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Discussion
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Discussion

Breeding for Resistance to Tree Pests: Successes, Challenges, and a Guide to the Future

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Forests in North America are threatened by a myriad of native and nonnative pests and pathogens, the latter of which are largely introduced via the international trade of raw wood products and live plants. The early twentieth-century arrival of white pine blister rust (WPBR) (*Cronartium ribicola*) and chestnut blight (*Cryphonectria parasitica*) on imported seedlings devastated forests across North America. Invasive species notably affect entire genera. For example, WPBR has now infected all North American five-needle pine (*Pinus*) species across the entire United States, which has affected species of commercial and noncommercial value and threatened sensitive, high-elevation ecosystems (Sniezko et al. 2011, 2014, Sniezko and Koch 2017). The entire Lauraceae family, which includes avocado (*Persea americana*), redbay (*P. borbonia*), and sassafras (*Sassafras albidum*), is threatened by laurel wilt disease. American chestnut (*Castanea dentata*), once a dominant, keystone species, survives only as an understory shrub because of constant dieback from repeated chestnut blight infections (Dalgleish et al. 2016). Less common *Castanea* species in North America, such as dwarf chestnut (*C. pumila*), are also susceptible to blight (Dane et al. 2003). The extensive, rapid mortality of ash trees (*Fraxinus* species) caused by emerald ash borer (EAB) (*Agrilus planipennis*) has spread to 35 states and resulted in the listing of five eastern North American ash species—green (*Fraxinus pennsylvanica*), white (*F. americana*), black (*F. nigra*), blue (*F. quadrangulata*), and pumpkin ash (*F. profunda*)—as critically endangered on the International Union for Conservation of Nature (IUCN) Red List (Westwood et al. 2017). Invasive pests threaten native forest species at a time when reforestation is considered one of our best options for mitigating the impacts of climate change (Goymer 2018, Bastin et al. 2019).

Invasive pests have devastated entire ecosystems across the eastern United States, affecting major urban centers to sensitive riparian areas in remote forests. Dutch elm disease (DED) (*Ophiostoma novo-ulmi*) essentially ended the existence of American elm (*Ulmus americana*) along streets and greatly diminished the presence of elm in riparian forests. In many instances, dead elms were replaced with green ash in urban forests across the United States and in riparian forests throughout the Midwest (Crocker et al. 2005, 2009). In a disheartening twist of fate, history repeated itself when EAB arrived in the late 1990s to ravage the ash that had replaced elm trees (Haack et al. 2002, Siegert et al. 2014). The impending loss of black ash in northern wetland forests because of EAB has the potential to convert forests into open marsh by altering the hydrologic cycles of these wetlands (Slesak et al. 2014). An entire North American forest type—beech-hemlock—is currently under threat by multiple invaders: hemlock woolly adelgid (*Adelges tsugae*), elongate hemlock scale (*Fiorinia externa*), beech bark disease, and beech leaf disease (Danoff-Burg and Bird 2002; Small et al. 2005, Morin and Liebhold 2015,

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Crocker et al. 2017, Carta et al. 2020). The plethora of dead and dying trees in natural forests, parks, and urban areas serves as a stark reminder of native tree vulnerability to novel pests from an infestation pipeline that is not expected to disappear anytime soon (Aukema et al. 2010). The need for pest-resistant seed is greater than ever, but capacity to generate this material is not in place, especially in the eastern United States (Nelson and Koch 2017).

Our national response to the first sign of an invasive species follows a protocol that includes eradication, containment, and mitigation (Pyček and Richardson 2010). Eradication and containment are usually executed by chemical, mechanical (removal of infested host trees), and physical (quarantine) means. Mitigation frequently employs biological control with various levels of success in lowering pest populations; in some cases little is known whether tree health or survival will be positively affected (Woods and Elkinton 1987, Kenis et al. 2017). Modified silvicultural practices can also provide mitigation by favoring the tree over the pest, but additional tools, such as biocontrol and resistance, are inevitably needed (Vose et al. 2013). In a few instances, pests may be locally eradicated (e.g., Asian longhorned beetle [*Anoplophora glabripennis*] in Illinois, New York, and New Jersey), but the threat of reentry entails relentless detection and response campaigns. Meanwhile, the Asian longhorned beetle continues to expand its reach with South Carolina recently becoming the sixth state to report an outbreak (USDA APHIS 2020). When invasive insects and pathogens overcome eradication and containment measures, and mitigation efforts fail, the lack of resistant seedlings for planting gives forest managers little choice beyond adapting management practices and switching to nonhost tree reforestation programs.

