting from coppice sprouting (Paillet, 1982, 1984).

canopy until being released by disturbance (i.e., logging, windthrow) and subsequently grew rapidly to assume canopy dominance.

Though American chestnut migration in the Paillet and Rutter (1989) study was estimated at only a few kilometers per century, the rate of spread was apparently escalating with an increase in volume of seed production. They suggested that hybrid chestnuts would successfully repopulate mixed oak woodlands where American chestnut was once an important canopy tree. Thus, although it may take several decades for blight-resistant hybrids to produce offspring that become established in the forest (Paillet and Rutter, 1989), the high competitiveness of American chestnut retained during breeding may lead to rapid spread of the species thereafter.

4. Pending challenges to American chestnut restoration

Unfortunately, chestnut blight is not the only pending impediment to American chestnut restoration. A variety of social and policy issues, biotic and abiotic stresses, operative limitations, and potential long-term adaptability and ecological considerations are likely to complicate development of effective strategies for American chestnut restoration. Prospective challenges and interactive natures are summarized, along with general approaches to overcome these inhibitions, in Fig. 3 and discussed in detail below.

4.1. *Public acceptance and policy issues*

The use of backcross breeding results in a hybrid chestnut tree for planting that cannot technically be considered pure American chestnut, and hybrid trees may eventually be classified as cultivars or new species. Thus, some ambiguity could emerge when using the hybrid chestnut tree with the auspices of restoring American chestnut to public lands. For instance, this could raise questions by those concerned with influences of alien invasions on ecosystem integrity. However, the hybrid will be more than 90% American chestnut and phenotypically indistinguishable from American chestnut (Diskin et al., 2006; Hebard, 2006), and thus may operatively be considered a native species and fit into exceptions in many current governmental policy regulations concerning introduction of non-native species. The USDA Forest Service, for instance, signed a memorandum of understanding with TACF in 2004 that establishes a cooperative relationship between the two organizations toward restoration of blight-resistant hybrid chestnut trees to Forest Service lands. National Park Service (NPS) policies may also be adapted in a similar means to facilitate American chestnut restoration.

It is important to note, however, that public opinion regarding harvesting and other forms of forest disturbance, particularly on NPS lands, may restrict the stand manipulations (i.e., large canopy gaps) required to create conditions best suited to American chestnut establishment (McEwan

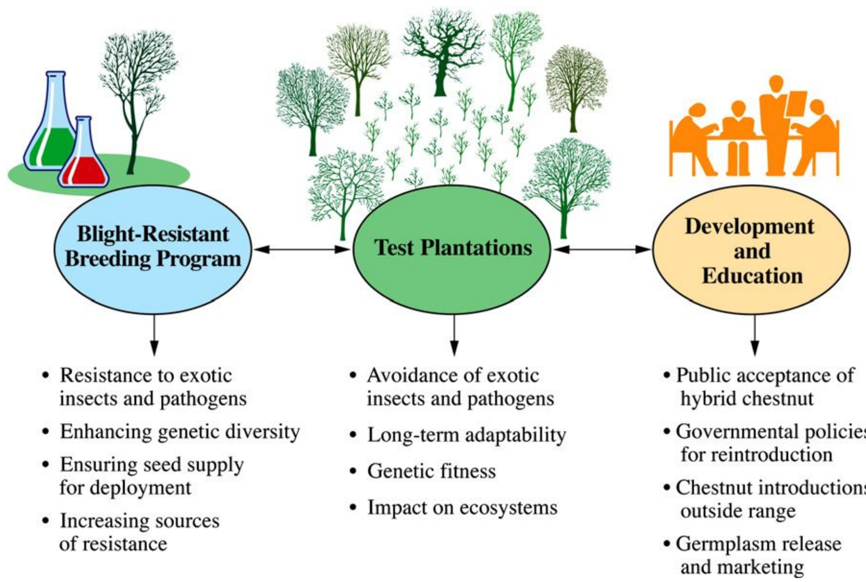

Fig. 3 – Overview of major challenges to effectuate and maintain successful American chestnut restoration in relation to strategic program areas. Specific details are provided in text, along with the interactive nature of program areas.

