The Future of Forest Pathology in North America

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The Future of Forest Pathology in North America

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HEALTHY FORESTS FOR A HEALTHY PLANET

Forests provide key ecosystem services globally, with economic values ranging from $125 to $145 trillion per year (Costanza et al., 2014). Forests are important not only for carbon sequestration goals and global biodiversity (Bonello et al., 2020a; Di Sacco et al., 2021; Palmer, 2021), but also for the economic (e.g., timber), environmental (e.g., water purification), and social (e.g., recreational activities) benefits (Trumbore et al., 2015) they provide (Bastin et al., 2019, 2020). Increasingly, forests are viewed as directly important to human health (Donovan et al., 2013); indeed, urban green environments are now considered essential in city planning (Nowak et al., 2006; Donovan and Butry, 2009; Donovan et al., 2013; Ideno et al., 2017).

The health of forests impacts their value and ability to deliver these ecosystem services. However, the definition of a healthy forest is actually quite complex and has long been debated (Raffa et al., 2009). In the absence of significant exogenous disturbances, forest ecosystems are ecologically dynamic, yet holistically stable and resilient. A healthy forest is not disease-free, but rather one that can self-perpetuate in a state of dynamic equilibrium, equivalent to a forest on its way to, or at, the climax state. A healthy forest, therefore, "encompasses a mosaic of successional patches representing all stages of the natural range of disturbance and recovery" (Trumbore et al., 2015). Indeed, a healthy forest supports pathogens and other disturbance agents that are essential for natural forest regeneration and nutrient cycling and, ultimately, increased resilience. Unfortunately, in the Anthropocene, forests have become increasingly threatened by human-mediated intensification of natural stressors, e.g., higher temperatures and lower water availability due to global warming, which make trees maladapted to their current habitats and thus more susceptible to insect pest and/or pathogen attacks (Sherwood et al., 2015).

THE ANTHROPOCENE IS DISRUPTING THE NATURAL BALANCE

Land-use changes and tree domestication aimed at large-scale plantations, often in monocultures, exacerbate susceptibility to insect pests and pathogens (Sturrock et al., 2011; Pautasso et al., 2015; Desprez-Loustau et al., 2016). With globalization proceeding unabated, natural, and planted forests are increasingly attacked by invasive alien insect pests and pathogens (Eriksson et al., 2019). Natural resources in Canada and the U.S. are becoming endangered at alarming rates because hosts that have not evolved resistance (i.e., naïve hosts) to such non-native insect pests and pathogens are inherently at risk of functional, if not actual, extinction (Pautasso et al., 2012, 2015; Santini et al., 2013; Trumbore et al., 2015; Albrich et al., 2020; Bonello et al., 2020a). While recently accelerating, this process has been ongoing since the onset of global commerce five centuries ago. In North America, some of the past non-native introductions, for example, *Cryphonectria parasitica* (chestnut blight) (Anagnostakis, 1987), *Cronartium ribicola* (white pine blister rust—WPBR) (Kinloch, 2003; Geils et al., 2010), and *Ophiostoma ulmi* and *novo-ulmi* (Dutch elm disease) (Gibbs, 1978), have caused irreversible changes to natural forest ecosystems. Examples of tree insect pests and pathogens that have changed forest ecosystems are not limited to the distant past: the last few decades have seen the appearance of damaging tree diseases such as sudden oak death (Rizzo and Garbelotto, 2003) and laurel wilt (Ploetz et al., 2017).

