Integrating Regeneration, Genetic Resistance, and Timing of Intervention for the Long-Term Sustainability of Ecosystems Challenged by Non-Native Pests – a Novel Proactive Approach

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Abstract

Global trade increases the likelihood of introduction of non-native, invasive species which can threaten native species and their associated ecosystems. This has led to significant impacts to forested landscapes, including extensive tree mortality, shifts in ecosystem composition, and vulnerabilities to other stresses. With the increased appreciation of the importance of healthy ecosystems for watershed protection, wildlife habitat, and aesthetics, we present a new management approach specifically designed for the long-term sustainability of ecosystems challenged by non-native pests for continued non-timber ecosystem services. Sustaining host population resilience in the presence of a non-native pest requires maintenance of the population's recovery capacity after disturbance, adaptive capacity over time, and multi-generational persistence. Therefore, the management approach must incorporate a long-term and evolutionary perspective which also incorporates continued adaptation to climate change. Management to promote self-sustaining host populations to support ecosystem processes and services can be implemented (1) in degraded ecosystems as reactive restoration management or (2) in threatened ecosystems not yet impacted as proactive intervention. When threatened ecosystems can be identified, we can choose to act proactively by gathering baseline genetic and ecological characteristics of the species and ecosystems to design timely interventions to increase resilience. Such a proactive approach herein referred to as the Proactive Strategy, can be contemplated for any threat that is anticipated to impact critical ecosystems. In this paper, we use the white pine blister rust – high elevation pine pathosystem as an example application. Genetic resistance is an essential management tool for both restoration and proactive management, yet the Proactive Strategy can also manipulate the timing of (1) resistance deployment and (2) landscape management of the mosaic of stand age class structures. These two additional tools provide further opportunities to sustain the host population and genetic diversity and mitigate the development of impacts over time. Populations having little disease resistance may need to be enhanced by direct planting. However, in other cases, manipulation of the age-class structure of stands across the landscape in populations in which heritable resistance is present at high enough frequency, can facilitate selection and accelerate the evolution of resistance after the pathogen eventually invades. Therefore, management that generates a mosaic of patches of different stand ages across a landscape can effectively generate patches with different rates of selection upon white pine blister rust invasion, thereby mitigating the effect of mortality in any one cohort or stand on overall ecosystem function of the greater landscape. Positioning ecosystems for greater resilience before invasion may avert impaired ecosystem conditions after invasion, when ecosystem services would be compromised, and reduce the need for later restoration. Regeneration is a stabilizing factor in populations; how and when it is managed in coordination with gene frequencies for resistance will play an important role in the establishment of a new sustainable condition for the host population and its ecosystems in the presence of a non-native pest.

Key words: genetic resistance, disease impacts, proactive strategy, *Cronartium ribicola*, invasive species

Proactive vs. Reactive Strategy

Global trade increases the likelihood of introduction of non-native, invasive species which can threaten native species and their associated ecosystems. This has led to significant forested landscape

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impacts, including extensive tree mortality, shifts in ecosystem composition, and vulnerabilities to other stresses.

Until recently, the use of genetic resistance to mitigate disease impacts in forest trees was focused primarily on plantation species, principally because of their obvious economic importance and the cost involved. However, as invasive species continue to decimate ecosystems beyond the traditionally managed forests, there is now an ever-increasing appreciation of the importance of sustaining healthy ecosystems that provide services such as snow capture, watershed protection, wildlife habitat, and aesthetics. As with the plantation species, there will be a cost involved, but we suggest that in some cases, it may be time to consider novel approaches specifically designed for the long-term sustainability of ecosystems challenged by non-native pests for continued non-timber ecosystem services. We present a proactive strategy that offers options for addressing a potential problem early and focuses on sustaining healthy ecosystems in the presence of an invasive species.

In some cases, non-native species spread slowly enough through a host species range to allow early-affected ecosystems to be studied and to identify threatened, but not-yet-impacted, ecosystems. For threatened ecosystems, we have a choice between acting proactively to increase resilience of the threatened ecosystem or waiting until it is degraded before doing restoration management (fig. 1). If ecosystems have been invaded and are already heavily impacted by a non-native species, the Restoration Strategy pathway (upper pathway, fig. 1) is the only option for restoring ecosystem function. In ecosystems threatened, but not yet heavily impacted by a non-native species, the Proactive Strategy (lower pathway, fig. 1) can be followed to minimize impaired ecosystem conditions and sustain ecosystem function during naturalization of the pest.