et al., 2005). National Park Service lands are generally managed to mimic natural disturbances and not subjected to harvesting. Thus, hybrid chestnut planting on NPS lands may primarily be limited to instances following natural disturbances such as fire, insect or disease outbreaks, or large-scale windthrow events. In contrast, National Forest lands are subject to harvesting, though public perception plays a role in enacting specific management regimes. Additionally, use of fire or herbicides on public land is becoming increasingly controversial, which could further constrain options to facilitate restoration success. The USDA Forest Service has been at the forefront of environmental litigations, which have effectively limited harvests in recent years, including those for restoration efforts. For instance, 3737 appeals from USDA Forest Service action were filed in the US Courts of Appeals from 1997 through 2002, including 139 appeals challenging restoration programs (Malmsheimer et al., 2004). Third party litigants concerned about potential adverse ecological effects may impose costly environmental impact studies that could inhibit reintroduction efforts. Restoration of American chestnut to private lands should circumvent these scenarios assuming that governmental cost-share programs, which provide critical funding to promote tree planting efforts on private lands (Ross-Davis et al., 2005), support restoration plantings of hybrid chestnut seedlings.

4.2. *Threats from other exotic insects and pathogens*

Chestnut blight is not the only threat to American chestnut restoration, as American chestnut is host to several other exotic insects and pathogens. Perhaps the principal risk among these is *Phytophthora cinnamomi* Ronds, an introduced soilborne oomycete pathogen favored by compacted soils with poor aeration and that tend to remain saturated (Anagnostakis, 2001; Rhoades et al., 2004), such as those highly disturbed by agriculture. The pathogen is transmitted as spores through the soil, and infection results in lesions in the roots that may eventually girdle the tree. Infection generally reduces seedling vigor and increases mortality (Anagnostakis, 2001; Rhoades et al., 2004). Symptoms associated with the disease were noted in the southern US prior to introduction of chestnut blight, and may have contributed toward a retraction of the southern portion of the American chestnut range (Russell, 1987; Anagnostakis, 2001). One possible mode of defense is to identify ectomycorrhizae that confer protection to roots (Rhoades et al., 2004). Alternatively, careful site selection may be needed to strategically locate hybrid chestnut plantings on very well-drained sites, substantially limiting site options (Rhoades et al., 2004). Chinese chestnut exhibits good resistance to *Phytophthora* (Anagnostakis, 2001), suggesting that selection for *Phytophthora* resistance may need to be integrated into future breeding programs, though this has yet to be implemented.

Another prospective threat to restoration is the oriental gall wasp, *Dryocosmus kuriphilus* Yasumatsu. The insect lays eggs in vegetative and floral buds, and galls form following larvae feeding, which can result in branch dieback, fruiting delay, and potentially mortality (Anagnostakis, 2001). Over the last two decades since its introduction, the pest has spread to natural American chestnuts growing in portions of the southern Appalachians (Anagnostakis, 2001). Gypsy moth, *Lymantria dispar* (L.), introduced into North America in the late 1800s presents another obstacle to reintroduction, particularly with recent evidence of enhanced gypsy moth performance on hybrid vs. pure American chestnut (Rieske et al., 2003). Ambrosia beetles (*Xylosandrus crassiusulus* Mot. and *Xylosandrus saxeseni* Blandford) are another introduced insect that may threaten American chestnut, as they are known to infect Chinese chestnut (Oliver and Mannion, 2001).

4.3. Deployment and genetic adaptability

Public interest in restoration of American chestnut is very high (Ronderos, 2000). It has been argued, however, that although backcross breeding holds promise for restoration of American chestnut to small-scale urban environments, it is unlikely to result in restoration of hybrid chestnuts to the nearly 4 million ha that represented the original American chestnut range (Ellison et al., 2005). Indeed, initial limited supplies of BC3F3 seeds will be disseminated by TACF toward field testing, cooperators and donors, and small landowner projects. Large-scale release to the general public will be delayed until field testing confirms the blight-resistance and American chestnut phenotypic character of BC3F3 plantations. At present, TACF imposes a strict germplasm agreement with any cooperators to ensure that germplasm remains property of TACF and is not independently released or marketed. The American Chestnut Foundation expects to develop cultivar names with trademark protections for deployment of blight-resistant germplasm. Though no specific details on costs of blight-resistant material have been formulated, this scenario suggests that economics may influence the capacity for public participation in wide-scale deployment. Maintaining adequate quantities of blight-resistant seeds is likely to pose another challenge. Seed orchards established at the primary TACF farm in Meadowview, Virginia and by TACF State Chapters may not meet demand; thus, innovative processes to increase seed production through commercial contracting may be necessary. Recent advances in somatic embryogenesis of American chestnut (Andrade and Merkle, 2005) offer an alternative means for rapidly producing large quantities of reproductive material.