At this critical junction we have a unique opportunity to meet these forest health challenges with new and reimagined resistance tree breeding partnerships. The purpose of this discussion is to review the current situation of resistance breeding and encourage the forestry community to embrace this emerging opportunity to enhance forest health. To this end, we will (1) describe the main features of resistance breeding to include phases detailed by Sniezko and Koch (2017), (2) provide examples of tree resistance breeding success stories, (3) delineate major challenges resistance tree breeding programs face, and (4) describe nascent partnerships and emerging themes to develop and deploy host resistance in forest trees. Resistance breeding considerations described here focus on the eastern United States but should be generally applicable to other regions.

What Is Resistance Breeding?

In general, the process of resistance breeding begins with a search in natural forests for trees that remain healthy, relative to their counterparts, after initial exposure to a pest or pathogen of interest. Optimizing timing of these selections is critical, but often difficult to perfect because some lag time after initial exposure is needed to ensure the pest or pathogen has spread throughout the forest. Initial attacks often kill the most susceptible genotypes, leaving behind trees that may have genetic resistance or tolerance (a condition where the host coexists with the pest). For example, “lingering” ash (trees selected for further testing) were defined as mature trees greater than 10 cm diameter at breast height (DBH) that retained a healthy canopy at least two years after more than 95 percent of the population died (Koch et al. 2015). Waiting too long to select and preserve candidate resistant trees, however, can result in losing these potentially resistant trees either from the primary pest or by other stressors (e.g., secondary pests, drought, or wind snap) on an already weakened tree.

Candidate trees are likely to have a range of resistance from none (e.g., trees that escaped infection or are simply the last to die) to moderate or higher levels that warrant further evaluation. Scientists capture genetic material by making clonal replicates of the candidate tree through vegetative propagation (generally grafting) or by collecting seed from the tree. Developing a screening method for a lab or field setting is necessary to determine the degree of resistance as well as the extent resistance is attributable to either genetic factors or environmental influences. The process requires trial and error to elicit a measurable response indicating a subtle, yet useful, genetic resistance without killing all inoculated seedlings or propagules (clones). Initial efforts to refine appropriate dose of inocula or insects (often a slow and painstaking process) is a preamble to efficiently mass screening large numbers of candidate genotypes. Mass screening employs quantitative genetics, the foundation of tree improvement, to identify the most promising parents for a breeding program out of hundreds or thousands of candidate survivors and their progeny while capturing enough genetic diversity to retain resilience to biotic and abiotic stressors (Namkoong 1991). The sheer number of candidate selections to propagate (seedling or clone) and screen creates a unique challenge for scientists who include resistance breeding in their research portfolios.

Once the first-generation parents are selected, breeding can commence. Breeding is an iterative process that enhances resistance in subsequent generations provided the trait is controlled by multiple genes and is genetically heritable (i.e., parents must transmit resistance to offspring in a reliable, quantifiable fashion, and clones must be repeatable in their resistance expression). Breeding designs vary but generally include crossing the most resistant, unrelated parents to further "stack" the genes for resistance in the next generation. The best performing trees (parents or progeny) from first and subsequent generations are propagated and planted in seed orchards to produce seed with improved resistance. Seed orchards with different genotypic compositions are needed to capture local adaptation and diversity for different geographic areas, or seed zones, amplifying the amount of screening that is needed to reforest across a species' range. Selected genotypes resulting from a large-scale screening program may become new cultivars for urban markets (i.e., clones that are named and marketed), such as American elm cultivars (Haugen and Benz 2016), some of which are widely available.

