

Resistance breeding against nonnative pathogens in forest trees — current successes in North America¹

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Abstract: Nonnative invasive pathogens have decimated North American forests for over 100 years, and additional pathogens continue to arrive. These pathogens are destined to be permanent fixtures in the ecosystem. In many cases, management activities have been unsuccessful in slowing the spread of these pathogens or in restoring forests. Genetic resistance potentially provides an invaluable management tool for restoring these species or using them in plantations. Although native tree species are highly susceptible to some nonnative pathogens, a low frequency of resistance is present in even those North American host species most affected. Classical breeding methods can produce genetically diverse and resistant populations for reforestation or restoration of natural forests. However, any operational program for developing resistant populations of forest trees must contend with relatively long generation times, as well as the long-lived nature of trees and the potential of the pathogen to evolve. Western white pine (*Pinus monticola*), Port-Orford-cedar (*Chamaecyparis lawsoniana*), American chestnut (*Castanea dentata*), and American elm (*Ulmus americana*) are examples of species for which there are successful breeding programs for disease resistance. Examples from these species, with a particular focus on western white pine and white pine blister rust [*Cronartium ribicola*] resistance, will be used to illustrate some of the successes in operational programs, as well as to discuss some of the research needs and current unknowns in developing durable resistance. Some of these programs have been ongoing for 50 years, while the Port-Orford-cedar program began only in the last decade. Resistant seedlings from several programs are now being used in reforestation and restoration.

Key words: resistance breeding, forest trees, blister rust, *Phytophthora lateralis*.

Résumé : Les organismes pathogènes envahissants exotiques ont décimé les forêts nord-américaines depuis plus de 100 ans et de nouveaux agents pathogènes continuent d'arriver. Ces agents pathogènes sont destinés à devenir des résidents permanents de l'écosystème. Dans plusieurs cas, des activités de lutte contre ces agents pathogènes n'ont pas réussi à ralentir leur dispersion ou à restaurer les forêts. La résistance génétique a le potentiel pour être un outil d'aménagement inestimable pour la restauration de ces espèces ou pour leur utilisation en plantation. Même si les essences indigènes sont très sensibles à certains agents pathogènes exotiques, un faible taux de résistance est présent, même dans les essences nord-américaines les plus affectées. Les méthodes classiques d'amélioration génétique peuvent produire des populations génétiquement diverses et résistantes pour la reforestation ou la restauration de forêts naturelles. Cependant, tout programme opérationnel de développement de populations résistantes d'arbres forestiers doit composer avec des durées de génération relativement longues, ainsi qu'avec la longévité des arbres et le potentiel d'évolution des agents pathogènes. Le pin argenté (*Pinus monticola*), le faux cyprès de Lawson (*Chamaecyparis lawsoniana*), le châtaigner d'Amérique (*Castanea dentata*) et l'orme d'Amérique (*Ulmus americana*) sont des exemples d'espèces pour lesquelles des programmes réussis d'amélioration génétique pour la résistance aux maladies existent. Des exemples parmi ces essences, plus particulièrement le pin argenté et la résistance à la rouille vésiculeuse du pin blanc [*Cronartium ribicola*], seront utilisés pour illustrer certains programmes opérationnels réussis, ainsi que pour discuter de certains besoins de recherche et des éléments actuellement inconnus du développement de la résistance durable. Certains de ces programmes existent depuis 50 ans, alors que le programme du faux cyprès de Lawson n'a commencé que dans la dernière décennie. Des semis résistants, issus de plusieurs programmes, sont maintenant utilisés en reforestation et restauration.

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Mots clés : amélioration génétique de la résistance, arbres forestiers, rouille vésiculeuse, *Phytophthora lateralis*.

Introduction

Nonnative invasive pathogens continue to have major impacts on North American tree species, causing widespread mortality in native forests, plantations, and urban plantings (Liebhold et al. 1995). These pathogens are likely to become permanent fixtures in North America. In many cases, the diseases they cause, e.g., white pine blister rust [*Cronartium ribicola* J.C. Fisch.], chestnut blight [*Cryphonectria parasitica* (Murrill) Barr], Dutch elm disease [*Ophiostoma ulmi* (Buisman.) C. Nannf. and *Ophiostoma novo-ulmi* Brasier], are well known throughout North America, while others such as Port-Orford-cedar root rot [*Phytophthora lateralis* Tucker and Milbrath L.] are more regional in scope. Pathogens such as *Cronartium ribicola* and *P. lateralis* continue to spread to new areas and intensify in areas already impacted (Blodgett and Sullivan 2004; Hansen et al. 2000; Kinloch 2003; USDI BLM and USDA Forest Service 2004).