Another challenge in deployment will be to limit hybrid chestnut plantings to areas representing the original American chestnut range. American chestnut has demonstrated its ability to thrive when introduced outside of its native range (Paillet and Rutter, 1989; Jacobs et al., 2004; McEwan et al., 2006). Increasing emphasis on hardwood afforestation plantings in the Midwestern US for carbon sequestration, conservation, wildlife, and timber (Jacobs et al., 2004; Nui and Duiker, 2006) suggests that these sites may be heavily targeted for hybrid chestnut plantings (Jacobs and Severeid, 2004) although this is incongruent with the fundamental mission to restore American chestnut to the original species range. The potential competitive dominance of American chestnut also raises important ecological considerations in regard to introduction of the species beyond its natural range. American chestnut was able to persist and spread into adjacent forest stands at a site in Wisconsin, despite being more than 600 km from its native range (Paillet and Rutter, 1989). Thus, introduction of hybrid chestnut into areas where American chestnut was not native may widen the range beyond historical conditions. Over time, this may act to suppress recruitment of tree species indigenous to regions of hybrid chestnut introduction in a manner similar to that of an aggressive, introduced exotic species.

Long-term adaptability and maintenance of genetic variation will present another key challenge to American chestnut reintroduction. The range of American chestnut spans five US climatic zones and 20 states. Although localized breeding programs have been initiated, a relatively narrow range of genotypes has served as the basis for the current backcross breeding program (Hebard, 2006). As natural sprouts continue to lose vigor, our ability to capture and integrate wide genetic variation into the current breeding program declines (Huang et al., 1998). This has risk of undermining restoration efforts due to potential for decreasing fitness and mal-adaptability of BC3F3 hybrid chestnut to localized environmental conditions, or the potential for mutation or adaptation of *Cryphonetria parasitica* to the resistance genes (Huang et al., 1998).

5. Conclusions

Through the efforts of a dedicated American chestnut breeding program generously supported by federal, state, private, and non-profit entities, perhaps the largest forest restoration effort of its kind is on the verge of initiation. Reintroduction of a hybrid tree that is nearly pure American chestnut to eastern forests of North America holds promise to restore the unique ecological niche that American chestnut once contributed. With the prospect of American chestnut restoration imminent, prioritization must shift toward careful and critical formulation of guidelines for reintroduction based on biological, management, policy, and ecological considerations.

Though much of our knowledge regarding American chestnut ecology and habitat requirements stems from analysis of stump sprouts, witness trees, or historical literature, current movements to study American chestnut development in plantation and forest settings are rapidly providing essential baseline information regarding site limitations, response to silvicultural treatments, and ecosystem interactions. This testing must be expanded upon to incorporate a wider range of site types across the original American chestnut range, extend the scope of silivicultural manipulations, and more carefully evaluate ecological interactions and impacts associated with American chestnut reintroduction. Additionally, most tests thus far have been conducted with pure American chestnut, and continued integration of hybrid chestnut material derived from breeding programs into future tests is necessary.

Many obstacles threaten to hamper restoration efforts following deployment of blight-resistant chestnut. Chief among these are social acceptance of a hybrid chestnut tree, policy limitations from governmental agencies, logistics associated with commercialization and wide-scale dissemination of blight-resistant hybrid chestnut germplasm, and sustained threats from exotic insects and pathogens. Furthermore, the likelihood of hybrid chestnut introduction and spread outside of the natural American chestnut range presents unique ecological uncertainties that require careful deliberation. A complex and well-integrated series of programs linked via cross-collaboration from a variety of disciplines is needed to ensure successful implementation of American chestnut restoration. Despite these pending challenges, reintroduction of American chestnut to forests of eastern North America holds promise to serve as perhaps the greatest ecological and conservation success story of modern time.

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