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A framework for establishing a rapid ʻŌhiʻa death resistance program

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Abstract

Metrosideros polymorpha Gaud. (ʻōhiʻa) is the most abundant native forest tree in Hawaiʻi and a keystone species of cultural, ecological, and economic importance. ʻŌhiʻa forests, particularly on Hawaiʻi Island, are being severely impacted by Rapid ʻŌhiʻa Death (ROD), which is caused by the fungal pathogens *Ceratocystis lukuohia* and *C. huliohia*. ROD is characterized by branch dieback, crown wilting, and mortality. Initial disease resistance screening of four varieties of *M. polymorpha* with *C. lukuohia* demonstrated that varieties may differ in susceptibility. Several survivors of field or screening-based infections still exist, providing strong impetus for the establishment of the ʻŌhiʻa Disease Resistance Program (ʻŌDRP). Here, we outline a framework for guiding the ʻŌDRP throughout the process of identifying and developing ROD resistance in *M. polymorpha* and, possibly, all Hawaiian *Metrosideros* species. Core ʻŌDRP projects include: (1) evaluating and operationalizing methods for greenhouse-based production and screening of test plants; (2) greenhouse screening of seedlings and rooted cuttings sampled from native *Metrosideros* throughout Hawaiʻi; (3) establishing field trials to validate results from greenhouse assays; (4) understanding environmental and genetic drivers of resistance to characterize the durability of resistance to ROD; (5) developing remote sensing and molecular methods to rapidly detect ROD-resistant individuals; and (6) conducting breeding trials to improve the degree and durability of ROD resistance. Ultimately, the ʻŌDRP seeks to produce ROD-resistant material for the perpetuation of *M. polymorpha* across Hawaiʻi, with the goal of preserving the ecology, culture, and communities that are dependent on this tree species.

Keywords *Metrosideros polymorpha* · *Ceratocystis* · Plant disease · Disease resistance · Forest pathogens · Fungal disease

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Introduction

Non-native pests and pathogens are serious and growing threats to forest tree species across the globe (Wingfield et al. 2001, 2017, Ghelardini et al. 2017). Some of these have seriously impacted native forest ecosystems, with resulting mortality causing disruptions to ecosystem services, declines in the quality and quantity of forest products, reduced biodiversity, and degraded access to species of cultural importance (Lovett et al. 2006, Boyd et al. 2013). These impacts are magnified when foundational species are impacted (Loo 2009). Development of genetically diverse populations of disease resistant trees is an effective way to restore systems damaged by exotic pests and pathogens, including returning a forest to a desired sustainable state of ecosystem composition, structure, and function (Showalter et al. 2018, Bonello et al. 2020).

Disease screening and resistance breeding programs have been developed for a number of forest tree species, with some successfully producing disease-resistant plant material (Sniezko 2006, Sniezko and Koch 2017). Successful programs include: elm (*Ulmus spp.*) resistance to Dutch elm disease (Martín et al. 2019), Port-Orford-cedar (*Chamaecyparis lawsoniana* (A. Murray bis) Parl.) resistance to *Phytophthora lateralis* Tucker and Milbrath (Sniezko et al. 2012, 2020), Sitka spruce (*Picea sitchensis* [Bong.] Carr) resistance to white pine weevil (*Pissodes strobi* Peck; Alfaro et al. 2013), and pine (*Pinus spp.*) resistance to fusiform and white pine blister rusts (Sniezko et al. 2014). A resistance program for koa (*Acacia koa* Gray), a dominant canopy species in Hawaiian forests, has identified a large number of tree genotypes across Hawai'i that show resistance to koa wilt (*Fusarium oxysporum* f. sp. *koae* Schlecht. Emend. Snyder & Hansen) and established seed orchards. This program, initiated in 2003, now includes field trials to examine resistance across diverse families from various eco-regions throughout the state (Dudley et al. 2015, 2017, 2020). The process of developing a successful applied resistance program is complex, typically involving multiple research groups and natural resource agencies (Woodcock et al. 2018), and often relying on a multi-faceted conceptual framework (Jacobs et al. 2013, Sniezko and Koch 2017).

Here, we propose a strategic framework for guiding the development of an ʻŌhiʻa Disease Resistance Program in Hawaiʻi to help produce *Metrosideros polymorpha* Gaud. (ʻōhiʻa) germplasm resistant to the novel species of *Ceratocystis* responsible for Rapid ʻŌhiʻa Death, *Ceratocystis lukuohia* and *C. huliohia* I. Barnes, T.C. Harr., and L.M. Keith. Our proposed framework relies upon lessons learned from disease resistance programs in other threatened forest tree species, while adapting specifically to the unique ecological, biological, and cultural characteristics of ʻōhiʻa. This work will add to the growing number of case studies on programs developing disease resistance in forest trees, as well as demonstrate how pioneering resistance programs can be leveraged to accelerate development of future programs.

ʻŌhiʻa: ecology, hydrology and cultural importance

Metrosideros polymorpha is a Hawaiian evergreen tree species belonging to the family Myrtaceae. It is the most abundant native forest tree in Hawaiʻi and is a major component (> 80% of biomass) of both wet and dry native forests across the archipelago (Loope et al. 2016). The ancestor to modern Hawaiian *Metrosideros* arrived in Hawaiʻi 3.1 to 3.9 million years ago on the island of Kaua‘i and subsequently colonized the other main Hawaiian Islands as they emerged from the ocean via volcanism. Over time, adaptive radiation led to multiple *Metrosideros* species occupying different ecological niches across the islands (Percy et al. 2008; Dupuis et al. 2019). As a result, there are now five species of endemic Hawaiian *Metrosideros*. Only one species, *M. polymorpha*, is found throughout the state. There are eight recognized varieties of *M. polymorpha*: var. *glaberrima* (found on all islands except Ni‘ihau and Kaho‘olawe), var. *incana*, var. *polymorpha*, var. *macrophylla*, var. *newellii* (a riparian variety endemic to Hawai‘i Island), var. *pseudorugosa* (endemic to Maui), var. *dieteri* (endemic to Kaua‘i), and var. *pumila*. These taxa are primarily distinguished by leaf traits (Dawson and Stemmermann 1990; Stacy et al 2016). The *M. polymorpha* varieties inhabit different environments and have adapted to selective pressures characteristic of these locations (Corn and Hiesey 1973; Cordell et al. 1998; Cornwell et al. 2007; Ekar et al. 2019). The maintenance of these phenotypic differences, despite frequent hybridization occurring in nature, coupled with evidence of strong genetic structure of *M. polymorpha* varieties supports the hypothesis that ‘ōhi‘a is undergoing incipient speciation (DeBoer and Stacy 2013; Stacy et al. 2014, 2016, 2020; Stacy and Sakishima 2018). Other *Metrosideros* taxa include *M. macropus*, *M. tremulolides*, and *M. rugosa* (all endemic to O‘ahu), *M. waialealae* var. *fauriei* (endemic to Maui, Lana‘i, and Moloka‘i) and *M. waialealae* var. *waialealae* (endemic to Kaua‘i).