Exclusion of new nonnative invasive pathogens, as well as new races of those already present, is paramount to keeping our forests and city landscapes healthy. However, once these pathogens are present in North America, a key factor in determining the fate of the affected species is the frequency and types of genetic resistance naturally present in the host. Although most trees in the severely affected host species are very susceptible, there are rare resistant individuals. These individuals can form the basis for a resistance breeding program for developing populations of genetically diverse and resistant trees. The rareness of the resistance to nonnative pathogens in North American host species and the potentially very limited types of resistance provide an additional challenge relative to native pathogens and their coevolved tree hosts. Management activities to slow the spread of the pathogen in native forests may be partially effective, but resistant seedlings will be the key to restoring most affected areas or to using these species in reforestation.

Breeding for resistance, using classical selection and breeding methods, is showing success for a small but diverse group of nonnative pathogens. Genetic engineering is not being used in these programs and is generally not yet feasible in most tree species (Adams et al. 2002), but discoveries using tools from molecular genetics should enhance the efficacy of conventional breeding programs in the future. Resistant seedlings or vegetative propagules are now available and are being used widely for several tree species.

General overviews and considerations relevant to resistance breeding in trees have been reviewed elsewhere (Burdon 2001; Carson and Carson 1989; Ekramoddoullah and Hunt 2002; Kinloch 2004; McDonald and Linde 2002; Parker and Gilbert 2004). This paper discusses some of the successes to date in several operational programs in North America in developing resistance to nonnative pathogens. White pine blister rust resistant western white pine (*Pinus monticola* Dougl. ex D. Don) has been used in reforestation for decades, and a discussion of the programs is highlighted here. Programs for developing resistance to three other pathogens: phytophthora root rot resistance in Port-Orford-

cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl.), Dutch elm disease resistance in American elm (*Ulmus americana* L.), and chestnut blight resistance in American chestnut (*Castanea dentata* (Marsh) Borkh.) are also discussed. Limitations to resistance, other management options for complementing resistance, and challenges ahead in several of the programs are also discussed. Knowledge from these programs can be used to plan more efficient programs for other species in the future.

Overview of classical disease resistance programs in trees

Because of the length of time to reach reproductive age for many tree species, coupled with often very limited and fluctuating budgets as well as other biological issues, most forest-tree resistance programs are in the early generations of breeding. Depending on the type of resistance present in the affected tree species, resistance programs may be based completely within species (e.g., western white pine, Port-Orford-cedar, American chestnut, American elm), may use hybridization with related, but highly resistant species (e.g., American chestnut), or may use hybrids of other related species to potentially fill the void created by high mortality in a native species (e.g., American elm). In some species, several of these approaches are being implemented (e.g., American chestnut and American elm).

The basic components of resistance breeding programs involve phenotypic selection in natural forests, plantations, or urban landscapes where the disease has infected a high percentage of trees. Selections can be trees that are free of disease symptoms or trees that appear to be less impacted by the disease. In some species (e.g. Port-Orford-cedar), resistance to the pathogen is the sole criteria used for selection, while in other species additional traits are a vital part of the selection to ensure acceptability of the final product (e.g., American elm). Subsequently, clonal propagules or seedling progenies of phenotypic selections are tested in a uniform environment, often using artificial inoculation, to ascertain the relative level of resistance and the type of resistance responses. Artificial inoculation may involve a mixture of pathogen genotypes or specific isolates. Testing may be short term (less than 1 year) or long term, depending on the nature of the disease and the array of resistance responses being assessed (e.g., Kegley and Sniezko 2004; Kinloch and Dupper 2002; Townsend et al. 2005). In testing, progenies of most phenotypic selections often show little or no resistance (e.g., Kegley and Sniezko 2004; Kinloch et al. 2003); thus the parent could be an escape, the resistance may have been overwhelmed under the conditions of artificial inoculation, or the parent tree could manifest ontogenetic resistance in the field.