Both approaches have uncertainty. While genetic resistance is an essential management tool for both, the Proactive Strategy can also manipulate the timing of resistance deployment and the mosaic of stand age-class structures across the landscape to utilize natural processes to further support resilience over time. These two additional tools provide further opportunities to sustain populations and genetic diversity and mitigate the development of impacts over time (Schoettle and Sniezko 2007). Additional opportunities of the Proactive Strategy include (1) gathering baseline genetic and ecological characteristics of the species and intact ecosystems, including the frequency of resistance to the non-native invader; (2) minimizing genetic bottlenecks through gene conservation and management efforts; (3) timing interventions relative to invasion for optimal benefit; and (4) manipulating natural processes to promote further intervention effectiveness.

Proactive Strategy approaches can be developed for many ecosystems challenged by invasive organisms, climate change, or other anthropogenic stress. For the purposes of this paper, the discussion will focus on its application to invasions by *Cronartium ribicola*, the non-native pathogen that causes white pine blister rust (WPBR), in North American five-needle pine (Family Pinaceae, Genus *Pinus*, Subgenus *Strobus*) ecosystems. The fungus was introduced to North America in the early 1900s and continues to spread. All of the North American five-needle pines have at least low frequencies of genetic resistance, yet high mortality is unavoidable (Sniezko et al. 2011a). The southern Rocky Mountains and Great Basin are currently at the expansion front for WPBR in the western United States. These landscapes are susceptible to invasion, and microclimate analyses suggest that invasion of the pathogen over time is inevitable (Howell et al. 2006). This paper provides an overview of some of the key elements of the Strategy and highlights some measures currently being implemented (e.g. gene conservation, screening seedling progenies for genetic resistance, stand dynamics studies, and modeling) as an integrated program in the southern Rocky Mountains.

The rust disease has caused high mortality in five-needle pine species in the northern Rocky Mountains (Tomback and Achuff 2010). The western white pine (*Pinus monticola* Douglas ex D. Don) timber industry collapsed and the incidence of this species is now a small fraction of its historic occurrence (Fins et al. 2001). As a consequence of WPBR, mountain pine beetle, and climate change pressures, whitebark pine (*Pinus albicaulis* Engelm.), a non-timber species, has recently been listed as a candidate species for endangered status under the Endangered Species Act in the United States, and is listed along with limber pine (*Pinus flexilis* James) as Endangered under the Alberta Wildlife Act in Canada. With early intervention, we can position the threatened populations of five-needle pines so that they do not follow the same trajectory as whitebark pine.

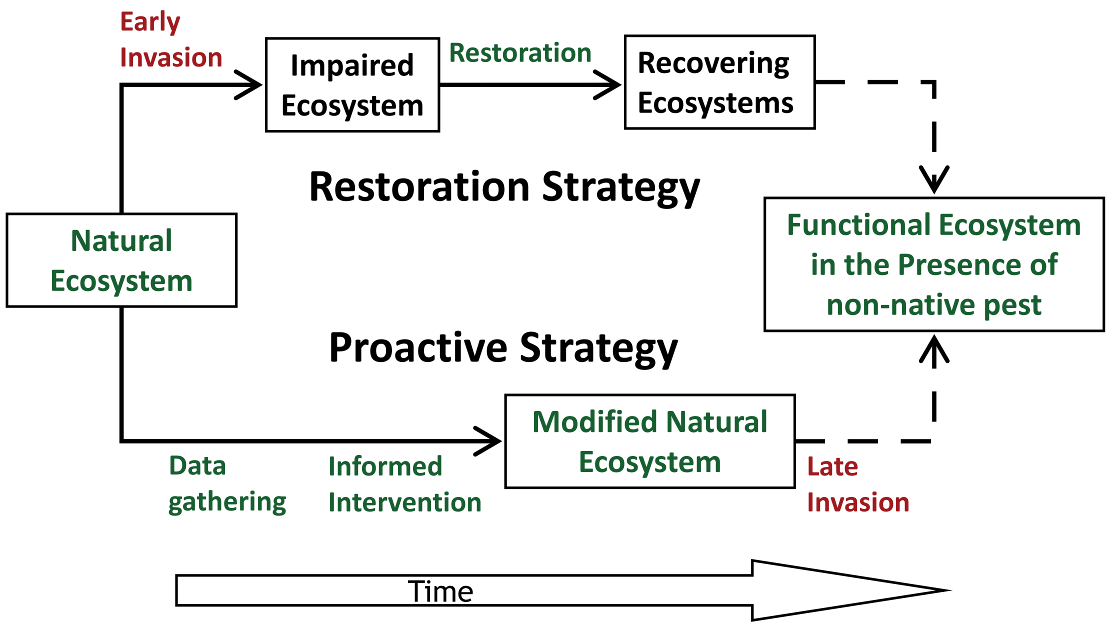

Figure 1—A schematic of pathways for facilitating transitions from native ecosystems threatened by a non-native species to functional ecosystems where the invader is present.