‘Ōhi‘a is a keystone species, providing habitat for endemic birds, insects, and plants, many of which are endangered (Loope et al. 2016). Many species of the diverse Hawaiian honeycreepers are found in ‘ōhi‘a forests and rely on this tree species for nesting sites and food (Ralph and Fancy 1996; Freed et al. 2007; Hart et al. 2011; Camp et al. 2019). Additionally, ‘ōhi‘a is a host for countless arthropod species. Arthropod surveys of ‘ōhi‘a conducted from 1996 to 2001 resulted in the detection of 711 insect species, 495 of which are Hawai‘i endemics with several being host-specific to ‘ōhi‘a (Gruner 2004). ‘Ōhi‘a forests are also critical habitat for species of Hawaiian *Cyrtandra*, *Clermontia*, *Cyanea*, *Gahnia*, and numerous other plants, many of which are federally listed as threatened or endangered (USFWS 1995, 1996, 1998). Thus, conservation of this species, and all Hawaiian *Metrosideros*, is vital for the conservation of countless other taxa. There is perhaps no other species in the US that supports more threatened and endangered taxa or that plays such a geographical dominant ecological keystone role (Gruner 2004; Paxton et al. 2018; Fortini et al. 2019).

Tantamount to the ecological importance of ‘ōhi‘a is its cultural importance. For Native Hawaiians, ‘ōhi‘a is a physical manifestation of multiple Hawaiian deities and the subject of many Hawaiian proverbs (‘ōlelo no‘eau), the subject of an enormous number of chants (oli) and stories (mo‘olelo) (Gon 2013), and foundational to the scared practice of many hālau hula. Native Hawaiians established many uses for the different parts of the tree. ‘Ōhi‘a wood is used for various structural components of temples and traditional Hawaiian houses, tool and weapon handles, carved into figures of Hawaiian gods, and used for firewood (Malo 1903; Gon 2013). The flowers, shoots, and aerial roots are used medicinally to treat many ailments (Friday and Herbert 2006; Gon 2013). Flowers and shoots are also used for making lei (Friday and Herbert 2006). Lastly, Native Hawaiians, Hawai‘i residents, and islands visitors alike value ‘ōhi‘a for its intrinsic beauty. The thriving biocultural link between ‘ōhi‘a and the people of Hawai‘i is a defining feature of Hawai‘i’s socio-ecological landscapes (Kealiikanakaoleohaililani et al. 2019; McMillen et al. 2020).

Hawai‘i is dependent on groundwater as a source of freshwater for residential and agricultural uses (Tribble 2008). A reduction in the availability of freshwater from this source could lead to the use of other, more expensive methods of freshwater production to meet public demand (Burnett et al. 2020). High elevation ‘ōhi‘a forests protect watersheds across the state, and, because of their lower water usage compared to fast-growing non-native species, allow for greater recharge of groundwater (Kagawa et al. 2009; Takahashi et al. 2011; Cavaleri et al. 2014). Additionally, a study by Burnett et al. (2017) found that the cost of protecting freshwater by conserving native Hawaiian forests is less than half the cost of freshwater production via large-scale reverse-osmosis of seawater per thousand liters.

Native Hawaiian forests are being impacted by multiple threats such as invasive pests, wildfire, and land-use. Substantial work has been invested into mitigating these threats and creating conservation areas where ‘ōhi‘a can thrive, sustaining the ecological, cultural, and economic importance of ‘ōhi‘a across the state. However, Rapid ‘Ōhi‘a Death now represents an unprecedented threat to this species, the loss of which would be devastating to Hawai‘i.

Rapid ‘Ōhi‘a Death

Starting in 2010, residents in the Puna District of Hawai‘i Island noticed an increasing number of dead and dying ‘ōhi‘a and brought this to the attention of state and federal agencies (Keith et al. 2015). Apparently healthy trees were observed rapidly deteriorating in a matter of weeks to canopies full of wilted, brown leaves (Fig. 1), and the phenomenon was given the name

Fig. 1 A *Metrosideros polymorpha* tree on Hawai‘i Island displaying a completely wilted canopy with leaves still attached to branches, typical symptoms of Rapid ‘Ōhi‘a Death

Rapid ʻŌhiʻa Death (ROD). Researchers dissected several diseased trees and found brown to black streaks and discoloration in the sapwood (Keith et al. 2015). Fungal isolates were isolated from sapwood samples and initially identified as *Ceratocystis fimbriata* Ellis and Halstead based on cultural morphology and DNA sequencing. Koch's postulates, the criteria used to demonstrate pathogenicity of a potential pathogen, were completed (Keith et al. 2015), and extensive sampling of diseased trees was conducted on public and private lands to identify the distribution of the pathogen and collect isolates from new detection areas.

Biology of the ROD pathogens

Genetic and morphological analysis of 64 additional fungal isolates revealed that two novel *Ceratocystis* species, not *C. fimbriata* (sensu strictu), were responsible for ROD: *C. lukuohia* and *C. huliohia* (Barnes et al. 2018). The two pathogens have been found to cause two distinct diseases. *C. lukuohia* extensively colonizes the sapwood of *M. polymorpha*, manifesting as brown to black staining, leading to rapid wilt of the crown (Hughes et al. 2020). This disease is now called *Ceratocystis* wilt of ʻōhiʻa (Keith et al. 2015; Hughes et al. 2020) and is present on Hawaiʻi Island and Kauaʻi (Brill et al. 2019), with the potential to devastate ʻōhiʻa forests across the state (Fortini et al. 2019). *C. lukuohia* belongs to the Latin American clade of *Ceratocystis*, which is known to include highly aggressive tree pathogens (Barnes et al. 2018). Due to this species' aggressiveness, it has been the main focus of ROD pathology work (Roy et al. 2019; Hughes et al. 2020; Luiz et al. 2020). *C. huliohia*, on the other hand, invades the living cells of the phloem, cambium, and outer xylem of ʻōhiʻa, resulting in a well-defined area of necrotic tissue typical of a canker disease (Manion 1991; Juzwik et al 2019). As such, the disease caused by *C. huliohia* is known as *Ceratocystis* canker of ʻōhiʻa. Multiple cankers are needed to girdle stems, resulting in slower mortality compared to *C. lukuohia* infection. *C. huliohia* has been detected on Hawaiʻi Island, Maui, Oʻahu, and Kauaʻi (Heller et al. 2019; ROD SRP 2020) and is a member of the Asian-Australian clade of *Ceratocystis* (Barnes et al. 2018). Both species of *Ceratocystis* produce sexual (ascospores) and asexual (endoconidia and aleurioconidia) spore types (Barnes et al. 2018). As the pathogens colonize the host tree, they produce asexual spores that colonize xylem tissues, leading to wilt and branch dieback. Sexual fruiting structures (ascomata) are rarely seen in natural infections, but they have been observed on surfaces of exposed sapwood of infected trees (e.g. stumps of recently felled trees and inoculation wounds). Analysis of neutral loci from the genomes of *C. lukuohia* isolates across Hawaiʻi Island and Kauaʻi, work that is ongoing, suggests that the species comprises clonal lineages derived from a single introduction, with little sexual recombination occurring within discrete populations. Comparatively, population structure of *C. huliohia* appears to be more diverse within and among populations, suggesting that the species may have been in Hawaiʻi for a longer period of time (T. Harrington pers comm). Research on the basic biology of these fungi will provide a solid foundation for future disease resistance research and aid in the development of best practices for mitigating their spread.