Another key component of a resistance breeding program is field testing. These tests are vital to evaluate whether resistance is expressed under field conditions and to examine the durability of the resistance over a range of environ-

ments. Relatively few tests examining genetic variation in field resistance or tolerance to nonnative pathogens have been established in North America (Sniezko et al. 2004a, 2004b, Sniezko et al. 2006; Townsend et al. 2005).

Trees are long-lived organisms and must be adapted to their environment and maintain disease resistance over many years, whether used in city plantings, forest plantations, or in restoration of native forests. For forest use, the aim is also to maintain relatively high levels of genetic diversity and adaptability. Within a single species, there may be separate resistance programs in different geographic areas (e.g., King and Hunt 2004; McDonald et al. 2004).

To ensure adaptability, breeding zones are established for most forest tree species, using common garden studies, molecular data, or environmental criteria. For each breeding zone, phenotypic selections confirmed as resistant or tolerant are propagated vegetatively and made available for immediate planting (e.g., American elm) or grafted into seed orchards to generate resistant seedlings for reforestation or restoration needs (e.g., western white pine and Port-Orford-cedar). Seed can also be collected from resistant parent trees in the forest, but resistance levels could be lower if only the female parent is resistant. Within-progeny selections can also be used for orchard establishment in place of the parental genotype (e.g., western white pine). Selections are also included in the breeding population for further resistance development. Multiple cycles of selection and breeding will generally be needed to develop resistance to nonnative pathogens, to increase levels of partial resistance, or to pyramid different types of resistance.

Resistance is not immunity (no infection or mortality in progeny), and often some sort of partial resistance appears to be present. For example, in western white pine even the most resistant families show a moderate to high percentage of trees with stem infection, but survival is much greater in these families than it is in most families evaluated (e.g., Kegley and Sniezko 2004). Use of resistant material will have to take into account the type of resistance and the disease hazard of the site to establish the number of trees to plant to reach a target number of survivors. The survival expected in plantings may depend on several factors, including the number of resistance mechanisms, nature of the resistance(s), mode of inheritance, the size of trees when infection first occurs, type of material (whether seedling progeny or clonal propagule), as well as pathogen variability and the environment. For many forestry operations, seedlings from open-pollinated seed orchards are the primary means of regeneration, but for higher value ornamental purposes vegetative propagation is often used.

Ultimately, tree breeders would like to know the full array of resistance mechanisms present, but this basic knowledge is still lacking. It is tempting to use only the most immediately effective types of resistance (in which no further breeding is needed), but this may prove to be a dead-end strategy (Kinloch et al. 2004a) and may prevent early incorporation of some forms of partial resistance into the population. In the programs that use wind-pollinated seed lots from forest selections (e.g., programs for white pine blister rust resistance), it might be difficult to observe any recessive resistance mechanisms that might occur.

R-gene resistance is present in several white pine species (Kinloch and Dupper 2002; Kinloch et al. 2003) and is usually the simplest to characterize (e.g., hypersensitive reaction in needles of western white pine and sugar pine (*Pinus lambertiana* Dougl.). In some tree species there also appears to be partial resistance or tolerance to these nonnative pathogens (e.g., Bingham 1983; Kegley and Sniezko 2004; Townsend et al. 2005).

For long-lived organisms such as trees, it is desirable to establish genetically diverse populations and to have types of resistance or combinations of resistance that are long lasting or durable. In some cases, it is expected that the resistant trees will live for hundreds of years, unlike most agricultural crops, which are replanted annually. Some types of resistance may provide relatively short-term utility in forest trees (Kinloch et al. 2004a). In addition, in many cases, once they are established, resistant trees will be expected to serve as the progenitors of future generations of forests and coevolve with the pathogen and new biotic or abiotic stresses.

The examples presented here represent successful programs involving an array of widely different pathogens and tree hosts. Operational reforestation or restoration using seedlings from the resistance programs has occurred for decades for western white pine; it has just begun for Port-Orford-cedar. Several cultivars of tolerant American elms are being distributed, and good progress has been made in developing resistant American chestnuts.

Examples of successful breeding programs

Cronartium ribicola resistance in western white pine

There are long established operational resistance programs in three of the nine North American species of white pines (*Pinus* L. subgenus *Strobus* Lemm.) (see Bingham 1983; Daoust and Beaulieu 2004; King and Hunt 2004; Lu et al. 2004; McDonald et al. 2004 for overviews of efforts to date). These programs have been established to provide resistant trees to use in reforestation or restoration of forests. Programs for western white pine and sugar pine have been active for decades (McDonald et al. 2004), while the programs in eastern white pine (*Pinus strobus* L.) have been more intermittent (Daoust and Beaulieu 2004; Kriebel 2004). Although the focus has been on the three species of most commercial value, recent concerns about the high mortality of several high-elevation species of white pines have raised awareness of the need to evaluate the level of resistance in these species to investigate possible management strategies (Samman et al. 2003).