In some cases, invasive pathogens affect historically and culturally significant species, such as the ʻohiʻa tree in Hawaii that is threatened by the fungal disease known as rapid ʻohiʻa death [causal agents: *Ceratocystis lukuohia* and *Ceratocystis huliohia* (Mortenson et al., 2016; Barnes et al., 2018)]. These diseases can also have very broad ecosystem repercussions and affect species that are not directly attacked by the pathogens, but depend on the services provided by trees for their survival. For example, landscape-level mortality caused by the oak wilt agent: [causal agent: *Bretziella fagacearum* (Juzwik et al., 2011)], in both rural and urban forests in the U.S., negatively impacts endangered species that depend on oaks, such as the golden-cheeked warbler in Texas (Appel and Camilli, 2010). Similarly, WPBR threatens high-elevation pines such as whitebark pine (*Pinus albicaulis*), a keystone species that provides ecosystem services such as food for grizzly bears, erosion prevention, and microhabitat provisioning for plants and animals (Keane and Arno, 1993; Tomback and Achuff, 2010). By severely damaging the self-perpetuating properties of healthy forests, newly introduced insect pests and pathogens reduce the ecological resilience of our forest landscapes (Pautasso et al., 2015; Abrams et al., 2021).

CLIMATE CHANGE IS THE CHALLENGE OF THE FUTURE

Climate change is having a compounding impact on forest health (Kolb et al., 2016; Ramsfield et al., 2016) because it makes trees maladapted to their current environments. Yet, little is known of the potential outcomes of a changing climate on forest health (Seidl et al., 2017). More prolonged and extreme periods of drought, or increasing rainfall, will likely increase the frequency of abiotic stress events making tree hosts more vulnerable to both insect pest and pathogen attack. Some of the new and future climatic conditions will also provide novel niches for non-native invasive insect pests and pathogens as well as expanding the niches of native ones. For example, *Dothistroma pini* (Dothistroma needle blight), *Nothophaeocryptopus gaeumannii* (Swiss needle cast), and *Diplodia sapinea* (Diplodia tip blight and canker) have increased in frequency and intensity, creating large-scale defoliation and mortality that is driven by new climatic conditions, whether caused by more rainfall or drought conditions depending on areas where each of these occur (Woods et al., 2005; Stone et al., 2008; Brodde et al., 2019). Moreover, climate change also causes shifts in forest tree species composition. Well-known examples include changes from large trees in conifer-dominated European mountain landscapes to those dominated by smaller, mainly broadleaved trees (Albrich et al., 2020), which fundamentally alters the underlying forest health framework. Climate shifts are also expected to result in novel ecosystems, driven by migration and species distribution expansion of both hosts and pathogens (Pautasso et al., 2015). Ultimately, this will likely lead to further unforeseen forest health issues, spanning across wider geographical regions and affecting ecosystem services across continents.

FOREST PATHOLOGISTS ARE NEEDED TO FIND SOLUTIONS

The combined impact of invasive alien insect pests and pathogens and climate change can create enormous economic and environmental costs to our society, in the range of $4.3–20.2 trillion per year in ecosystem service losses (Costanza et al., 2014). Mitigating those losses is one of the most pressing challenges to ensure future healthy forests and continued provision of services. Forest health research can lead to innovative solutions and is central to both short- and long-term approaches. Predicting the outcome of host–pathogen–pest interactions in a changing climate will be a very important research avenue for future forest health (Desprez-Loustau et al., 2016). Highly trained forest pathologists are needed to mitigate this crisis. Forest tree pathogens attack long-lived organisms with highly differentiated woody tissue types, which requires a specialized understanding of tree–microbe–environment interactions. This skill set differs greatly from that required for agricultural crop plants, which are primarily annual, herbaceous, and confined to highly simplified agroecosystems. Forest pathology thus represents the necessary fusion of forest ecology and plant pathology required to understand the complexities of forest community structure and composition, pathogen-based biology, biogeography, forestry, genetics, and genomics within the context of host defense and resistance. By necessity, all of these diverse scientific domains pose challenges for the non-specialist, who is not adequately armed with the integrated knowledge necessary to formulate cogent management strategies.