Dispersal and transmission of the ROD pathogens

While much effort has been invested into the epidemiology of these two pathogens, potential dispersal agents, vectors, and the roles they play in pathogen dispersal are still being researched. Frass (boring dust) created when ambrosia beetles (*Xyleborus ferrugineus*

(Fabricius), *X. affinis* Eichhoff, *X. perforans* (Wollaston), *X. simillimus* Perkins, and *Xyleborinus saxesennii* (Ratzburg)) attack and tunnel into diseased trees can harbor viable fungal propagules (Roy et al. 2019, 2020). One hypothesis is that windblown *Ceratocystis*-contaminated frass particles are involved in the spread of these pathogens (Barnes et al. 2018), but the role of beetle frass in long- and short-range dispersal of fungal spores is not understood. While beetle frass has been one of the main foci of ROD research, new evidence suggests that ambrosia beetles can directly vector fungal propagules between trees. It is unknown how frequent this method of transmission occurs and how much of a contribution it makes to the overall spread of ROD (K. Roy, pers comm). Humans are suspected of dispersing *Ceratocystis*-contaminated materials via contaminated tools, infected firewood and other plant parts, and contaminated soil on the tires and undercarriage of vehicles (Friday et al. 2015). Humans can also create infection courts when they wound ʻōhiʻa. Similarly, evidence suggests that feral ungulates are suspected of creating wounds on ʻōhiʻa trees, leading to increased mortality rates of ʻōhiʻa in stands where ungulates are present versus ungulate-free stands (Perroy et al. 2021). Understanding how these potential transport and wounding mechanisms contribute to the spread of the ROD pathogens is integral for the long-term management of Hawaiʻi's native forests.

Epidemiology of ROD

The extensive distribution of ʻōhiʻa across Hawaiʻi (roughly 250,000 hectares of ʻōhiʻa on Hawaiʻi Island alone) makes rapid identification of new ROD outbreak areas difficult. Routine state-wide helicopter surveys are conducted with Digital Mobile Sketch Mapping software to note areas of suspected ROD mortality, followed by tree-sampling by ground crews (ROD SRP 2020). Additionally, advanced aerial imaging systems using video, camera, and spectral data are being developed to improve detection and monitoring capabilities (Asner et al. 2018; Vaughn et al. 2018; Perroy et al. 2020). Hawaiʻi Island, where the first ROD outbreaks were identified, has the most extensive ʻōhiʻa forests in the state. ROD has had the greatest impact on this island, with significant mortality occurring over 72,000 hectares of ʻōhiʻa across all nine districts of the island (ROD SRP 2020). The ROD mortality patterns observed via ground-based and remotely sensed mapping can be complex. For example, Mortenson et al. (2016) found that average mortality in ROD-impacted forest plots in Puna and South Hilo from 2014 to 2015 was 28% of total stems on average and mortality ranged from 3 to 50%. In the worst cases, mortality of ʻōhiʻa in some stands can reach over 90% (Fig. 2; R. F. Hughes pers comm). This variability has resulted in some stands being decimated by ROD and others barely impacted. The finding that some ʻōhiʻa continue to survive in forests despite the presence of ROD indicates that resistance may be present in natural stands of ʻōhiʻa and these trees should be studied further.

Two strategic plans have been created to describe current knowledge, accomplishments, and frame the work required to achieve goals of the ROD research, management, and outreach communities. The first strategic response plan for 2017–2019 outlined the need for expanded field detection efforts via remote sensing, research on the epidemiology of the pathogens, optimized management practices, and exploration of other avenues for outreach (ROD SRP 2016). These goals were largely met and discussed in the latest strategic plan for 2020–2024 (ROD SRP 2020). Current needs include continued support of surveillance efforts and improvement of these technologies, expanding outreach efforts and public engagement, research on possible vectors of the pathogens, collection and preservation of

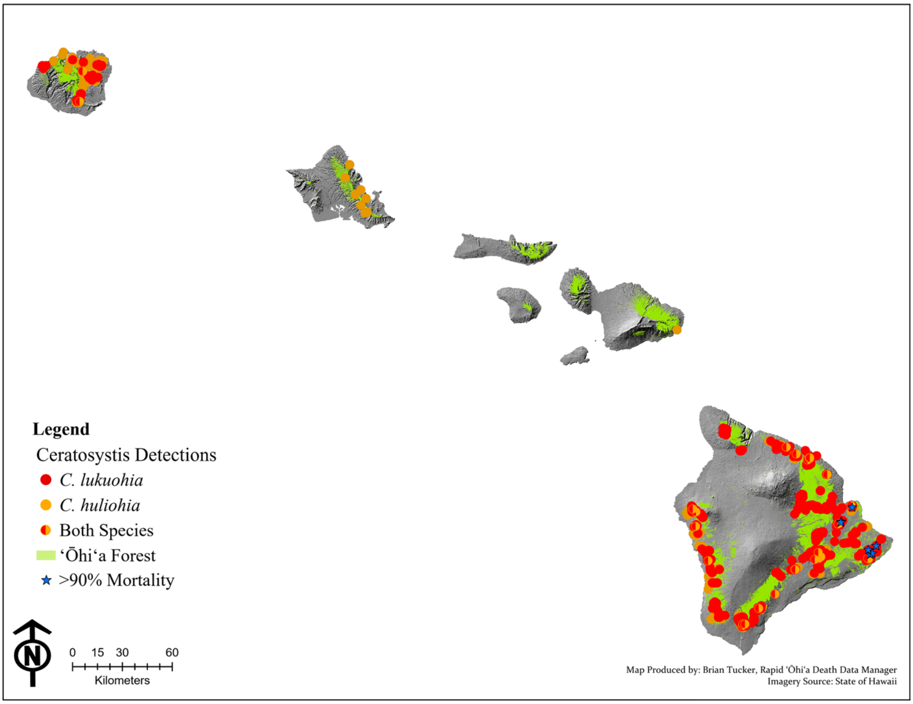

Fig. 2 The distributions of *Ceratocystis lukuohia* and *C. huliohia* positive diagnostic detections in relation to the distribution of ʻōhiʻa (*Metrosideros polymorpha*) forest across the state of Hawaiʻi. Mortality in some stands of ʻōhiʻa can be greater than 90%, as evidenced by forest inventory plots on Hawaiʻi Island (R. F. Hughes, pers comm)

seeds for research and future restoration, and comprehensive evaluation and development of disease resistance in ʻōhiʻa. Here, we focus on the complexities of developing ROD-resistant ʻōhiʻa.