The most progress among white pines has been in western white pine (WWP), where hundreds of selections are now in orchards, and where resistant seed has been used for several decades from the USDA Forest Service programs based in Oregon and Idaho. Four resistance programs are currently in place in the United States and Canada, covering the range of WWP north of California (King and Hunt 2004; McDonald et al. 2004). Several of these programs have been ongoing for more than 40 years.

Parental or progeny selections from the short-term tests have been used to establish seed orchards for all the major breeding zones, and seed from the first or second generation

of selections is available for most zones. All WWP orchard seed lots are open pollinated and will therefore yield a mixture of resistant and susceptible seed. Land managers will have to take this into account in using resistant seed.

Artificial inoculation of 2-year-old seedlings has been the principal method of assessing resistance in all programs. Most of the first generation testing has involved using half-sib progeny of phenotypically resistant trees selected in forest stands; full-sib families are being used in advanced-generation resistance-screening trials. Several types of resistance have been found in WWP (Kinloch 1982; Zambino and McDonald 2004). The best characterized resistance is a hypersensitive reaction (HR) in the needles that generally prevents stem infection (Kinloch et al. 1999, 2003). HR in WWP is found only in populations in California and parts of Oregon (Kinloch et al. 2003). Separate *R* genes conditioning HR have been found in two other North American white pines (Kinloch and Dupper 2002). Generally, 50% to 100% of progenies of parents with HR would be expected to be canker free. However, virulence to these *R* genes is documented in both western white pine and sugar pine (Kinloch et al. 2004a), and 95% to 100% infection of WWP trees with HR has occurred in several cases (R.A. Sniezko, unpublished data). HR will have very limited utility for WWP in parts of western Oregon where the virulent race of the rust is already established.

Short-term artificial inoculation trials have helped characterize differences among WWP families in resistance responses other than HR (e.g., Bingham et al. 1983; Hoff 1986; Hoff and McDonald 1971; Kegley and Sniezko 2004; McDonald and Hoff 1970; Sniezko and Kegley 2003a, 2003b). However, much less is certain about these, including the number of mechanisms, their inheritance, their geographic distribution, and their effectiveness in different test environments. The relatively heterogeneous mixtures of rust inoculum used in inoculations should help ensure the likelihood of resistance in field plantings in North America. However, research with single spore isolates would be useful to refine knowledge of inheritance and number of resistant mechanisms.

High levels of resistance are very rare in WWP. The USDA Forest Service Region 6 program (covering Oregon and Washington) has screened progeny of more than 4200 field selections and has found both HR (Kinloch et al. 1999, 2003) and other types of resistance (Kegley and Sniezko 2004; Sniezko and Kegley 2003a, 2003b). In two typical trials in the Oregon program, family survival 5 years after inoculation of the top open-pollinated families (excluding HR families) was 20% to 55% versus 3% to 9% for the average of all open-pollinated families (Kegley and Sniezko 2004). In another trial, the top full-sib family (excluding HR families) had 83% survival 3 years after inoculation compared with 8% survival of the most susceptible open-pollinated family (Sniezko and Kegley 2003b); 5 years after inoculation survival was 68% for this resistant family and 0% for the susceptible family (R.A. Sniezko, unpublished data). Many of the seedling families with highest survival (excluding families with HR) in these trials have an array of resistance responses, including longer period to stem symptom appearance, higher levels of bark reaction or canker inacti-

vation, lower incidence of stem symptoms, and higher survival of trees with stem symptoms (Kegley and Sniezko 2004; Sniezko and Kegley 2003a, 2003b). Research is needed to determine whether these responses are separate mechanisms or differential expression of the same type of resistance in different genotypes within a seedling family.