Shifting to an Evolutionary Perspective

Historically, the context for management of genetic resources to mitigate disease impacts has been plantation forestry. However, the management goals for non-timber species differ from those for species for extracting timber resources. Restoration efforts for timber species focus primarily on managing tree growth to merchantable size and are supported by intensive resistance breeding programs (e.g., Kearns et al. 2012, Schwandt et al. 2010). Five-needle pines that are not timber resources, but are important components of natural ecosystems, such as whitebark, limber, and Rocky Mountain bristlecone (*Pinus aristata* Engelm.) pines, and in some areas western white pine, provide ecosystem services (e.g., watershed protection and wildlife habitat) that depend not just on the health of the pines, but the overall ecosystem (Schoettle 2004, Tomback and Achuff 2010). These pines and their ecosystems are traditionally not managed and are in remote, high-elevation areas, including wilderness. They are also considered foundation and keystone species and are often the only tree species that can tolerate the extreme environmental conditions at treeline. As a consequence, other species are not available to replace the trees' ecological functions, should the five-needle pines be lost from the ecosystem (Tomback et al. 2011). The management goal for these ecosystems is promotion of self-sustaining pine populations in the presence of WPBR and other stresses to support ecosystems processes and services (Keane and Schoettle 2011, Schoettle and Sniezko 2007). Therefore, success is evaluated on multi-generation outcomes of the treated landscape in contrast to the stand-based, generation-by-generation, outcomes for plantation forestry.

Sustaining population resilience requires maintenance of populations' (1) recovery capacity after disturbance, (2) genetic diversity to support adaptive capacity over time, and (3) multi-generational persistence. Therefore, the management approach must incorporate a long-term and evolutionary perspective which also incorporates adaptation to climate change. Maintaining a functioning regeneration cycle is essential as it is the engine that supports post-disturbance recovery and enables selected traits to accumulate within populations (fig. 2 – solid narrow arrows). Unfortunately for the high-elevation, non-timber five-needle pines, generation time is very long. The species are not prolific seed producers and establishment of seedlings after disturbance is protracted in the harsh high-elevation habitats and is constrained by competition by other species on more moderate sites (e.g., Coop and Schoettle 2009). Once established, high-elevation five-needle pine seedlings mature very slowly and only begin to produce full cone crops after 100 years under natural conditions. The mature trees can be long-lived, commonly reaching ages of 1,000 years. These species are tolerant of stresses under which they have evolved, but are not well equipped, without additional regeneration opportunities, for rapid adaptation to novel stresses such as those imposed by the introduction of *C. ribicola* in a changing climate.