Rapid ʻŌhiʻa Death and disease resistance research

To understand and model the future impact of ROD, it is necessary to determine whether genetic resistance exists in ʻōhiʻa, as well as its frequency throughout Hawaiʻi, the level of resistance, and its geographic distribution. Disease resistance research in ʻōhiʻa was initiated in 2016 by the USDA Agricultural Research Service, with the goal of conducting a preliminary assessment of ROD resistance in local populations of ʻōhiʻa (Luiz et al. 2020). In this study, 124 plants across four varieties of *M. polymorpha* were screened for resistance to *C. lukuohia*, resulting in the survival of 4 individuals of *M. polymorpha* var. *incana* and 1 individual of *M. polymorpha* var. *newellii* 3 years post-inoculation. Currently, the five survivors from the study are being kept for long-term monitoring and will be used to produce rooted cuttings and seeds for further evaluation of these genotypes. The results of this first study suggest that natural resistance to ROD may be present in wild populations of at least some varieties of *M. polymorpha.* However, a more comprehensive screening of the species throughout its range is needed to provide an accurate baseline on the frequency, level, and the distribution of genetic resistance to both pathogens.

This initial effort expanded into a collaborative partnership among state, federal, and non-profit agencies and entities, which in 2018 became the ‘Ōhi‘a Disease Resistance Program (‘ŌDRP). The ‘ŌDRP is comprised of the Akaka Foundation for Tropical Forests, the USDA Forest Service (Regions 5, 6, and the Pacific Southwest Research Station’s Institute for Pacific Islands Forestry), the USDA Agriculture Research Service Pacific Basin Agricultural Research Center, the University of Hawai‘i at Mānoa College of Tropical Agriculture and Human Resources, University of Hawai‘i at Hilo Spatial Data Analysis and Visualization Lab, Purdue University, the Tropical Hardwood Tree Improvement and Regeneration Center, the Hawai‘i Division of Forestry and Wildlife, Arizona State University, the Hawai‘i Agriculture Research Center, and Kalehua Seed Conservation Consulting. The overarching goal of this inter-disciplinary group is to provide baseline information on the genetic resistance present in all varieties of *Metrosideros polymorpha*. Additionally, the group aims to develop sources of ROD-resistant germplasm for a range of restoration purposes including cultural plantings, landscaping, and ecological restoration of areas that have been heavily impacted by ROD. This goal is being achieved through: (1) evaluating and operationalizing methods for inoculation-based screening and greenhouse-based production of test plants and (2) short-term greenhouse screenings of seedlings and rooted cuttings sampled from native *Metrosideros* throughout Hawai‘i. The ‘ŌDRP will then expand by: (3) establishing field trials, with the help of local communities, to validate the short-term greenhouse assays and monitor durability and stability of resistance; (4) understanding environmental (climate, soils) and genetic (vascular architecture, wound response) drivers of susceptibility and resistance to characterize the durability and stability of genetic resistance to ROD; (5) developing remote sensing and molecular methods to rapidly detect ROD-resistant individuals; (6) if necessary, conducting breeding to increase the efficacy of resistance and improve durability of ROD resistance; and (7) support already established and ongoing *Metrosideros* conservation work (state-wide seed collection and banking) with information on genotypes resistant to ROD and ROD-resistant seed production.

Operationalizing ROD-resistance methodologies for *Metrosideros* screening

Useful levels of resistance to non-native pathogens are often rare, necessitating screening progeny of thousands of parent trees to develop base populations for breeding or restoration. Current growing and screening capacity for ROD is limited to approximately hundreds of plants per year, in contrast to established disease resistance programs that screen tens of thousands of individuals annually. For instance, over 12,600 field selections of Port-Orford-cedar, with collections spanning two states and occurring over three decades, were collected to examine resistance to *Phytophthora lateralis* (Sniezko et al. 2012). To expand screening into potentially many thousands of plants per year, material collection, propagation methods, growth management, and screening must become the focus of efforts to operationalize each step in the process of securing diseases resistant material. The enhanced efficiency and accuracy of screening due to optimization of methods will allow the program to more rapidly grow and screen *Metrosideros* plants, decreasing the overall time to identify and produce ROD-resistant plants to satisfy the urgent needs of the conservation, restoration, and landscaping sectors.

Inoculation methodology

Considered a foundational step in any disease resistance program, the ʻŌDRP is working to optimize an artificial inoculation methodology or set of methodologies. Artificial inoculation methods need to consistently cause infection (low false negative rate) that mimics natural infection to provide useful results (McKenna et al. 2011). Additionally, fine-tuned inoculation methods will allow for more nuanced observation of intermediate levels of disease resistance (Hansen et al. 2012, Sniezko et al. 2014, 2020).

Testing different inoculation methods and continuously improving upon them as new data become available ensures that resistance responses like those expressed under field conditions are consistently produced. To date, several inoculation methods have been tested separately using *C. lukuohia* isolates: (1) colonized agar chunks, (2) inoculated grains of brown rice, (3) soil drench with a spore suspension (L. Sugiyama pers comm), (4) stem inoculation with liquid spore suspensions (B. Luiz pers comm), (5) agar slurry (Hughes et al. 2020), and (6) inoculated filter paper disks (Keith et al. 2015). The filter paper disk method has been the only artificial inoculation method to consistently produce disease symptoms under constant growth chamber conditions and is the current standard for inoculations. Using this method, wilting occurs on 1- to 2-year-old plants in as little as 2 to 4 weeks post-inoculation under constant conditions in a growth chamber (Keith et al. 2015, Brill et al 2019, Luiz et al. 2020).

Despite a high degree of success with the filter paper disk method, our initial comparisons of inoculation method efficacy relied upon small sample sizes, focused on *C. lukuohia*, and used young plants, all of which point to a need for more robust testing. Thus, an expanded set of plants capturing a wider range of varieties, sizes, and genotypes is needed. The ʻŌDRP will be comparing inoculation methods using hundreds of ʻōhiʻa individuals to compare different inoculation techniques and concentrations, with the goal of optimizing and operationalizing mass screening of ʻōhiʻa.