Ultimately, it is field performance over time that will be the key determinant of the utility of resistant white pines. All WWP orchard seed lots are open pollinated and will therefore yield a mixture of resistant and susceptible seed. Land managers will have to take this into account when using resistant seed. However, levels of field resistance are still to be tested for most orchard seed lots. In operational plantings in Idaho, F_2 orchard seed lots consistently had lower infection and lower mortality than unimproved seed lots (Fins et al. 2002). In four replicated field tests in Idaho (12 to 26 years after planting), infection averaged 60% and mortality 25% for the bulked F_2 orchard seed lot versus 95% infection and 67% mortality for the unimproved seed lot (Fins et al. 2002). However, on some sites the F_2 orchard lots were much more heavily infected than expected based on predictions made from a short-term nursery test (Fins et al. 2002; Hunt 2004a). Thus, avoidance of planting current resistant stock or planting a mixture of tree species on the highest hazard sites for white pine blister rust may be prudent. However, further research is needed to characterize which sites have the highest hazard for blister rust (Goddard et al. 1985; Hagle et al. 1989; Hunt 1983; Muller 2002). Large geographic movement of WWP seed sources also may affect rust resistance or general survival and growth (Hunt 2004a; King and Hunt 2004). For example, F_2 orchard seed from the Idaho breeding program does not hold up well for resistance in low-elevation plantings in coastal British Columbia (Hunt 2004a).

Field evaluation of individual families should provide researchers and breeders with more detailed information than that available from the plantings of bulked seed lots. Recent summaries from several of the oldest known field plantings show that some resistant families can survive for more than 25 years in areas with high levels of infection (Kinloch et al. 2004b; Sniezko et al. 2004a). Very few replicated field plantings of WWP half-sib or full-sib families have been established, but early results are encouraging (Kinloch et al. 2004b; Sniezko et al. 2000, 2004b). Recent family trials indicate that there is good correspondence between infection levels following artificial inoculation and early field results for WWP (Sniezko et al. 2004b). In one test, 5 years after planting, the percentage of trees with stem symptoms ranged from 10% to 50% for 12 resistant families versus 83% for the susceptible control family (Sniezko et al. 2004b). In another test, established in 1998, stem infection 6 years after planting averaged 89%, with means ranging from 25% to 100% for the 49 families (R.A. Sniezko, unpublished data). Based on seedling screening results, some families with a high percentage of trees with stem symptoms are expected to show high survival in the field. However, since mortality in these tests lags behind infection, data are just now becoming available. Evidence also exists that the effectiveness of some types of resistance is dependent upon the test environment (Hunt 2004a) and the nature

of the resistance (Kinloch et al. 2004a, 2004b). Additional field tests have recently been established for several programs.

Answers to several key questions are needed to enhance the efforts to breed for resistance and maximize utility of resistant materials: How many types of resistance are present in WWP? What is the inheritance and nature of each resistance mechanism? What is the influence of inoculum level and environment on resistance? To what degree does the source of inoculum influence resistance? How many cycles of breeding will be needed for some partial resistances to reach silviculturally useable levels? Are there types of resistance that are effective in older trees (i.e., larger trees), but not in the 2-year-old seedlings used?

Asian and European species of white pines are generally much more resistant to white pine blister rust than are North American species. It would be useful to more fully understand the types of resistance and their distribution within populations and regionally within these species. Similar information from other natural pathosystems would also help guide long-term breeding efforts within WWP.

The evolutionary potential of *Cronartium ribicola* is a key factor in whether resistance programs will be successful in achieving durable resistance and restoring WWP and other white pines in North America. The geographic origin of white pine blister rust is unknown, but is believed to be in Asia or Russia (Hunt 2004b). Relatively few studies of genetic variation (using molecular markers) of the rust have been undertaken, and generally only North American sources have been examined (Hamelin et al. 2000; Hei et al. 2003; Kinloch et al. 1998). Perhaps more informative are direct tests of susceptibility of resistant WWP families to races of blister rust from different areas of the world. Studies undertaken in the early 1970s generally showed higher susceptibility of resistant WWPs to rust races outside of western North America (see summary in Hoff and McDonald 1993). New trials underway will examine a wider array of resistant families to blister rust in Germany, China, and eastern North America.

Some WWP trees develop pollen cones or seed cones within 6 to 8 years of sowing, but flowering in others may take 10 to 15 years. Generally, seed cones begin to appear at an earlier age than pollen cones. The long breeding cycle will slow the development of increased resistance within WWP somewhat but should not be a major obstacle. Research on techniques to accelerate flower development in WWP would expedite both breeding and seed availability for restoration and reforestation.

