II. PATHOGENS

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Invasive fungal pathogens have caused immeasurably large ecological and economic damage to forests. It is well known that invasive fungal pathogens can cause devastating forest diseases (e.g., white pine blister rust, chestnut blight, Dutch elm disease, dogwood anthracnose, butternut canker, Scleroderris canker of pines, sudden oak death, pine pitch canker) (Maloy 1997; Anagnostakis 1987; Brasier and Buck 2001; Daughtrey and others 1996; Furnier and others 1999; Hamelin and others 1998; Davidson and others 2003; Gordon and others 2001). Furthermore, invasive pathogenic fungi have disrupted many forest ecosystems and threaten to eliminate some tree species (Liebhold and others 1995). RMRS research has historically emphasized white pine blister rust, caused by *Cronartium ribicola*, because of the extensive damage to five-needled white pines that are a keystone species to many forest ecosystems in the Interior West since its introduction to North America in the late 1800s. However, this disease continues to spread to new areas and environments. RMRS scientists are instrumental in providing synthesized information concerning research on invasive species, including white pine blister rust (Geils and others 2010; Hunt and others 2010; Kim and others 2010c; Richardson and others 2010a; Zambino 2010). Another emerging invasive pathogen in the Rocky Mountain region and elsewhere is *Geosmithia morbida*, the cause of 1,000 cankers disease. This disease can cause mortality of walnut trees (*Juglans* spp.) and is transmitted by the walnut twig beetle, *Pityophthorus juglandis* (Tisserat and others 2009). In recent years, RMRS has not had the resources to address this disease. Currently, a research group from Colorado State University is evaluating methods to prevent movement of the pathogen and insect vector.

In 2006, the USDA Forest Service R&D Invasive Species Strategic Program Area obtained input from a formal peer review of diverse user groups in order to develop long-term planning for the program. The Invasive Species Strategy was revised to reflect this guidance, and research efforts were prioritized to address the future challenges to managers. As a result of this process, a publication series was produced (Dix and Britton 2010) that includes 12 visionary papers developed to address future invasive species research issues and priorities. RMRS scientists who work on invasive pathogens contributed to papers on overarching priorities (Britton and others 2010) and invasive plant pathogens (Klopfenstein and others 2010). Similarly, a summary of invasive species research and an expertise directory for the RMRS was recently published (Butler and others 2009), which included a section on invasive pathogen research (Klopfenstein and Geils 2009). RMRS has also contributed to regional forest pathology groups, such as Western International Forest Disease Work Conference, which cover diverse aspects of invasive pathogens (Geils 2004b). In another review paper, several authors from Federal and State institutions produced a collaborative review on impacts of non-native invasive species on U.S. forests (Moser and others 2009). This review addresses ecological, economic, and social impacts of invasive species such as pathogens, insects, plants, and aquatic organisms in forests. Recommendations for policy and management were provided.

RMRS research programs have developed critical information for four key areas of invasive pathogens and microbes.

(1) Prediction and Prevention. Because invasive pathogens are virtually impossible to eradicate after establishment, predicting and preventing them is the most efficacious method to minimize impacts. However, considerable baseline information on precise distributions of hosts and pathogens and interactions with the environment is needed to develop effective prediction tools. When compiling inventories of pathogenic fungi, it is important to include pathogens that cause only minor disease problems, because invasive pathogens frequently cause only minor damage in the area of their origin. Also, representative samples are needed for pathogens that are widespread, because subspecies groups may exist that have distinct ecological behavior. Surveys of existing fungi of forests and nurseries are difficult to conduct because numerous species exist, fungal taxonomy is constantly changing, and species are difficult to identify accurately. However, DNA-based diagnostics provide a reliable and cost-effective means to survey existing pathogens (or hosts) within a region (Hoff and others 2004b). Because of the diverse utility of DNA-based characterization, it is extremely short-sighted to preclude DNA-based approaches from any pathogen survey.

Prediction of invasive pathogens requires an understanding of (1) current geographic distributions of forest pathogens and hosts; (2) genetic relationships among pathogen species, subspecies, and populations; (3) potential for intraspecific or interspecific hybridization to create novel pathogens with unique biological behavior; (4) genetic relationships among host species, subspecies, and populations; (5) environmental factors (e.g., temperature, moisture, soil types) that are suitable for survival, growth, and reproduction of forest hosts and pathogens; (6) how changing climate will affect the suitable climate space for forest hosts and pathogens; and (7) pathways of pathogen movement and introduction.