Within the context of these inoculation trials, the ʻŌDRP will also examine the effects of temperature and season on infection rates and disease progression to inform optimal timing for inoculating and experiment duration. This information is vital for fine-tuning screening methods and avoiding experiments that are too short to distinguish types of resistance or capture intermediate levels of resistance (Sniezko et al. 2020). In vitro experiments of *C. lukuohia* cultures demonstrate that mycelial growth and sporulation are optimal at 25 °C and quickly diminish at temperatures $\leq$ 20 °C or $\geq$ 35 °C (Luiz and Keith 2020). There is a possibility that these growth and sporulation patterns are similar once the pathogen has infected host tissues. While seasonal temperature change in Hawaiʻi is mild, average temperature can fluctuate in a greenhouse or field environment by season, prevailing weather, and elevation, possibly affecting plant responses to inoculation (Hughes et al. 2020). Additionally, factors such as plant age and size (Hu and Yang 2019), branch architecture (Costes et al. 2013), and mechanical stress (Ishihara et al. 2021) have been shown to affect disease resistance responses in woody plant species and will be explored to identify optimal parameters for inoculations.

Operationalizing propagation and culture of *M. polymorpha*

The current minimum size requirement for *M. polymorpha* plants to be inoculated is a 6 mm stem diameter, as this diameter allows a stem wound to be made easily with a scalpel and reduces the chance of adverse effects due to wounding. Most viable seeds germinate within 4–6 weeks; however, *M. polymorpha* stem diameter increases at a rate of

1–3 mm annually under optimal conditions (Friday and Herbert 2006), so seedlings can take roughly 2 years to obtain the minimum 6 mm stem diameter required for the filter paper disk method. Previous studies on *M. polymorpha* have focused on the effects of irrigation type (subirrigation vs. overhead), fertilizers, temperature, and light levels on *M. polymorpha* seedling growth and survivorship (Dumroese et al. 2006; Morrison and Stacy 2014; Sakishima 2015), and these studies, along with input from native plant nurseries in Hawai‘i, have shaped the ‘ŌDRP’s ‘ōhi‘a growing methods. Experiments comparing container types and sizes are being established using *M. polymorpha* seed families, as similar studies with *Acacia koa,* another Hawai‘i native forest tree, have found that seedling growth rate increased as container volume increased (Dumroese et al. 2011; Jacobs et al. 2020). In theory, seedling production can be scaled up quickly, be readily available for all populations and varieties, and provide key information on level and inheritance of resistance. Seedlings will be the bulk of the material tested by the ‘ŌDRP, so optimizing *M. polymorpha* seedling growth will reduce the time required to produce plant material and increase screening efficiency.

M. polymorpha can also be propagated through vegetative cuttings (Rauch et al. 1997), which has several advantages over propagation by seeds including: the ability to acquire multiple copies of identical genotypes, much shorter time to reach target size, and relative ease of propagation due to year-round access to vegetative material. However, rooting success varies widely by mother tree (Bornhorst and Rauch 1994; Hughes and Smith 2014), with cuttings from cultivated trees most likely having higher rooting success than trees in the wild. The effects of indole-3-butyric acid concentrations on rooted cuttings has been studied on easy-to-root *M. polymorpha* using a single hormone product (Rauch et al. 1997). However, a direct comparison of rooting hormone products and potting media has not been published. Both factors have been found to significantly affect rooting success of other woody angiosperms (Pijut 2004; Antwi-Boasiako and Enninful 2011; Mabizela et al. 2017), and an experiment to study their effects on rooting success of *M. polymorpha* cuttings is being established. This propagation method is particularly useful for obtaining clonal material of promising trees for disease resistance, such as survivors in areas heavily impacted by ROD, and further refinement of this method could improve overall rooting success of cuttings taken from trees in the field that may be hard to root.

Resistance screening of survivor *M. polymorpha* trees

As previously mentioned, asymptomatic survivor trees may be found in ‘ōhi‘a stands severly impacted by ROD. These remnant live trees represent potential survivors and, therefore, are prime candidates to focus screening efforts (Pike et al. 2021). Curiously, there are instances of lightly impacted stands of *M. polymorpha* near these high-mortality stands. These adjacent, lightly impacted stands serve two important functions: they serve as a control for studying survivor trees in high-mortality sites and, in light of their proximity to areas with high disease pressure, may be largely comprised of disease resistant trees. Screening seedlings and cuttings from these trees together will allow us to distinguish if they are alive because they are resistant to *Ceratocystis* infection or because they were not infected by either pathogen (escapes) and will eventually become infected. Currently, the program is sampling four different forest sites in the Hilo and Puna Districts of Hawai‘i Island with the appropriate conditions to form paired plots within each site: one with low ROD-induced mortality ($\leq 20\%$ of stems) and one with high mortality ($\geq 80\%$ of stems).

Cuttings and seeds are being collected from trees in these sites, with the goal of screening the resulting plants for *C. lukuohia* and *C. huliohia*. This study will be the first to assess the susceptibility of naturally occurring survivor *M. polymorpha* in heavily ROD-impacted areas.

Remote sensing and pre-screening of survivor trees

Previous efforts, supported by U.S. Forest Service Region 5 and the State of Hawaiʻi, combined leaf and airborne spectroscopy with measurements of canopy chemical (i.e. water, nitrogen, non-structural carbohydrate, phenols) concentrations from ʻōhiʻa foliage to develop spectral-chemical signatures (Asner et al. 2018) that were used to map individual tree crowns exhibiting symptoms of active (brown/desiccated ʻōhiʻa crowns) and past (leafless tree crowns) wilt, most likely due to ROD, across Hawaiʻi Island (Vaughn et al. 2018). Combined, these data provided the first landscape-scale, spatially explicit maps of probable ROD for managers. Documentation of ROD presence using these geospatial tools will satisfy the growing need to identify how quickly the pathogens are spreading and quantify resistance in ROD-impacted landscapes.

The search for survivor trees represents a critical bottleneck in the resistance-screening process, as ground-based surveillance requires a significant time investment by field crews. To alleviate this bottleneck, we are using unmanned aerial system technology (drones) to identify potential survivor trees in *M. polymorpha* forests in the Hilo and Puna districts of Hawaiʻi Island for disease resistance screening. Additionally, we are developing remote sensing methodologies (lidar and hyperspectral imagery) to identify ROD-resistant ʻōhiʻa trees. The goal of this work is to develop a spectral-chemical indicator of ROD resistance using a comparative time-series analysis of spectral-chemical signatures in ʻōhiʻa foliage from ROD-resistant ʻōhiʻa versus escapes. Successful results will accelerate identification of survivor trees by remotely pre-screening candidate survivor trees, allowing for targeted field sampling of trees with the spectral-chemical signature that corresponds to ROD resistance.