Even with sufficient resistant seed available, a long-term concerted effort will be needed to restore WWP in forests over its range. Because of lower timber harvests on federal lands and limited budgets for reforestation after fires, fewer hectares are available to restore. Making seed available to nonfederal landowners will be invaluable in enhancing the spread of resistance over the range of WWP.

The wide use of resistant WWP seed for several decades and its general success are encouraging. Future efforts should include monitoring field plantings for any breakdowns in resistance, maintaining or increasing the levels of genetic diversity in seed orchards, and enhancing levels of resistance through breeding. Other management activities

such as site hazard rating and branch pruning (Hagle et al. 1989; Hungerford et al. 1982; Hunt 1998; Schwandt et al. 1994) can be useful complementary tools.

***Phytophthora lateralis* resistance in Port-Orford-cedar**

Port-Orford-cedar (POC) is the only species known to be highly susceptible to the root pathogen *P. lateralis* (Goheen et al. 2003a). Because of the nature of this root pathogen, management activities such as seasonal road closures may slow the spread of the pathogen to new areas (Goheen et al. 2003b), but availability of resistant seedlings is the main method of restoring already impacted areas. In addition to its use in restoration on public lands, there is interest in planting disease-resistant POC on private lands. As a result of a combination of the favorable biology of POC, the testing regime used, personnel experienced in tree breeding and resistance work, and cooperation of many people from USDA Forest Service, USDI Bureau of Land Management, Oregon State University, and private groups, this resistance program may be among the fastest moving in forest trees.

The presence of genetic resistance to *P. lateralis* was first noted in the late 1980s (Hansen et al. 1989). The operational resistance program began in 1996, and over 10 000 field selections have been through the first phase of testing, a stem dip test (USDI BLM and USDA FS 2004). For POC, the sole selection criterion has been resistance to *P. lateralis*. Many of the most susceptible progenies show 100% mortality in greenhouse testing, but a small percentage of selections show 50% to 100% survival (Sniezko and Hansen 2003; Sniezko et al. 2003). Preliminary results from the second phase of testing, a root dip test, indicate that several types of resistance may be present (Sniezko 2004). Initial work to investigate the underlying nature of resistance has recently been completed (Oh 2004).

Prospects for durability of resistance may be good: the pathogen appears to have little genetic variation (Goheen et al. 2003a), it is relatively slow moving, and no indications of new virulent strains are known. Since 2000, over 20 plantings have been established to examine field resistance. Early results from a few sites, 53 months after planting (~4.5 years), are very encouraging, with the most resistant families showing 50% higher survival than the most susceptible families (Sniezko et al. 2006). Further information over an array of sites, including sites that experience periodic flooding as well as higher overall mortality, is needed to determine any limitations of current resistance. Other data supporting the potential durability of resistance come from revisits to some of the earliest field selections. Selections such as 510015, 117490, and CF1, made prior to 1991 in areas of high *P. lateralis* infestation, and confirmed as resistant in short-term greenhouse testing, have been visited in the last few years, and they are still alive.

Provisional breeding zones have been delineated based on common garden and isozyme studies (Kitzmiller and Sniezko 2000; Kitzmiller et al. 2003; USDI BLM and USDA FS 2004). These are currently under revision based on additional data. An anticipated reduction in the number of breeding zones (from 29 to 13) will simplify and expedite any future aspects of the program.

Containerized seed orchards have already been established in several breeding zones. An advantage of containerized

seed orchards is ease of management; POC orchards can be upgraded yearly or whenever new resistant trees are identified. Approximately 100 selections showing high survival in short-term testing have been incorporated into these orchards. Many additional selections are expected to be confirmed as resistant in the next 5 years.

When flower induction treatments are used, POC can produce large quantities of seed within a few years of orchard establishment (Elliott and Sniezko 2000). The first seeds for reforestation and restoration were produced in 2002, within 7 years of when most selections were made. Large amounts of seed and seedlings from open-pollinated orchards are now available to landowners. In the first greenhouse test of bulked orchard seed lots, the orchard lots showed 44% to 50% less mortality than wood-run seed lots for the three orchards with >22 parents (R.A. Sniezko, unpublished data).