Successes in Resistance Breeding

Recent successes in resistance breeding are notable. Port-Orford-cedar (*Chamaecyparis lawsoniana*) in the western United States was downgraded from "vulnerable" to "near threatened" by the IUCN; the results were attributed to both planting resistant stock and efforts to eradicate the pathogen (Farjon 2013). Resistant seed lots were available for seven out of 10 breeding zones within 10 years of program initiation (Sniezko et al. 2012). Breeding programs improved resistance of nearly all five-needle pine species currently planted on national forest land in the West (Sniezko et al. 2014, Sniezko and Koch 2017). The prospects for restoring whitebark pine (*Pinus albicaulis*), reduced to less than ten percent of its natural populations in some areas (Keane and Arno 1993), improved with WPBR disease resistance breeding advancements (Sniezko et al. 2008) coupled with developments in seed handling and germination (Riley et al. 2016). Efforts to improve resistance of koa (*Acacia koa*) to a vascular wilt disease in Hawaii are also yielding promising results (Dudley et al. 2015). All these western US programs were possible with the sustained support of the US Department of Agriculture (USDA) Forest Service regional genetic improvement program located at the Dorena Genetic Resource Center (DGRC) near Cottage Grove, Oregon, as well as efforts by the Institute of Forest Genetics, Forest Service Pacific Southwest Research Station, in Placerville, California, and the Coeur d'Alene Nursery in Idaho (Sniezko et al. 2011).

In the eastern United States, where the vast majority of forest land is privately owned and national forests comprise less than seven percent of forest land (Oswalt and Smith 2014), resistance breeding is undertaken by a variety of state, federal, and private partners. For example, advancements in resistance to fusiform rust (*Cronartium quercuum* f. sp. *fusiforme*), a native but problematic pest for the southern US commercial forest industry, are supported by the Resistance Screening Center (RSC), a Forest Service–operated facility in Asheville, North Carolina. The RSC provides standardized disease resistance screening services to the tree improvement community on a cost recovery basis. Forest industry, often through membership in university-industry tree improvement cooperatives (discussed below), used the RSC extensively in its breeding programs to improve fusiform rust resistance in loblolly (*Pinus taeda*) and slash (*P. elliottii*) pine. The benefit to investment ratio in rust resistance research ranged from 2.2 to 20.4 (Cubbage et al. 2000) for a region that grows 18 percent of the world's pulpwood for paper (Hanson et al. 2010).

Resistance breeding for noncommercial hardwoods depends heavily on public-private partnerships, a model exemplified by The American Chestnut Foundation (TACF) and programs predating it (Nelson et al. 2013, 2014). The TACF program uses backcross breeding with chestnut species of Asian origin to transfer resistance from the Asian species to American chestnut (Steiner et al. 2017). The TACF provides a model for cooperative resistance breeding where individuals and organizations make contributions to the foundation and the workload is managed across a series of chapters organized at the state level (Jacobs et al. 2013). This model has provided funding for over 30 years with the goal of delivering American chestnuts for restoration planting across the original species range. The sustained level of public engagement surrounding resistance breeding in American chestnut is exceptional. Multiple universities and organizations have undertaken DED resistance efforts for American elm since the early 1930s but with no comparable publicly supported base. DED work initially focused on screening wild germplasm (seed collections or clonal propagules of large surviving trees) and resulted in most of the seven commercially available cultivars today

(Haugen and Bentz 2016). Decades-long American elm breeding programs at the USDA National Arboretum and the University of Wisconsin, which began around 1970, were based off parents from the earlier work (Smalley and Guries 1993, Townsend 2000). In the last decade, Forest Service researchers, with support from a private foundation, focused on expanding the genetic base of American elm to produce DED-resistant seed sources (as opposed to cultivars) through conventional tree breeding practices for forest restoration (Knight et al. 2017).

Demand for genetic resistance in hardwood trees is rising, especially for minor species such as butternut (*Juglans cinerea*), and it may be bolstered by recent successes. For example, in less than 10 years, the American beech (*Fagus grandifolia*) breeding program produced resistant seedlings for restoration in the Upper Peninsula of Michigan where forests suffered severe losses from beech bark disease (Koch and Heyd 2013). In the southern United States, resistance programs for redbay afflicted with laurel wilt disease have progressed rapidly (Hughes et al. 2018). Surviving trees were found in decimated stands, clonally propagated (Hughes and Smith 2014), and tested with newly developed screening protocols. At present, several genotypes are exhibiting resistance that appears to be genetically based (Hughes 2013). Breeding to produce the next generation of trees for further evaluation is underway (J. Smith 2020, pers. commun.).