Statewide *Metrosideros* screening

Ceratocystis lukuohia and C. huliohia have only been reported on *M. polymorpha*, and most of the pathology work thus far has been conducted on Hawaiʻi Island *M. polymorpha* varieties. Little is known about the susceptibility of other Hawaiian *Metrosideros* taxa, but this knowledge is important for protecting the remaining native forests throughout the state. Therefore, an exploratory screening study is underway for seedlings from endemic Kauaʻi and Oʻahu *Metrosideros*. Four seed families of both *M. polymorpha* var. *dieteri* and *M. waialealae* var. *waialealae* from Kauaʻi were provided by the National Tropical Botanical Garden and sown in 2018. Seeds from *M. rugosa*, *M. macropus*, *M. tremuloides*, and *M. polymorpha* var. *incana*, var. *glaberrima*, and var. *polymorpha* from Oʻahu were provided by the University of Hawaiʻi Lyon Arboretum and the Hawaiʻi Department of Forestry and Wildlife, and sown in late 2019. Screening these initial accessions from Kauaʻi and Oʻahu will provide a first look at whether native *Metrosideros* other than *M. polymorpha* are susceptible to infection by either *C. lukuohia* or *C. huliohia* and guide our larger disease screening experiments in the future.

The ROD Seed Banking Initiative was established to collect and store *Metrosideros* seeds from naturally occurring trees throughout Hawai‘i, with the goal of preserving the genetic diversity of these taxa for restoration and disease research efforts (Chau 2020). Provisional seed zones were established based on climatic and environmental parameters, providing the foundation for a collection strategy in this large, multi-agency initiative (Chau 2020; Laukahi 2020). Representative seed samples from populations across the islands will be screened for resistance to ROD, with the seed bank providing the ‘ŌDRP easy access to seeds from a diverse set of *Metrosideros* taxa and genotypes. The plan is to grow and test seedlings from three seed families of each *Metrosideros* taxon per seed zone in which the taxon occurs. Due to constraints in growing and screening space, families from seed zones that are highly threatened by ROD will be prioritized (Fig. 3).

Resistance testing in the field

Greenhouse trials provide important baseline insights into genotypic variation in disease resistance and are necessary for quickly screening out families that are highly susceptible, which are likely to be the majority of families that are tested. However, greenhouse trials will use young plants (2–3 years old) and artificial conditions for inoculating and

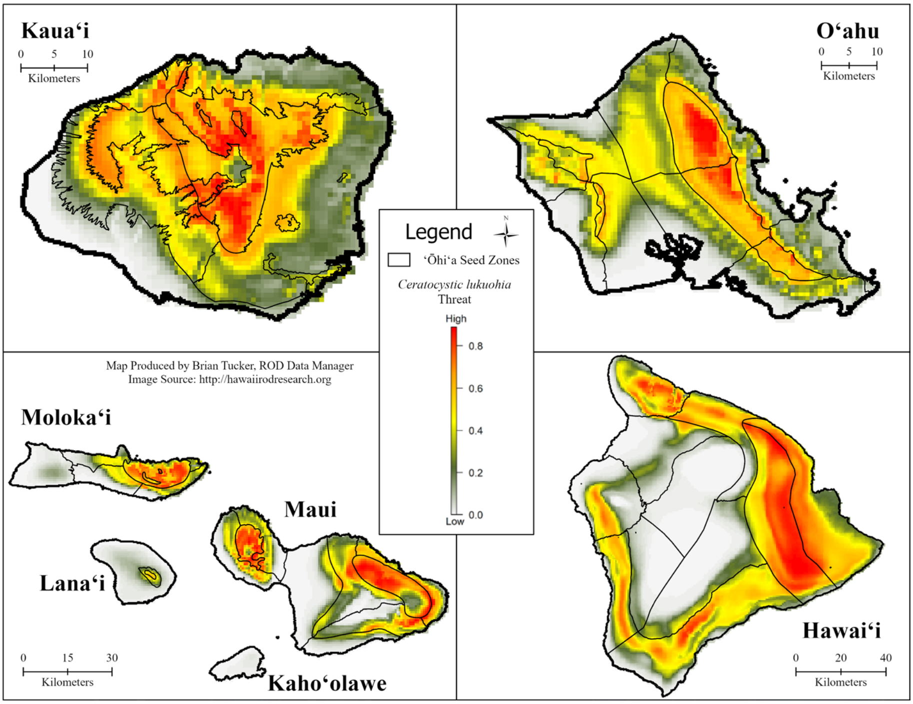

Fig. 3 The threat of *Ceratocystis lukuohia* is geographically variable, with middle elevation, windward *Metrosideros polymorpha* seed zones (delimited by black lines) predicted to be most vulnerable to *C. lukuohia* (based on threat models constructed by Fortini et al. 2019). *C. lukuohia* threat level data provided by hawaiirodresearch.org. Seed zone shapefiles created and provided by Ben Nyberg, Seana Walsh, Dustin Wolkis, Adam Williams (Kaua‘i), and Alex Loomis (all other islands)

monitoring these individuals, which may not accurately represent how disease resistance will manifest under field conditions. For this reason, the ʻŌDRP will initiate field trials for Stage II screening with the goal of further testing less susceptible genotypes identified during Stage I screenings. Stage II screening will be necessary for examining the durability of resistance potentially present in candidate plants (Dudley et al. 2017; Sniezko and Koch 2017), which is the effectiveness of resistance over time and space in the presence of a potentially evolving pathogen (REX Consortium 2016; Sniezko and Koch 2017). ʻŌhiʻa is a long-lived tree species, so the type of resistance present, whether resistance genes are expressed more strongly at particular life stages of the host (i.e. adult plant resistance), and the evolutionary potential of the pathogen will have an impact on the potential durability of resistance (McDonald and Linde 2002).

ʻŌhiʻa is a long-lived tree species, so the type of resistance present, such as adult plant resistance, and the potential for pathogens to evolve and overcome it may impact it's durability (MacDonald and Linde 2002). Different modes of infection can be evaluated in field trials that include: (1) natural infection, i.e. pathogen introduced via inoculum present on the site that infects naturally occurring wounds, (2) intentional wounding to provide a suitable infection court for infection by inoculum present on the site, and (3) using laboratory produced inoculum of *Ceratocystis* applied to artificial wounds. Each has benefits, requirements, and method-specific monitoring requirements. For designs 1 and 2, field sites will be located where ROD occurrence is high to improve the chances of planted trees being challenged by the pathogens. This criterion will be applied to some extent to 3, as we will not introduce the disease to a location that is free of ROD. Designs 1 and 2 will be useful for testing resistance under pressure from naturally occurring inoculum but may take decades to adequately assess. In the instance of 1, and 2 to a lesser extent, escapes would be difficult to distinguish from truly resistant trees without destructive sampling of wood tissues.