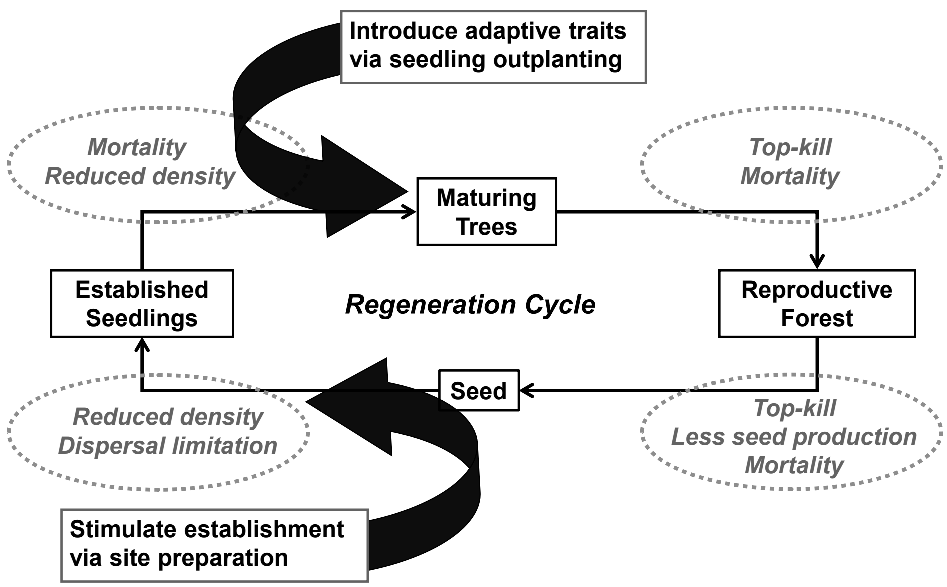

Figure 2—Flow diagram of the forest regeneration cycle and the points of interaction with white pine blister rust and management. White pine blister rust can cause impacts (ovals) at all life stage. Broad arrows depict intervention options for increasing blister rust resistance and population resiliency. (Redrawn from Schoettle et al. 2009)

Managing Host Demography to Offset Disease-Caused Mortality

In some cases, the regeneration cycle can be managed to increase the resilience of the host population to mortality from non-native disease even without genetic disease resistance. *Cronartium ribicola* impacts the regeneration cycle of the pines at each life stage; rapidly killing young seedlings, reducing cone production in infected mature trees, and later causing mature tree mortality (fig. 2 – ovals) (Schoettle and Sniezko 2007). At locations where infection is high, the number of survivors may be insufficient to sustain populations. Maintaining a functioning regeneration cycle requires trees from multiple age classes distributed across landscapes.

Using a population infection model parameterized for high–elevation, five-needle pines and WPBR, Field et al. (2012) reveal that pine populations with high seedling recruitment are sustainable under moderate levels of WPBR infection (table 1). In contrast, in a situation where regeneration is suppressed by inter-specific competition, the model predicts that WPBR-caused mortality and inter-specific competition further depress regeneration and the population enters a downward spiral. Alternatively, if regeneration is stimulated by removing inter-specific competing trees prior to rust invasion, the population remains sustainable under the same infection conditions. The greater the regeneration capacity of a population, the greater is its recovery ability and tolerance of the population to mortality under moderate disease pressure. Therefore, management to promote regeneration in low to moderate rust hazard sites will contribute to populations' resilience upon *C. ribicola* invasion (fig. 2 – lower broad arrow). Under conditions of greater infection, regeneration can slow, but not offset, population decline (table 1). These model runs are conservative as they do not include other important disturbance agents such as bark beetles that further compromise the population and impose demographic imbalances by selectively reducing mature cohorts at their peak of fecundity.

Table 1—Model predictions of population projections for three high-elevation, five-needle pine populations[a]

Competition	Zero Infection Probability		Mod. Infection Probability		High Infection Probability	
	MA	TotPop	MA	TotPop	MA	TotPop
None	354	624	171	815	70	165
High	200	354	59	145	38	60
High → Low	404	472	176	746	42	99

[a] The initial stage structure for the no inter-specific competition and high inter-specific competition are at equilibrium densities (trees per hectare at zero infection probability) and the initial conditions for the high to low competition condition are equilibrium five-needle pine densities with inter-specific competition and then competitors are removed at time zero. White pine blister rust is introduced (except for the "zero infection probability" case) at time zero, and projections are for 200 years. The density (per hectare) predictions include mature adults (MA), total population (TotPop) at 200 years. See Field et al. (2012) for more details. Data adapted from Field et al. (2012).

The ability of a population to respond to site manipulation for increased seedling establishment is time dependent in the rust-pine pathosystem. Because WPBR kills trees of all ages, and therefore directly impacts the pine regeneration cycle, intervention to increase seedling establishment is best accomplished before or during the early stages of WPBR invasion. Attempts to stimulate regeneration in whitebark pine forests heavily impacted by WPBR have failed to produce established seedlings, even after more than a decade (Keane and Parsons 2010). Therefore, this intervention option is a tool unique to the Proactive Strategy.

The model suggests that management of regeneration can favorably affect the outcome of a population under low to moderate rust hazard conditions. We know regeneration capacity varies among habitats (Coop and Schoettle 2009). Integrating this understanding into risk and hazard models can provide further guidance for the spatial design and prioritization of treatment areas and improved outcome projections. Regeneration capacity information can be gained through field surveys and studies of healthy ecosystems and is much more difficult to ascertain in ecosystems already impaired by disease.