Concepts to examine the genetic structure of hosts and pathogens at the landscape level have been developed (Klopfenstein and others 2001; Lundquist 2005b; Lundquist and Hamelin 2005a, 2005b; Lundquist and Klopfenstein 2001; Richardson and others 2005). DNA-based analyses are currently underway to examine the genetic relationship of white pine blister rust pathogens worldwide (Richardson others 2010b). Such studies will evaluate risks associated with new introductions and seek the evolutionary and/or geographic origin of white pine blister rust that was introduced to North America. Studies on the distribution of genetic groups of *Armillaria* spp., root-rot pathogens of diverse trees, are providing a framework to predict potentially invasive pathogens and hybrids (Hanna and others 2007b; Hanna and others 2009). Studies are ongoing to examine the distribution and genetic relationships among *Armillaria* spp. in the Northern Hemisphere (Cannon and others 2008).

Recently, considerable interest has developed on eucalypt rust (*Puccinia psidii*), also known as guava rust, ohia rust, or myrtle rust. Eucalypt rust has been introduced to Hawaii, where it poses a current threat to myrtaceous trees, which represent ~80% of the native forest in Hawaii. This pathogen is also the subject of worldwide concern, because of its capacity to infect eucalypts. Collaborative work with Universidade Federal de Viçosa (Viçosa, Brazil), Washington State University, the University of Hawaii, Forest Health Protection-Region 5, Western Wildland Environmental Threat Assessment Center, and RMRS is examining the population genetic structure of the eucalypt rust in Brazil, the putative origin of this rust, and other countries where the rust has been found. One goal of this project is to identify eucalypt rust populations that pose additional threat to Hawaiian forest and eucalypts (Cannon and others 2010; Graca and others 2010). Other evaluations were performed to assess the invasive risk of western gall rust (caused by *Peridermium harknessii*) to *Pinus radiata* in New Zealand (Ramsfield and others 2007). In addition, RMRS scientists were instrumental in developing a response plan for Scots pine blister rust, caused by a potentially invasive pathogen that is not yet present in the United States. (Geils and others 2009)

Other factors, such as climate and means of dispersal, must also be considered when predicting potentially invasive pathogens. Studies are underway that will use climate variables to predict areas with suitable climate space for invasive pathogens and evaluate potential effects of climate change (Klopfenstein and others 2009a). Other studies have investigated the possible mode of transport for invasive pathogens (Frank and others 2004, 2008; Geils 2004a).

(2) Early Detection and Rapid Response. Early detection of forest pathogens is dependent on identification to species, subspecies, and population level. Taxonomic identification of forest pathogens is largely dependent on herbaria and culture collections that allow comparisons among microbes. RMRS has a Forest Pathology Herbarium under the supervision of B.W. Geils. In addition, over 10,000 living culture archives of forest pathogens, endophytes, decomposers, and potential biological control agents are housed in the Forestry Sciences Laboratory in Moscow, Idaho. Because most forest pathogens and associated fungi cannot be easily detected or identified, techniques are needed to detect and identify forest pathogens and associated fungi (Kim and others 2005). DNA-based diagnostic methods were developed and/or applied for root rot fungi (Hanna and others 2007a; Kim and Klopfenstein 2011; Kim and others 2000, 2001, 2006, 2010a, 2010b, 2011; Klopfenstein and others 2009b; Stewart and others 2006), white pine blister rust (McDonald and others 2006; Zambino 2002; Zambino and others 2007a), powdery mildew pathogens (Mmbaga and others 2000, 2004), endophytes, and potential biological control agents (Hoff and others 2004a, 2004b; Stewart and others 2006).

RMRS research has contributed over 500 diagnostic DNA sequences to national databases to help in the identification of forest pathogens and microbes. These DNA-based diagnostic tools allow surveys of the present distributions of pathogens and microbes. These surveys are necessary to recognize an introduced pathogen and allow predictions of potentially invasive pathogens and microbes. Furthermore, such DNA-based diagnostic tools can be adapted for screening procedures designed to prevent movement of invasive pathogens and microbes.

One striking example of the need for DNA-based identification is associated with a conifer nursery (Stewart and others 2006). In this situation, isolates of *Fusarium commune* are highly pathogenic to Douglas-fir (*Pseudotsuga menziseii*), but morphologically indistinguishable from nonpathogenic *Fusarium oxysporum*. However, multiple DNA-based techniques were developed to detect and identify the pathogenic *Fusarium* species (Stewart and others 2006). Because nurseries represent a primary route by which invasive pathogens are spread, it is critical that DNA-based tools are used to survey pathogens that exist in nursery settings.