Current efforts are focused on confirming resistance of field selections made from 1997 to 2005; making additional field selections to enhance the genetic base and diversity of resistant selections for several breeding zones; advance-generation breeding to increase levels of resistance; assessing field trials to examine durability of resistance; examining the mechanisms of resistance and their underlying inheritance; and producing resistant seed for reforestation and restoration. A key information gap includes the number of resistance mechanisms. Updates and overviews of the program are available at the resistance program Web site (<http://www.fs.fed.us/r6/dorena/poc/index.shtml>).

Tolerance to Dutch elm disease in American elm

Before the advent of Dutch elm disease (DED) in North America, American elm was the predominant street tree in many urban areas, as well as an important component of forests. DED is a vascular wilt and can kill trees within a few weeks of first appearance of symptoms (Schreiber and Peacock 1980). DED has spread throughout the United States, vectored by two species of elm bark beetles, *Scolytus multistriatus* (Marshall) and *Hylurgopinus rufipes* (Eichoff) (Schreiber and Peacock 1980). No elm species is immune to DED. Chemical control of DED has met with only limited success (Schreiber 1993), and development of resistant elms has been a major focus. In North America, resistance programs have been established for many years with the objective of finding or breeding elms to replace those in cities (Townsend 2000; Townsend and Santamour 1993; Townsend et al. 2005). A small number of highly tolerant selections have been documented (Townsend and Douglass 2001; Townsend et al. 2005).

To meet the objective of replacing the stately American elms killed by DED, multiple selection criteria have been incorporated, including tree form and tolerance to DED. Trees selected for tolerance show only slight impacts of DED (Townsend 2000; Townsend et al. 2005). Trees with tolerance to DED and possessing the other desirable attributes are rare, but several cultivars have now been released for public use (Townsend 2000). Recent testing using both *O. ulmi* and *O. novo-ulmi* has identified other parents with high tolerance to DED (Townsend et al. 2005).

Few long-term field results exist, but survival of two of the most disease tolerant selections or their clones ('Valley

Forge' and 'New Harmony') for more than 40 years is encouraging (Denny Townsend, personal communication). Breeding among the top selections and resistance testing of these progenies is also continuing (Steve Eschita, personal communication; Townsend 2000).

In addition, several small restoration plantings in forested areas have recently been established (Jim Slavicek, personal communication). Between 2003 and 2005, eight very small restoration plantings (21 to 25 trees per site) were established in forested areas in Ohio, Iowa, Minnesota, and Wisconsin using tolerant clones of American elm. Five cultivars, 'Valley Forge', 'Princeton', 'New Harmony', 'Delaware-2', and 'R-18' were used. Since very young seedlings tend to be resistant to DED, it usually takes 5 to 7 years after planting to assess tolerance (Jim Slavicek, personal communication). About 10% of the trees in the first plantings have flowered, and some natural regeneration is expected.

In addition to work with American elm, resistant hybrids between elm species from Europe and China are also being developed for use in North America, and several cultivars have been released (Townsend 2000). Work in these other species indicates that DED tolerance is controlled by many genes and that specific combining ability is important (Townsend 2000).

Resistance to chestnut blight

Chestnut blight has been present in North America for over 100 years. Two organizations, The American Chestnut Foundation (TACF) and American Chestnut Cooperators Foundation (ACCF), lead much of the current efforts to develop resistant populations of American chestnut (Griffin et al. 2005; Hebard 2004; Sisco 2004). Their efforts span several decades and build on earlier efforts that produced relatively few selections with a combination of desirable growth, form, and resistance (Griffin et al. 2005). The two organizations have generally taken different approaches to developing resistant American chestnut.

TACF is using hybridization and backcrossing to incorporate resistant genes from Chinese chestnuts (*Castanea mollissima* Blume) into American chestnut (Hebard 2004). After the initial hybrid is made, selections are backcrossed to American chestnut for several generations. Intercrosses among selections from the backcrosses are then made (Hebard 2004; Sisco 2004). The intent is to incorporate the high level of resistance from Chinese chestnut while retaining most (93.75%) of the genetic makeup and form of the American chestnut. Since blight resistance in Chinese chestnut appears to be due to just a few genes, it should be relatively straightforward to incorporate strong resistance (all parents homozygous for blight resistance at all loci) while retaining much of the character of American chestnut (Hebard 2004). The sixth generation of crossing (BC3F3) is expected to achieve this goal. Some activities in the current new 10-year plan include developing seedling seed orchards, investigating additional sources of resistance, continued breeding in surviving American chestnut to see if useful levels of resistance can be obtained, and initiating of wide-scale planting and the monitoring of resistant materials (Hebard 2004).