Managing the Regeneration Cycle for Increased Disease Resistance

Due to the harsh sites that high-elevation, five-needle pines occupy, protracted regeneration dynamics on those sites, and persistence of introduced pathogens, management of demographic structure and distribution alone will not sustain all pine populations in the presence of WPBR. Reducing the effect of disease on survival and fecundity by increasing heritable disease resistance is essential to sustaining many of these populations and ecosystems services. Fortunately, some level of natural genetic resistance to this non-native pathogen is present in each North American five-needle pine species, and many trials are underway to discern geographic patterns of resistance and identify parent trees and populations for protection and from which seed collections can be made (Schoettle et al. 2011b; Sniezko et al. 2007, 2011a). Ultimately, we need to increase the frequencies of resistance genes over landscapes to help establish a new equilibrium from which pine species and associated ecosystems will have the best opportunity to exist and function in the face of the permanent residence of *C. ribicola*. We can also learn from studying ecosystems where the disease is native. Resistance, life history traits and disturbance dynamics of white pine species that have co-evolved with *C. ribicola*, such as in Russia and other parts of Asia, provide optimism as well as insights into possible equilibrium population outcomes for North American species.

Early deployment of genetic resistance through artificial regeneration and stimulating natural regeneration to facilitate selection of genetic resistance are key tools for preparing a threatened landscape for invasion (Schoettle and Sniezko 2007). The natural frequency of resistance will determine if supplemental resistance is required through outplanting (fig. 2 – upper broad arrow) or if the natural frequency of resistance can be increased sufficiently via natural regeneration (fig. 2 – lower broad arrow).

Benefits of Estimating Baseline Resistance Frequencies

Estimates of disease resistance frequencies and their geographic distributions in threatened native pine populations provide valuable information for designing, prioritizing, and evaluating proactive management options. Similar to assessing variation in regeneration capacity, estimating the frequencies of disease resistance in the host populations is best accomplished in non-invaded populations where sampling is not biased by disease-caused tree mortality or reduced cone production. Likewise, collections of seed, pollen, buds/scion, and DNA in intact ecosystems offer opportunities for gene conservation of the full genetic diversity of the host before it is reduced by the disease.

Information on resistance mechanisms and their frequencies helps identify the populations that are least and most susceptible to disease-caused mortality. For example, the proportion of seedlings from different seedlots collected from healthy populations of Rocky Mountain bristlecone pine that were disease-free 3 years after heavy artificial inoculation with *C. ribicola* ranged from 17 to 60 percent, demonstrating both high levels of natural resistance and high variability across the range of this host species (Schoettle et al. 2011b). In combination with mapping disease risk and regeneration potential of the site, the types and geographic distribution of genetic resistance can be used to prioritize and implement proactive management options (Schoettle et al. 2011a). North American white pine species show a number of types of resistance to WPBR (Hoff and McDonald 1980, Kegley and Sniezko 2004, Kinloch and Davis 1996, Kinloch and Dupper 2002, Kinloch et al. 2003, Sniezko and Kegley 2003, Sniezko et al. 2007, 2008). Early identification of areas with simply-inherited resistance mechanisms (e.g., R genes) versus those with complex polygenic inheritance also offers insight into resistance durability which should be included in management planning.

Supplementing Resistance Through Artificial Regeneration

If resistant stock is planted in a mosaic across the landscape before or at the time of WPBR invasion, young resistant trees will be maturing as older, diseased trees are dying (Schoettle and Sniezko 2007). Not only would these resistant trees be providing ecosystem services in the eventually disease-impacted landscape, they would also provide pollen, and eventually seed, for the flow of resistance genes to neighboring native populations. Therefore, the earlier resistant seedlings can be planted before WPBR invasion the shorter the window of time the recovery capacity (i.e., ability to produce sufficient seed to regenerate) of the overall population is compromised upon invasion. Planting also offers opportunity to provide ‘assisted migration’ if needed to help counter-balance the projected impacts of climate change. With a proactive deployment of genetic resistance, the amount of time that ecosystem services are at risk for interruption by the disease is reduced.