The field of forest pathology is not new: it has developed over 130 years, stimulated by the severe impact of non-native, pathogen-caused epidemics during the first half of the twentieth century and with the purpose of preventing or controlling such events in the future (Boyce, 1961). Since the early 1980s, forest pathology positions in academia and the federal government in North America have undergone a steep decline, despite the significant increase in emerging pest issues (Martyn, 2009; Santini et al., 2013; Bonello et al., 2020b). Lack of trained personnel has occurred in tandem with reductions in organizationally visible forest pathology programs across forestry and plant pathology departments throughout the U.S. and Canada. The latter is a result of smaller departments being combined into larger units/divisions or simply being dissolved. This has resulted in the further erosion of forest pathology training (including faculty positions) in higher education, often with forest pathology as a subject being relegated to a singular course or being combined into a forest protection/forest health course focused on diseases, insect pests, and/or fire.

The number of classically trained forest pathology faculty positions at U.S. universities has declined from over 40 positions in the 1980s to 22 positions in 2021. This includes 14 universities in which a forest pathologist faculty position was not replaced following retirement. In the federal government sector, there has also been a steep reduction in the total number of USDA-FS-Research and Development research scientist positions since 1985. Between 1985 and 2007, the number of all research scientists decreased by 44% (from 985 to 547) (USDA FS, 2007). The proportional change in position numbers, however, did vary by research series classification. Currently, the series with larger numbers of FS researchers include Research Ecologist, Research Forester, and Research Social Scientist. In comparison, there are currently nine Research Plant Pathologists employed (estimated 2.2% of the research scientist cadre) (NFC Insight data, USDA OCIO Enterprise Analytics Team). Between 1985 and 2007, the proportion of scientists in this series per total research scientists decreased from 5.1 to 2.9% (USDA FS, 2007). The USDA FS also employs Plant Pathologists (non-research positions) with responsibilities for detection and monitoring, oversight of federally funded disease suppression programs, and technical assistance. These plant pathologists (39 in 2021 per NFC Insight data, USDA OCIO Enterprise Analytics Team) may be considered the "first responders" while research plant pathologists are often the initial investigators of new and emerging tree disease.

SUCCESS STORIES IN FOREST PATHOLOGY

Forest-pathology-based research has generated some considerable successes in tree disease management. One important case is represented by Heterobasidion root disease (HRD), caused by the *Heterobasidion annosum* species complex. HRD is found throughout coniferous forests of the Northern Hemisphere (Garbelotto and Gonthier, 2013). *Heterobasidion irregulare*, one of the species in this complex, is considered a native species in North America and it has a very low impact in unmanaged or extensively managed forests but causes high mortality in intensively managed pine plantations (Otrosina and Garbelotto, 2010). An innovative solution was developed, based on the pathogen infection cycle (which occurs *via* freshly cut stumps with additional spread through root contacts) by treating stumps with borate compounds (e.g., disodium octaborate tetrahydrate or DOT) or by inoculating the stumps with saprobic wood decay fungi such as *Phlebiopsis gigantea* that outcompete the pathogen. These strategies are considered "among the most effective and sustainable in forestry" and are commercially available around the world, preventing the death of millions of trees (Garbelotto and Gonthier, 2013).

Tree breeding for disease resistance is another successful avenue for controlling tree diseases. Fusiform rust (*Cronartium quercuum* f. sp. *fusiforme*) is a very damaging pathogen that attacks the stems and branches of pines, causing high levels of mortality. Breeding for disease resistance has made it possible to control fusiform rust to maintain low disease levels in loblolly and slash pine plantations in the southern U.S. (Schmidt, 2003). Breeding for disease resistance can also help protect endangered tree species. Several white pine species, including high elevation white pines, have now been bred for resistance to WPBR, making it possible to restore white pines in areas where these pines were previously endangered (Sniezko et al., 2014). Breeding and developing resistant Port-Orford-cedar (POC) for resistance to the exotic root pathogen *Phytophthora lateralis* (Zobel et al., 1985) is another success story (Sniezko et al., 2012). Planting resistant POC and developing operational use of multiple disease management practices have been credited with the recent downgrade of POC status from "vulnerable" to "near threatened" by the IUNC (Pike et al., 2021).