The utility of DNA-based diagnostics was also demonstrated with the white pine blister rust pathogen, *C. ribicola*. In North America, this pathogen was long assumed to utilize only *Ribes* spp. as its alternate (telial) host. Recently, natural infections of *C. ribicola* were found on three other alternate host species, *Pedicularis racemosa*, *Pedicularis bracteosa*, and *Castilleja miniata* (McDonald and others 2006; Zambino and others 2007a). The *C. ribicola* telia on these non-*Ribes* alternate hosts are morphologically indistinguishable from those produced by *C. coleosporioides*, an endemic pathogen that causes stalactiform rust on lodgepole pine (*Pinus contorta*) and utilizes *Pedicularis* spp. and *Castilleja* spp. as alternate hosts (Farr and others 1995; Vogler and Bruns 1998). Thus, DNA-based diagnostics were essential to recognize natural *C. ribicola* infection of non-*Ribes* alternate hosts in North America. Understanding the pathogen ecology and host utilization is essential to managing and predicting ecological behavior of invasive pathogens. RMRS scientists prepared a synthesis of molecular approaches for investigating white pine blister rust pathosystems (Richardson and others 2010a).

The fungal genus *Armillaria* is associated with diverse tree species worldwide. However, some *Armillaria* species are virulent pathogens, while others exhibit low pathogenicity and play beneficial roles in forest ecosystems. Thus, accurate identification of *Armillaria* species is a critical component of surveys of forest pathogens. Because many *Armillaria* species are difficult to identify by morphology, DNA-based techniques were developed to help identify *Armillaria* species (Kim and others 2000, 2001, 2006). These techniques were used to identify *Armillaria* species collected in a survey of *Armillaria* spp. in the inland northwestern United States. Surprisingly, an area in south-central Idaho was identified where the primary pathogenic *Armillaria* species (*A. solidipes = A. ostoyae*) was not found, even though suitable habitat types, suitable host trees, and other *Armillaria* species were present (McDonald and others 1987). Based on this information it appears that any introduction of *A. solidipes* into south-central Idaho represents an invasive species risk. This situation also emphasizes the key role of DNA-based diagnostic methods for pathogen surveys, without which this unique phenomenon would remain unrecognized.

(3) Control and Management. Because of the enormous and growing impacts of white pine blister rust, considerable research in RMRS has be devoted to control and management of this disease that impacts diverse forest ecosystems that comprise several species of five-needled white pines (Geils 2001, 2003; Hoff and others 2001; Kendall and Keane 2001; McCaughey and Schmidt 2001; Schoettle 2004a; Tomback and others 2001a; Zambino and McDonald 2003). Continuing studies have documented the spread of white pine blister rust (Geils 2000; Geils and others 2003; Kearns and Jacobi 2007) and the development of hazard rating systems (Van Arsdale and others 2006). Additional studies have been conducted on infection episodes of comandra rust, a related native rust disease, on lodgepole pine (Jacobi and others 2002). A white pine blister rust model has been developed that simulates the life cycle of the pathogen and resulting tree mortality (McDonald and others 1981), and further developments of this model are still in use as an extension to the Forest Vegetation Simulator (FVS; http://www.fs.fed.us/foresthealth/technology/wpbr_model.shtml). Research on disease resistance has contributed to breeding programs of western white pine and eastern white pine (Hudgins and others 2005; Jurgens and others 2003; McDonald and others 2004; Woo and others 2001, 2002, 2004a, 2004b), and genetic research has evaluated the impact of resistance breeding on the genetic diversity of western white pine (Kim and others 2003). Research by RMRS scientists to assess resistance in limber pine and Rocky Mountain bristlecone pine is ongoing (Sniezko and others 2008; Vogler and others 2006; Schoettle and others 2007; Schoettle and others 2009). Methods to identify genetic markers for rust resistance have been developed for other tree species (Tabor and others 2000). Because the white pine blister rust pathogen requires an alternate host to complete its lifecycle, research has documented the distribution and role of *Ribes* spp. in this disease (Van Arsdel and Geils 2004; Zambino 2010). Recently, other alternate hosts of white pine blister rust were confirmed in North America (McDonald and others 2006; Zambino and others 2007a). This finding may significantly impact our understanding of risks posed by this disease (Kearns and others 2004; Zambino and others 2006, 2007b). Genetic research is assessing whether the blister rust pathogen is changing in a manner that could affect disease development, potential risks of new introductions, and genetic relationships among pathogen populations (Hamelin and others 2000; McDonald 2000; Richardson 2006; Richardson and others 2007, 2008a).

Other research is being directed toward developing proactive approaches in management of high-elevation white pines to reduce the impact of white pine blister rust (Schoettle 2004b; Schoettle and Sniezko 2007; Schoettle and others 2007; Schoettle and others 2009). This new intervention paradigm moves past the idea of protecting the hosts from exposure to the established non-native invader and shifts toward facilitating naturalization by preparing the landscape to sustain ecosystem function into the future in the presence of the invasive. For white pine blister rust, this means facilitating evolution of genetic resistance in the pine host to the non-native pathogen. Positioning the ecosystem for greater resilience upon invasion is especially important for traditionally minimally managed ecosystems where the risk of ecological impacts is high. These ecosystems may be remote but they are not out of reach for invasion by non-native organisms.