There are diverse considerations for the establishment of field trial sites. *M. polymorpha* varieties occur across a wide range of climatic and edaphic conditions, from desert to sub-alpine and from newly formed lava substrates to Hawaiʻi's oldest soils (Cornwell et al. 2007; Fisher et al. 2007; Martin and Asner 2009; Morrison and Stacy 2014; Ekar et al. 2019; Stacy et al. 2020; Barton et al. 2020; Stacy and Johnson 2021). The ʻŌDRP will consider the likelihood of genetic differences among populations found along these gradients. Due to the vast habitat range of the species, resource managers and conservation biologists prefer to outplant trees following geographic considerations, where *M. polymorpha* for any field trials or for restoration are derived from local populations. For this reason, the ʻŌDRP will identify a range of field sites for the establishment of disease resistance field trials, and to the extent possible, rely on local seeds or cuttings from local plants. There are clearly complications to this strategy, including the need to avoid introducing ROD to new areas of *M. polymorpha* habitat range where ROD is not yet found. The proposed site selection approach is different than that taken for field trials evaluating koa resistance to *Fusarium oxysporum*. Specifically, the koa pathogen appears to be ubiquitous across the lower elevation areas of koa's range on Hawaiʻi Island, Maui, Oʻahu, and Kauaʻi, while the *Ceratocystis* species responsible for ROD still have a fairly limited range in the Hawaiian archipelago.

Stage II ʻŌDRP screenings of the will rely on seed zone-based strategies that account for environmental variation found across *M. polymorpha* range, with the restriction that field trial sites need to be established across Hawaiʻi Island and on other islands only where *C. lukuohia* and/or *C. huliohia* are already present. Because some islands are currently and hopefully will remain ROD free, testing *M. polymorpha* genotypes, and other *Metrosideros* taxa, from those islands will require finding climatically and edaphically representative field sites on a different island to ascertain whether disease resistance will be maintained under site-specific conditions (Dudley et al. 2017; Sniezko and Koch 2017). Collaborating with governmental and non-governmental land managers will be vital for finding and securing access to appropriate field sites.

Establishment of seed orchards

Demand for ROD-resistant *M. polymorpha* (and other *Metrosideros* taxa) is high amongst ʻŌDRP partners, conservation organizations, and resource managers, so the ʻŌDRP must assess the size of the need, anticipate its future growth, and develop a program for producing seeds and rooted cuttings for widespread use. Fortunately, a single ʻōhiʻa tree can produce hundreds of thousands of seeds in a single season, and is highly compatible with a seed orchard-based approach to meeting demand. A seed orchard is a stand of disease-resistant trees planted with the goal of producing seeds that inherit the resistance phenotype while promoting genetic diversity of resulting offspring through cross-pollination between genetically different parent trees (Koch and Heyd 2013). The resulting genetic variability will be key for maintaining long-term disease resistance and improve the resiliency of forests comprised of these offspring (Telford et al. 2015). If these two criteria are met, then a network of seed orchards will be established to provide the first round of ROD-resistant seeds for restoration.

Site selection for seed orchards will need to consider appropriate pairing of environmental conditions and climate to *Metrosideros* taxa. Ideally, seed orchards would be established in the same seed zone that they were collected from and provide seeds for their respective regions, like establishment of seed orchards for wilt-resistant koa (Dudley et al. 2017; 2020). Establishment of seed orchards, from local seed sources when possible, on most of the islands in the state would be an important tool for supplying local restoration efforts. One challenge will be selecting the appropriate sites for seed orchards throughout the state. Sites would, ideally, be eco-region specific and easily accessible by the entities maintaining them. On Maui, for instance, seed orchards for ROD-resistant *Metrosideros* will be planted in the same sites where current wilt-resistant koa seed orchards sites exist. A second challenge lies in providing the propagative material to start these localized orchards. A permanent quarantine banning the movement of *Metrosideros* plants, plant parts, and soil from a ROD-infested island to a ROD-free island has been in effect since 2016. These materials can be transported under permit provided by the Hawaiʻi Department of Agriculture, but requires the material be free of ROD based on a destructive diagnostic qPCR test (Heller and Keith 2018). Since all disease screening work will be done in areas where ROD is present, permits will need to be obtained to send any propagative material, most likely seeds.

While seeds produced by initial ROD-resistant selections will satisfy the immediate need for resistant ʻōhiʻa in native forest restoration, selective breeding of the most resistant families and successive breeding of those progeny can improve resistance (Carson and Carson 1989; Sniezko et al. 2012). If only partial resistance exists, recurrent selection of individuals that show the highest levels of resistance could produce offspring with similarly high levels of resistance at a higher frequency. If multiple resistance mechanisms occur and are heritable, trees containing these mechanisms could be selectively bred to form progeny with combinations of the various disease resistance genes, known as pyramiding, to produce resistance with a higher likelihood of being durable (REX Consortium 2016). The establishment of seed orchards will allow the ‘ŌDRP to explore these potential avenues of selective breeding to produce highly durable ROD-resistant seeds that will persist in the landscape for decades.

For resistance characteristics that can be detected via remote sensing data, including morphophysiological differences and any spectral-chemical indicators that may exist, high-throughput phenotyping of the seed orchard plantings will be attempted via repeat collection of high-resolution imagery using aerial and ground-based sensors (Aasen et al. 2020; Singh et al. 2020). Imagery-based phenotyping is becoming widely adopted in agricultural and agroforestry settings (Ludovisi et al. 2017; Yang et al. 2017; Tsouros et al. 2019; Rallo et al. 2020) and is increasingly being used in forestry and conservation (Santini et al. 2019; Camarretta et al. 2020).