Pathogen identification and detection have revolutionized how we diagnose tree diseases (Stewart et al., 2018). Plant health clinics now routinely use DNA-based methods (Martin et al., 2009; Wu et al., 2011; Lamarche et al., 2015; Yang and Juzwik, 2017; Oren et al., 2018; Parra et al., 2020; Rizzo et al., 2021; Stackhouse et al., 2021) that provide rapid and accurate diagnostics. Regulatory agencies have adopted the tools developed by forest pathologists for their day-to-day testing for invasive species. This has been instrumental in preventing the spread and tracking sources of pathogens such as *Phytophthora ramorum* (sudden oak death) (Grünwald et al., 2019). PCR tests targeting this pathogen have now been used millions of times around the world to provide rapid and reliable molecular identification and help contain this pathogen to western states and provinces of North America (Martin et al., 2009).

Ultimately, it is the integration of multiple approaches that offers the best long-term solutions. This is the case with oak wilt, initially recognized as a mysterious rapid wilting of black oaks (*Quercus velutina*) that was discovered in the early 1940s (Henry 1944), shortly after the discovery of chestnut blight and Dutch elm disease in North America. The fungus *B. fagacearum* spreads above-ground by insect vectors and below-ground through naturally grafted root systems and is known to occur only in the eastern U.S., where it is arguably considered non-native (Juzwik et al., 2008). Control tools and management approaches developed by forest pathologists over the past 75 years and implemented in both urban and rural forests have resulted in effective multi-pronged disease management. Above-ground pathogen transmission by sap beetles (Coleoptera: Nitidulidae) is minimized by timely removal of wilted red oaks, avoidance of oak wounding during high-risk season(s), and restricting movement of firewood and logs with bark from oak wilt-affected areas. Below-ground transmission is stopped by mechanical disruption of common or grafted root systems between diseased and nearby healthy oaks. These selected success stories demonstrate the need for increased research capacity for multidisciplinary approaches that range from basic research for knowledge acquisition to applied research to find solutions.

THE NEED FOR FOREST PATHOLOGISTS IN THE FUTURE

Forest pathology researchers and practitioners are our first *line of defense*, one that is constantly under pressure from a variety of stakeholders facing new and re-emerging forest health issues. Although there are a number of success stories related to mitigating forest diseases, new, unknown, and emerging pest issues are on the rise (Santini et al., 2013). The challenge of predicting outbreaks under future climates and the increasing global movement of invasive pathogens will require novel skills. The need for a traditional "forest specialist" worked well in the past because there were enough "unknown" disease etiologies to investigate and sustain the career of several forest pathologists to tackle a single disease system for decades. However, future generations of forest pathologists will require even more multidisciplinary training and approaches. They will need to acquire multidisciplinary knowledge to better characterize diverse pathosystems (Martyn, 2009). Furthermore, it is critical that resource opportunities sufficient to support the clear needs identified here be strategic, focused, and applied across the continuum of basic to applied research and solution implementation. An expanding cadre of research forest pathologists with the modern training necessary to tackle these problems is urgently needed.

The current forest health crisis brought about by climate change and globalization creates the need and opportunity to train the upcoming generation of forest pathologists. For example, multidisciplinary research consortia are increasingly necessary to tackle the societal grand challenges that forest decline syndromes represent. Such consortia must include forest pathologists, forest entomologists, forest ecologists, silviculturists, traditional forest geneticists, modelers, remote sensing specialists, as well as experts in artificial intelligence, microbial ecology, and novel genomics approaches such as CRISPR-Cas9, to name a few. This will require constant inputs and multiple resource providers and careful and intentional strategic planning to achieve defined forest health objectives. The past and current generations of forest pathologists have demonstrated the value of their work by providing innovative solutions to forest health challenges. The next generation of forest pathologists will have access to an extraordinary toolbox ranging from classical to cutting-edge tools to address and provide solutions to current and future forest health crises. They should be at the forefront of the fight against invasive tree pest and pathogen invasions in the era of climate change.

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All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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