Challenges for Resistance Breeding

Across the world, primarily public agencies lead resistance breeding efforts to combat evolving climate patterns and novel pests (FAO 2014). The United States currently lacks the trained professionals and facilities needed to conduct resistance breeding to meet current and future demands, especially in the East where most land is privately owned (Wheeler et al. 2015). Breeding programs require costly infrastructure (e.g., laboratories, greenhouses, field test sites) and the staff to manage operations. Additional expertise is needed in data management and analysis, to maintain and track accession performance over space and time, and in genetics (trained geneticists), to lead the operation. With the exception of the DGRC in the West and the RSC in the East, these activities typically are not coordinated into applied operational resistance breeding programs. As a result, programs are often unable to fulfill the large-scale demand for improved materials for deployment, restoration, and reforestation of urban and rural forests. Translating research findings into improved seed remains a major shortcoming of our response to the ongoing forest health crisis.

University-industry tree improvement cooperatives are tremendous assets for resistance breeding in the East, but their programs are driven by members' needs and focus on species of commercial value. Examples include southern pines (North Carolina State University's Tree Improvement Program, University of Florida Cooperative Forest Genetics Research Program, and Texas A&M University Western Gulf Forest Tree Improvement Program) and northern conifers (University of Minnesota Tree Improvement Cooperative). These cooperatives are composed of private- and public-sector dues-paying members and led by university faculty with specific technical expertise and capability. Member organizations typically manage seed orchards for their own reforestation programs and, therefore, control their seed supplies. These programs endure periodic declines in membership as industry investment fluctuates over the decades (Wheeler et al. 2015) with federal, state, and county agencies providing consistent, critical membership dollars. The dependence on these public land agencies to support tree improvement cooperatives is likely to continue, but funding may be subject to political forces and budget shortfalls.

Scientists who pursue resistance for species of ecological concern but limited commercial interest, such as ash, hemlock (*Tsuga* species), beech (*Fagus* species), and redbay, remain dependent on small-scale, short-term grant funds to support research and development activities. Continuous funding for long-term tree breeding programs is necessary for efficient, tangible outcomes, but remains a challenge for institutions, whether university or government supported, to fund sustainably. Some aspects of resistance breeding can be accomplished within the short time frame that is well suited to university research, including new pathogen biology studies, pathogen interactions within ecosystems, histological interactions between host and pathogen, inoculum concentrations needed to elicit host responses, and phenological synchrony (Smith et al. 2006, Beier and Blanchette 2018). Long-term components of resistance breeding, such as controlled crosses and progeny testing, exceed the duration of typical university research cycles and usually depend on tree improvement cooperatives or federal agencies to address. The ability to scale up products of this type of research into operational resistance breeding efforts is limited in regions without an active tree improvement cooperative, such as the central hardwood region, and similarly affects species that lack commercial markets. Even worse, without industry or government participation, these research outcomes may never be translated into breeding programs or seed orchards that produce seed, seedlings, or propagules with improved resistance for planting stock.

The implementation of resistance breeding requires expertise in multiple disciplines including seedling culture, pathology/entomology, and genetics. Failures to identify heritable resistance because of suboptimal practices from incomplete knowledge can lead to mistaken beliefs that resistance is unattainable. For example, breeding for WPBR resistance in eastern white pine (*Pinus strobus*) lagged for decades as methods to screen for resistance met with meager success compared with other five-needled pines in western North America (Kriebel 2004). Efforts to mass screen thousands of seedlings were hindered by heightened foliage sensitivity to infection; artificial inoculations either killed too many seedlings or, in some cases, not enough, to generate meaningful data. These findings led to the conclusion that no heritable resistance existed in eastern white pine, but that conclusion was reconsidered when a histological assessment of one selection (P-327, first identified by Robert Patton, University of Wisconsin–Madison) demonstrated elevated resistance (Smith et al. 2006). A refinement of the screening protocol changed the trajectory of the program and revealed significant heritability for resistance (Pike et al. 2018a). The eventual success for eastern white pine is attributable to interdisciplinary efforts to refine and conduct the screening program with contributions from federal and university scientists.