Science information has been synthesized for various users and forest managers. A website established by B.W. Geils entitled “The Peridium” contains diverse information about rust diseases and their management (http://www.rms.nau.edu/rust/). A website developed by A.W. Schoettle is devoted to high-elevation white pines, their ecosystems, and the factors that threaten them (http://www.fs.fed.us/rm/highelevationwhitepines/index.htm). Information about whitebark pine was also compiled in book form (Tomback and others 2001b). In addition, B.W. Geils has established an RMRS database that contains comprehensive historical publications related to white pine blister rust. USDA research on biological control of native and invasive pathogens was also summarized (Klopfenstein and others 2000).

Other pathogens, such as *Armillaria* spp. and other root pathogens, have the potential to behave as invasive pathogens following disturbances, such as fire or fuels treatment. Science-based syntheses have developed reports and online tools to guide managers in the application of fuels treatments and potential impacts on root disease (*Armillaria* Response Tool http://forest.moscowfsl.wsu.edu/fuels/art/; Rippy and others 2005; McDonald and others 2005). A number of studies have developed methods and models to evaluate the effects of disease-induced disturbances at various landscape scales (Kallas and others 2003; Lundquist 2000, 2005a; Lundquist and Beatty 2002; Lundquist and Hamelin 2005a, 2005b; Lundquist and Lindner 2000; Lundquist and Negron 2000; Lundquist and Sommerfeld 2002; Reich and Lundquist 2005). Other studies have developed methods to assess non-timber impacts of disease (Lundquist and Ward 2005; Stubblefield and others 2005).

(4) Rehabilitation and Restoration. Information has been compiled for restoration of forest ecosystems impacted by white pine blister rust (Arno and others 2001; Burns and others 2008; Conklin and others 2009; Fins and others 2002; Harvey and others 2008; Keane 2001; Keane and Arno 2001; McCaughey and Tomback 2001; Neuenschwander and others 1999; Tomback and others 2001b; Wagner and others 2000). Science synthesis reports have been developed to demonstrate how molecular genetic tools can contribute to rehabilitation and restoration (Kim and others 2005; Richardson and others 2005). RMRS research has been active in defining host populations that are affected by white pine blister rust, such as white bark pine (Dekker-Robertson and Bruederle 2001; Richardson 2001; Richardson and others 2002a), western white pine (Kim and others 2003, 2011), and limber pine (Schoettle and Rochelle 2000). Understanding of population dynamics and capacity for regeneration is critical to sustaining healthy ecosystems and restoring impacted ecosystems (Coop and Schoettle 2009; Coop and others 2010; Richardson and others 2002b). Fire-scar and tree-recruitment chronologies have been developed from two limber and bristlecone pine sites in Colorado (Brown and Schoettle 2008). Population structures in both sites document relationships with disturbances and changes in climate and land use over the past several centuries, and they provide the longest such records yet developed for this area of North America. A population genetic model parameterized for the high elevation white pines is being constructed to examine the effects of white pine blister rust on the ecological and evolutionary dynamic of rust resistance in the pines (Antolin and others 2009; Schoettle and others 2010). Incorporation of these natural disturbance regimes with management intervention is critical to the long-term sustainability of the host population in the presence of the invasive species (Coop and Schoettle 2009). Lessons learned from long-term research toward enhancing natural recovery of impacted ecosystems has been synthesized for management professionals (McDonald and others 2005; McDonald and Hoff 2001; Zambino and McDonald 2003).

Genetic conservation is an important strategy for sustaining white pines threatened by white pine blister rust and other stressors. RMRS scientists and cooperators are developing and applying molecular and quantitative tools for investigating genetic diversity, correlations among adaptive traits, and disease resistance in several species of white pines. Kim and others (2011) examined the range-wide genetic diversity of western white pine (*Pinus monticola*) populations across the western United States. In related studies, Richardson and others (2009) demonstrated that spatial patterns of western white pine derived from molecular and quantitative genetic data were congruent with regional climates. Issues related to the conservation of limber pine have been addressed by Schoettle and others (2008).

Ongoing research is addressing how climate change will further threaten forest ecosystems that are at risk from white pine blister rust (Richardson and others 2008b; Warwell and others 2007, 2008). Influences of other disturbances such as mountain pine beetle epidemics and climate change on management of white pine blister rust impacts is also being explored (Schoettle and others 2008).

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