Understanding mechanisms of ROD resistance

Disease resistance is a biological arms race where pathogens and host defenses are constantly coevolving to overcome each other (McDonald and Linde 2002; Anderson et al. 2010). Understanding the genetic basis and host defense mechanisms in a given pathosystem can aid in the development of potentially durable, long-lasting resistance (Carson and Carson 1989). Host resistance to disease can manifest in the form of major gene resistance (MGR), often conferred by a single dominant gene, or quantitative disease resistance (QDR), resistance conferred by multiple genes (Woodcock et al. 2018; Sniezko et al. 2020). MGR confers complete resistance to a disease, but when it is overcome by a pathogen, all of the previously resistant individuals become susceptible (Kinloch et al. 2004). QDR confers partial resistance to a disease and is harder for a pathogen to overcome. These types of resistance are not exclusive; it is possible for a host to express both MGR and QDR (Vigoroux and Olivier 2004; Sniezko et al. 2014, 2020). A common resistance mechanism in *Ceratocystis* pathosystems generally involves the occlusion of the pathogen within the xylem by the rapid production of tyloses, phenolic compounds, and other defense compounds, as seen in resistance responses of mango (*Mangifera indica* L.; Araujo et al. 2014a; Araujo et al. 2014b) and *Eucalyptus urophylla* × *E. grandis* hybrids (Silva et al. 2020) to *Ceratocystis fimbriata* infection. In both cases, resistance is polygenic and thus, QDR (Rosado et al. 2010; Arriel et al. 2016). Host anatomical factors such as xylem architecture has also been associated with resistance to vascular wilt diseases like Dutch elm disease and Esca disease of grapevines, where smaller xylem vessels dimensions were linked to quicker and more complete host xylem occlusion (Solla and Gil 2002; Pouzoulet et al. 2014). In ‘ōhi‘a, higher elevation populations were shown to contain smaller vessel diameters (Fisher et al. 2007), which, coupled with cooler temperatures associated with decreased fungal growth (Luiz and Keith 2020), may be associated with the less aggressive expansion of ROD seen in high elevation sites. Further research is planned to investigate the potential associations between climate, ‘ōhi‘a xylem architecture, and susceptibility to *C. lukuohia*.

Once ROD-resistant *M. polymorpha* are discovered and the groundwork has been laid to satisfy initial stakeholder needs for trees that are resistant to ROD, research into the genetic basis of ROD resistance can be conducted to improve breeding efforts. Several methods for identifying trait-related loci, such as linkage mapping, linkage-disequilibrium mapping, and studying gene expression via transcriptomics, proteomics, and metabolomics can be employed to develop markers for rapid identification of ROD resistance in *M. polymorpha* individuals (Boshier and Buggs 2015). The ability to genetically identify ROD-resistant *M. polymorpha* will speed up the process of a future breeding program and allow us to cull any susceptible progeny without having to grow them to size and inoculate them (Boshier and Buggs 2015).

Production of *M. polymorpha* that are resistant to both *C. lukuohia* and *C. huliohia* is one of the main goals of the ʻŌDRP, since both ROD pathogens are concerning to stakeholders. While trees resistant to a single pathogen could be outplanted, trees resistant to both pathogens will be the most useful and a safer investment for stakeholders, particularly on Kauaʻi and Hawaiʻi Island where both pathogens are present. Thus, resistance mechanisms that are effective against both pathogens will be prioritized for study, breeding, and production. It is possible that resistance to one pathogen does not confer resistance to the other pathogen, and both mechanisms may not be present in the same tree. If this is the case, selective breeding between *C. lukuohia*- and *C. huliohia*-resistant trees would need to be conducted in an attempt to produce progeny that have both resistances in the event that they do not already coexist in the same tree or use the same mechanism.

Community science involvement in resistance research

Community science can be an effective approach for overcoming limitations in program resources while providing opportunities for community education on the ROD pathosystem and inclusion of community members in the protection of their local forests (Ingwell and Preisser 2011; Pike et al. 2021). Community science has been effectively used to augment the activities of several resistance programs, including those for Chestnut blight (Westbrook et al. 2020) and Emerald ash borer (the Monitoring and Managing Ash Program; monitoringash.org). Incorporating community science projects into the ʻŌDRP will be critical for maximizing operational output while building public awareness and support for the program. The ʻŌDRP has already established one community science project with Teaching Change (teaching-change.org), an organization that provides environmental stewardship experiences for public and private school students. This project focuses on teaching students from local schools how to plant ʻōhiʻa seeds and care for them. A portion of the resulting seedlings are donated to the ʻŌDRP for resistance screening, providing an opportunity for students to take part in critical research while increasing the program's inventory of ʻōhiʻa. There is potential to expand the scope of this work to include more volunteers from local communities throughout the state (schools, community associations, environmental organizations) and incorporate them into all aspects of disease research, from identification of potentially resistant trees in the wild to maintenance of ʻōhiʻa seed orchards. These activities take considerable financial and time investments to conduct, but with the help of Hawaiʻi's local communities, the program can achieve greater outcomes than it could achieve on its own.

Overall management strategy for ROD

Developing ROD-resistant ʻōhiʻa is one part of the overall program to save Hawaii's ʻōhiʻa forests. Statewide efforts are under way to control the spread of the pathogen through local quarantines on movement of infected material and increased public education on bio-sanitation for forest users. Tests are also being done on repellants to reduce beetle attack on infected trees and subsequent frass production. Since there is limited ability to control windblown frass, efforts are also being made to reduce injuries to trees that can subsequently become infected. Fencing more pristine forests and removing feral ungulates such as cattle, goats, sheep, and pigs can reduce injury to trees, and fenced and protected forests have shown much lower levels of disease than forests with high populations of feral animals (Perroy et al. 2021). Natural ʻōhiʻa regeneration is occurring at higher elevation forests (above 1,000 m), and seedlings seem less susceptible to the diseases than larger trees (R. F. Hughes pers comm). For most lower elevation forests, natural ʻōhiʻa regeneration is largely absent, likely because of competition with invasive species and the presence of diseases such as *Austropuccinia psidii* (G. Winter) Beenken. Control of invasive plants and replanting with disease-resistant ʻōhiʻa and other native trees could restore limited areas of ecologically important forests and smaller forests managed by private landowners. Ultimately, an integrated pest managment program can be developed by incorporating all of the tools that have been or are currently being developed to combat ROD (ROD-resistant ʻōhiʻa, ambrosia beetle and feral ungulate control methods, ROD education and biosanitation protocols).

Conclusion

Due to the threat that ROD poses to the Hawaiian culture, ecology, and hydrology, there is an urgent need for ROD-resistant ʻōhiʻa. The time to produce such a product relies on the frequency of natural resistance and the ability of the program to capture and develop it. This will be achieved by the core activities of the ʻŌDRP: short-term greenhouse screenings, long-term field screening of survivors from greenhouse experiments, potential breeding of the most resistant individuals to provide seed for restoration, research on the mechanisms responsible for resistance, and the development of technology to rapidly detect ROD-resistant ʻōhiʻa and reduce the need for screenings. All of these objectives can be achieved with the valuable collaboration of entities that is the ʻŌDRP. The support of our work by the local communities of Hawaiʻi and sustained funding will provide the ʻŌDRP with the ability to complete such long-term goals. The existence of *M. polymorpha* seedlings that have survived the initial disease screenings in the greenhouse and survivor trees present in forests where ROD mortality is high provide hope that we may be able to mitigate the effects of ROD through the deployment of ROD-resistant ʻōhiʻa.

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