State nurseries have been key partners in resistance breeding, providing land and staff to manage seed orchards and progeny tests; however, the number of nurseries has steadily declined across the United States. Eight states have lost their state nursery since 2005 (NASF 2016), and more may close in the future. Private nurseries are primary producers of containerized seedlings for reforestation in the United States (Haase et al. 2019) but are less inclined than state-run nurseries to support research or invest in screening work that lacks an immediate cost return. Hardwood trees are grown primarily as bareroot stock and constitute less than five percent of all seedlings produced across the United States (Haase et al. 2019). Across the Northeast, public nurseries grow roughly half of hardwood trees (Pike et al. 2018b). A diverse nursery sector, consisting of federal, state, and private nurseries, is needed across the eastern United States to grow and distribute seed with improved resistance to pests, especially for hardwood trees.

Keys to Success in Resistance Breeding

In the eastern United States, partnerships across private and public sectors have proved essential to breed resistant trees and increase seed production for eventual deployment. Although each partnership is unique, several themes emerge, including the following:

1. A group of people committed to saving or restoring a species and its associated values—socioeconomic and ecological.
2. An array of researchers, usually including scientists at federal agencies, interested in the underlying science of the problem independent of the committed group.
3. Multiple sources of funding that provide enough buffer to compensate for year to year fluctuations.
4. A network of leaders (formal and informal) focused on obtaining effective resistance that maintains open communication by sharing information, including setbacks, progress, and data.
5. Effective public engagement, including active volunteers and interested citizens.

The TACF exemplifies this combination of themes but is unlikely to be replicated, or closely modeled, for species less charismatic than American chestnut. The vast amount of genetic resources created through TACF allowed a wide array of scientists (NIMSS 2020) to research the mechanisms and genetic architecture of resistance (Kubisiak et al. 2013, Zhebentyayeva et al. 2019, Staton et al. 2020) and potential control of the pathogen (MacDonald and Fulbright 1991). The production of genetic resources for chestnut (trees of known pedigree and phenotype) is a hurdle that, once overcome, may be attractive to collaborators whose research can accelerate or enhance resistance breeding efforts (Lane et al. 2016, Ćalić et al. 2017). This information can help integrate breeding, biocontrol, and biotechnology programs for future restoration of American chestnut (Jacobs et al. 2013, Nelson et al. 2013, 2014). For example, research conducted by the State University of New York College of Environmental Science and Forestry (SUNY-ESF) in Syracuse, running in parallel to the TACF breeding program, produced a genetically modified (GM) American chestnut that shows strong resistance to the blight fungus (Newhouse et al. 2014, Steiner et al. 2017).

This GM tree may offer the best chance for restoring American chestnut once the federal process for its release is completed. The inclusion of GM genotypes in future restorations hinges on whether the modified genes can be successfully transmitted into a variety of populations covering the range of photoperiods and climates the species formerly occupied (Westbrook et al. 2019). SUNY-ESF restoration efforts can only be accomplished through cooperation with TACF chapters and partners that have supported breeding efforts since the 1980s, which includes federal and state agencies.

Resistance breeding programs in the eastern United States depend on support from federal and state agencies to develop and distribute the improved seed. This full complement of resources currently only occurs in Great Lakes region states of Minnesota, Wisconsin, and Michigan. J.W. Toumey Nursery, a federal nursery in Watersmeet, Michigan, and Oconto River Seed Orchard, a federal seed orchard in White Lake, Wisconsin, support grafting and seed orchards for Region 9 (Eastern Region) National Forests. Various state and private nurseries also reside in these three states of the region. Minnesota's Department of Natural Resources manages one nursery in Akeley (Badoura State Forest Nursery) and is planting new seed orchards on the grounds of General C.C. Andrews State Forest Nursery, which closed in 2013, in partnership with the University of Minnesota Tree Improvement Cooperative. The Badoura nursery sells seedlings to nonindustrial private landowners in the state and provides plant material for reforesting state-owned land. The state's Soil and Water Conservation Districts have an active program to sell small bundles of seedlings grown at Badoura (as opposed to the 500-seedling minimum order for direct purchases) to private landowners. Grafting can be supported, seed can be stored, and seed orchards managed at all these different locations. This multiagency collaboration can supply seed and seedlings to public (county, state, and national forest) and private landowners across the region, fulfilling all phases of resistance breeding, provided that plant material with improved resistance is available.