Development of disease-resistant planting material for proactive deployment requires (1) transport of seed from resistant parent trees identified from distant areas already impacted by the disease or (2) identification of resistant seedtrees in local, healthy host populations. In populations already invaded, seeds are traditionally collected from individual trees that appear disease-free or have less severe disease symptoms than most of the other trees in the population. The progeny from these putatively resistant trees are then screened for heritable resistance under controlled conditions and further tested under natural growing conditions (Sniezko et al. 2011a). In combination with genecological studies, the consequences of seed movement (i.e., using non-local seed sources) can be evaluated and appropriate seed sources identified. The development of seed orchards is one option to maximize the level of, and availability of, resistant seed. However, because maturation of high-elevation, five-needle pines is slow, orchards will not provide seed in the near future. For immediate and near future needs, the only option is to utilize seed collections from parent trees in natural ecosystems. To identify resistant seed trees in populations not yet invaded by the pathogen, pre-selection of seed trees for putative resistance traits is not possible, so trees are essentially random samples from the population. This may appear to be inefficient compared to identifying putatively resistant seedtrees in impacted areas; however the benefits of early resistance identification and deployment for sustained ecosystem benefits could be substantial and warrant the extra effort. Fortunately, rust screening facilities can evaluate progenies from 100s to 1,000s of parent trees in a relatively short time. With proper sampling, these studies also offer added significant benefits for gene conservation and providing estimates of the baseline population frequencies of disease resistance, allowing a forecast of the likely direct impacts of the disease before it happens and enabling managers to make more informed decisions (see above; Schoettle et al. 2011b,Sniezko et al. 2011a, 2011b).

In the southern Rocky Mountains, genetic resistance to WPBR has been identified in healthy limber pine and Rocky Mountain bristlecone pine populations (Schoettle et al. 2011b) and summaries of the geographic distribution of some resistances are underway. Screening studies allow us to discern (1) if there is resistance, (2) what level of resistance is present, and (3) how it is distributed over landscapes. They also provide some first ideas on how resistance might be inherited (which influences strategies) and how many types of resistance are present and whether they would be durable under different sets of circumstances. This provides a foundation for further work on the underlying mechanisms and the genes involved. This early detection of resistance has enabled *in situ* protection of WPBR-resistant seed trees and populations from the recent mountain pine beetle (*Dendroctonus ponderosae*) epidemic, collection of resistant seed stocks for outplanting and gene conservation, and refinement of management plans (Schoettle et al. 2011a).

Facilitating Selection for Resistance Through Landscape Management

Planting resistant stock will be needed in populations with little disease resistance. However, in populations in which heritable resistance is present at high enough frequency, manipulation of the age class structure of stands across the landscape can facilitate selection and therefore accelerate the evolution of resistance throughout the population once WPBR invades (Schoettle and Sniezko 2007). After infection with WPBR, young trees are killed more quickly than older, larger trees, so selection for resistance proceeds more rapidly in younger cohorts. The model of Field et al. (2012) demonstrates high mortality of young seedlings even when all age cohorts have the same probability of infection (see fig. 11 in Field et al. 2012). When an R gene for WPBR resistance is incorporated into the model, it shows accelerated increase in the allele frequency in younger cohorts (Schoettle et al., unpublished information). Consequently, selection against susceptible genotypes (i.e., disease-caused mortality) will occur more rapidly in young stands than older stands. Therefore, management that generates a mosaic of patches of different stand ages across a landscape can effectively generate patches with different rates of selection upon WPBR invasion, thereby mitigating the effect of mortality in any one cohort or stand on overall ecosystem function of the greater landscape.

A landscape of diverse age class structures will also reduce the susceptibility of the populations to future impacts by mountain pine beetle. Likewise, in other host-pest systems, a diversified host age-class structure may affect not only the distribution of mortality, but also susceptibility to infection or infestation by those pests that preferentially infest one host age or size over another. The scale of the landscape, the patch sizes, and the portion of the landscape that is managed can be adjusted to optimize gene flow and management objectives. At a minimum, establishment of some refugia populations with resistance and genetic diversity would serve as progenitors of future generations and re-establishment. The landscape perspective can help manage the effects of mortality and retain overall population resilience and ecosystem services.

Continued Management to Promote Further Adaptive Capacity

Whether the genetic resistance was in the native population or added via artificial regeneration, maintaining a diverse mosaic of stand structures across the landscape will sustain the benefits of initial interventions, facilitate further adaptation to changing climate conditions, and reduce susceptibility to mountain pine beetle impacts. Future estimates of resistance frequencies in populations can be compared to original baseline resistance frequencies to assess management efficacy and detect changes in durability of resistance. Likewise, changes in environmental condition with climate change may also affect the expression or efficacy of resistance.

The introduction of a non-native pathogen changes many dynamics for host species (McDonald et al. 2005). The disturbance regime to best promote adaptation to this novel stress is not likely to be the same as the historic pattern for the species (Coop and Schoettle 2011); monitoring and research is needed on these new landscapes as they develop to optimize the mosaic for adaptation and sustainability of the pine and ultimately naturalization of the rust.