One of the key questions is whether the highly resistant trees developed using germplasm from Chinese chestnut will retain their ability to compete in native forests (Hebard 2004). Another concern is whether the resistance incorporated from Chinese chestnuts will be durable. Chinese chestnuts have been planted widely in the United States and continue to show intermediate to high levels of resistance (Hebard 2004). To aid in minimizing the prospects of breakdown of resistance, more than one Chinese chestnut parent is being used as a source of resistance germplasm, and the merits of using Japanese chestnut (*Castanea crenata* Sieb. & Zucc.) or American chestnut in the program are also being investigated. Both classical and molecular techniques will aid future activities (Hebard 2004). Common garden tests will be used to compare the performance of resistant chestnuts developed in each of TACFs chapters (Hebard 2004).

The ACCF is taking a different approach, working only within American chestnut with the goal of increasing the low levels of partial resistance that have been found in a small number of surviving large American chestnut trees (Griffin et al. 2005). Large surviving American chestnuts are very rare, and survival may be influenced by low levels of partial resistance, hypovirulence, and site (Griffin et al. 1983, 2005). In the ACCF program, acceptable levels of resistance have been found in a recent test of some crosses among four large surviving trees, and F_2 progeny are now being grown from crosses between F_1 progeny of these earlier crosses (Griffin et al. 2005).

In addition to resistance, site selection and use of hypovirulence are important components to consider when maximizing the utility of disease-resistant chestnut (Griffin et al. 2005). Sites with high levels of hardwood competition, low-temperature stress (high altitude), or drought appear to lower the effectiveness of resistance (Griffin et al. 2005). Although chestnut blight is the major pathogen of concern, in some parts of the chestnut's range, *Phytophthora cinnamomi* Rands is also a potential major constraint to restoration.

Summary

Nonnative pathogens present a serious threat to a number of forest trees and their associated ecosystems, and in many cases there are few effective management tools. Disease-resistance breeding may hold the key to restoration of these species. Illustrations from resistance programs to four nonnative pathogens discussed here demonstrate that high levels of genetic resistance are available to these introduced pathogens, either within the host species or through hybridization with related species. The programs discussed have relied on classical breeding methodology, but advances in techniques in molecular genetics should increase efficiency of breeding efforts in the future. Although genetic resistance is the keystone to future restoration or reforestation with these species, other management activities such as site hazard rating, branch pruning, and use of biocontrols (e.g., hypovirulence, hyperparasites, and endophytes) will help ensure success.

Breeding programs in trees are long term in nature, and continuity of staff and funding are essential to progress. Funding challenges could slow or prevent further development in some of the programs. Public support will be vital in ensuring the future success of the program; volunteers can also play an important complementary role (e.g., in the two chestnut programs). An additional challenge is the availability of sufficient sites for restoration, and solutions may depend upon concerted efforts of many groups.

Short-term artificial inoculation and evaluations (or indirect selection using molecular markers) can be invaluable in reducing the time and expense to develop resistant populations. However, they do not replace the need to establish plantings to examine resistance under field conditions and over long time periods. Environment can have a large effect on utility of some types of resistance. At least in the early generations of breeding, resistance may not hold up on some of the sites of highest disease hazard. Test results from artificial inoculation may vary depending on many factors, including seedling age, inoculum density, inoculum source, growth environment of the seedlings, and time period of assessments.

Although current evidence indicates that moderate to high levels of resistance are available, little is known about the genetic variation of the pathogens and their evolutionary potential. Further understanding of the evolutionary potential of pathogens should help to determine the types of resistance needed and the best deployment strategies (McDonald and Linde 2002). Strains of pathogens introduced to North America may have much less genetic diversity as well as lower virulence and aggressiveness than in their native range. If so, then a first line of defense would be to prevent new races from entering North America. However, we need to evaluate the possibility that new introductions will happen or that evolution will lead to more diversity in the pathogen. International tests of the best resistant materials should provide useful data.

In addition, knowledge of host-pathogen interactions in native range of the pathogens could provide insights on durable resistance, such as how many resistant mechanisms are present, what types of resistances are present in these species, and how are they distributed within and among populations of the host species. The answers to these questions would help breeders discern whether they have the mix of resistances that may be needed and give guidance on how to best incorporate or deploy them for long-term durability of the resistance.

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