A new multiagency forest health collaborative serving the Great Lakes region recently formed and may become a model for conducting resistance breeding for species with few commercial markets. This collaborative, a partnership between the Forest Service and American Forests, was recently developed with support from the Great Lakes Water Basin Forest Health Collaborative (funded by the Environmental Protection Agency through the Forest Service). It does not yet have a web presence but is described in a recent *Washington Post* article (Popkin 2020) and blog post (Leahy 2020). The collaborative will be housed at the Holden Arboretum in Kirtland, Ohio, and initially will focus on ash and hemlock. Their primary mission is to establish and train a network of partners who will share the work of establishing seed orchards, collecting seeds, and restoring sensitive habitat. In addition, the Roots of Rock, another innovative partnership, is a collaboration between the Forest Service, American Forests, and the Fender Musical Instrument Company that evolved out of shared concerns about the potential loss of imperiled species in both urban and rural forests. This partnership will support efforts to identify additional lingering ash trees on the Allegheny National Forest and work in conjunction with Greening of Detroit (greeningofdetroit.com), a nonprofit focused on enhancing the lives of citizens by planting trees, educating youth, and providing job training.

Recent advances in mobile phone technology and social networking have increased opportunities to engage with the public, including citizen volunteers (a critical part of both the Roots of Rock and Forest Health Collaborative), in resistance breeding. For example, the Ecological Research Institute (ERI) (monitoringash.org) and associated platform, anecdata (anecdata.org), in close consultation with Forest Service scientists, developed a training program to help land managers identify and incorporate lingering ash into their management strategies. Development of the ERI training program was driven by volunteer groups, state and local parks, state conservation departments, universities, nature preserves, and many others interested in contributing to ash conservation. In addition, National Science Foundation funding helped launch TreeSnap (treesnap.org), a free application for mobile phones that allows citizens to report information such as size, health status, and locations of trees to support scientific research on conservation and breeding programs (Crocker et al. 2019). Although any species can be reported, six species are currently featured, including American chestnut, ash, hemlock, white oak (*Quercus alba*), American elm, eastern larch (*Larix laricina*), and butternut. This type of model (federal agencies provide foundational support and nonfederal partners contribute educational programming, publicity, land, and labor) is less costly than a program built entirely on federal support (Bonello et al. 2020) and has the added benefit of built-in public engagement.

Conclusions

Breeding for host resistance is often overlooked as a tool to help with the growing problem of invasive pests and pathogens that threaten our forests, especially in the eastern United States where the majority of forest land is under private ownership. Resistance breeding is sometimes viewed as being too long term and too expensive to be practical, but decades of success in resistance breeding for fusiform rust and blister rust diseases, Port-Orford-cedar root disease, and beech bark disease demonstrate otherwise. In the past, resistance breeding was conducted by federal and state agencies, university faculty members, and industry-supported tree improvement cooperatives, apart from TACF, which has garnered widespread public support for the cause of restoring American chestnut. Successful breeding programs in the future will rely on flexible partnerships among state and federal agencies, nonprofit organizations, industry groups, and citizen scientists to allocate resources and produce outcomes. Fostering this collaboration through innovative partnerships (Nelson and Koch 2017) designed to identify, develop, and deploy host resistance is required to meet the forest health challenges we are facing.

Supplementary Materials

Supplementary data are available at *Journal of Forestry* online.

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Disclaimer

The findings and conclusions in this article are those of the authors and should not be construed to represent any official USDA or US government determination or policy.

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