Applying the Proactive Strategy – Southern Rockies Example

In 2008, the USDA Forest Service Rocky Mountain Research Station (RMRS), Rocky Mountain National Park (RMNP), USDA Forest Service, Rocky Mountain Region Forest Health Management, several National Forest districts, and USDA Forest Service Dorena Genetic Resource Center initiated an application of the Proactive Strategy to conserve and develop management plans for limber pine in Rocky Mountain National Park and northern Colorado. Approximately 42,000 ha of limber pine occur in this area. Most are threatened and not yet impacted by WPBR.

The objectives of the cooperative program to conserve and sustain limber pine on the northern Colorado landscape are five-fold: (1) protect limber pine from the mountain pine beetle epidemic so seed collections can immediately be made for WPBR resistance tests, genetic conservation, and research; (2) screen seedlings for WPBR resistance to determine the frequency of resistance across the landscape and to identify resistant parent trees and populations for further seed collections; (3) estimate population differentiation along the elevation and latitudinal gradient to refine seed transfer guidelines; (4) survey forest health, biotic damage incidence, regeneration capacity, and advanced regeneration condition to project persistence of these populations after MPB invasion; and (5) prepare proactive management plans for northern Colorado. The program is described in detail by Schoettle et al. (2011a).

The Northern Colorado Limber Pine Conservation Program contributes site-specific scientific data and tools for decision making about the need for and/or trade-offs of intervention to promote sustainability of limber pine populations in the presence of multiple stressors (WPBR and mountain pine beetle). Some of the information, tools, and activities, such as estimating rust resistance frequency, understanding natural regeneration dynamics, and capturing the pine's full genetic diversity via seed collections, can only be taken advantage of in healthy forests that have not yet had their processes disrupted by these stressors. Common garden studies are also underway to refine seed transfer guidelines. The early availability of information facilitates justification and direction for interventions if prescribed and permits the inclusion of science-based information in prioritizing sites for strategic planning. It also provides the opportunity for early implementation of some management options, such as stimulating regeneration in populations with high frequencies of rust resistance, that are best implemented when those forests are still healthy. Gathering and using this information before the loss of ecosystem functions allows land managers the widest range of management options to sustain limber pine populations and mitigate future impacts in these ecologically important ecosystems.

The Proactive Strategy framework can be adapted for other five-needle pine species threatened by WPBR and/or mountain pine beetle and possibly for other pathosystems. It is currently also being applied in Rocky Mountain bristlecone pine and Great Basin bristlecone pine (*Pinus longaeva* D.K. Bailey) ecosystems and is being adopted for some remaining healthy whitebark pine ecosystems. An intensive location-based program, such as that implemented in northern Colorado, is especially appropriate for administrative units that want to use local genotypes as much as possible, such as national parks. Understanding the interaction of the species' life history traits and ecology with resistance mechanisms will highlight factors that limit the species' sustainability in the presence of the pathogen. Focusing timely management on maintaining genetic diversity and a functional regeneration cycle will promote sustained adaptive capacity and ecosystem resiliency. Early intervention activities also allow better potential maintenance of overall genetic diversity within the species which provides the foundation for the species to continue to evolve in a changing environment.

Summary

Managing threatened populations and ecosystems that are not yet impacted by a non-native pest can position the population or ecosystem for greater resilience. The Proactive Strategy is especially appropriate for long-lived, slow-maturing species. Utilization of genetic tools in conjunction with timely management of natural demographic processes can facilitate the transition of the native ecosystems to a new and sustainable condition in the presence of the introduced pest. Early research on healthy populations enables regeneration capacity and disease resistance frequencies and their geographic distributions to be estimated, enabling more accurate forecasting of impacts and providing valuable information for designing, prioritizing, and evaluating management options. Early intervention allows management to (1) increase regeneration to increase genetic combinations and offset disease-caused mortality; (2) deploy resistance in a temporal and spatial array to promote population persistence and gene flow; (3) diversify the age class structures on the landscape to affect selection rates, mitigate impacts of mortality, and promote further adaptive capacity; and (4) preserve genetic diversity with in situ and ex situ conservation. Positioning the ecosystems for greater resilience before invasion may avoid the impaired ecosystem condition after invasion when ecosystem services are compromised and reduce the likelihood of the need for restoration later. Information learned while conducting the Proactive Strategy can likewise help inform restoration efforts in impacted ecosystems. Effective implementation of the strategy requires a concerted effort by researchers, forest health professionals, and land managers working together.

The existing genetic management programs (including development of disease resistance) for the timber species provide infrastructure and a solid foundation of knowledge about genetic disease resistance and management from which to more efficiently build management plans for ecosystems that deliver essential ecosystem services. Building on this foundation and shifting from a stand-based plantation perspective to a landscape evolutionary perspective requires considerations, and provides opportunities for managing host demographics and timing of intervention to achieve multi-generational sustainability of populations that can maintain ecosystem functions. Regeneration is a stabilizing factor and is an important factor in determining if a new sustainable condition is established or the population spirals into decline in the presence of the disease.

Gathering information in threatened, but not-yet-impacted, ecosystems also allows time to explore the interactions of life-history traits of the host with (1) pathogen infection, (2) regeneration capacity, (3) heritable resistance, (4) cost of infection on survival and fecundity, and (5) transitory population dynamics (Field et al. 2012). All of these factors affect the outcome of invasion on the populations, and through modeling, insights can be gained to optimize the type and timing of management interventions for the best outcomes. Co-evolution dynamics between the host and pest are also important to consider when implementing either proactive or restoration approaches. As we learn more about these interactions for specific pathosystems and develop silvicultural prescriptions to manipulate regeneration dynamics, it will enable us to further address these and other key questions: (1) What frequency of resistance(s) is enough to sustain a population under an array of conditions? (2) What spatial arrangement of structural and genetic diversity on the landscape is best to optimize selection, regeneration, gene flow, and adaptive capacity for long-term host population sustainability? (3) When during the invasion process does intervention achieve optimal ecological effectiveness? (4) What will be the characteristics of the new population condition and how will it behave in relation to natural disturbances after pathogen naturalization? (5) What are the public preferences and economic and ecological trade-offs of different management options implemented at different times during the invasion process?

The recent national-level directive on the management of invasive species across aquatic and terrestrial areas of the U.S. National Forest System (U.S. Department of Agriculture, Forest Service 2011) includes an aspiration to sustain healthy native ecosystems through proactive detection and mitigation of ecosystems threatened or impacted by non-native species. High-elevation pine forests, under the threat of multiple stressors, serve as an excellent flagship to lead the paradigm shift away from crisis management and toward proactive management for ecosystem resilience. The Proactive Strategy is a novel approach to providing information and technologies to make informed decisions to better sustain mountaintop ecosystems. The components of the strategy are also amendable to other biotic and abiotic agents that will impact forest ecosystems.

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Literature Cited

Coop, J.D.; Schoettle, A.W. 2009. Regeneration of Rocky Mountain bristlecone pine (*Pinus aristata*) and limber pine (*Pinus flexilis*) three decades after stand-replacing fires. Forest Ecology and Management. 257: 893–903.

Coop, J.D.; Schoettle, A.W. 2011. Fire and high-elevation, five-needle pine (*Pinus aristata* & *P. flexilis*) ecosystems in the southern Rocky Mountains: What do we know? In: Keane, R.E.; Tomback, D.F.; Murray, M.P.; Smith, C.M., eds. The future of high-elevation, five-needle white pines in western North America: proceedings of the high five symposium. Proc. RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 164–175. http://www.fs.fed.us/rm/pubs/rmrs_p063/rmrs_p063_164_173.pdf. (03 May 2012).

Field, S.G.; Schoettle, A.W.; Klutsch, J.G.; Tavener, S.J.; Antolin, M.F. 2012. Demographic projection of high-elevation white pines infected with white pine blister rust: a nonlinear disease model. Ecological Applications. 22: 166–183.

Fins, L.; Byler, J.; Ferguson, D.; Harvey, A.; Mahalovich, M.F.; McDonald, G.; Miller, D.; Schwandt, J.; Zach, A. 2001. Return of the giants: restoring white pine ecosystems by breeding and aggressive planting of blister rust-resistant white pines. Station Bulletin 72. Moscow, ID: University of Idaho, College of Natural Resources. 20 p. http://www.fs.fed.us/rm/pubs_other/rmrs_2001_fins_l001.pdf . (02 May 2012).

Hoff, R.J.; McDonald, G.I. 1980. Improving rust-resistant strains of inland western white pine. Res. Pap. INT-245. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 13 p.

Howell, B.; Burns, K.S.; Kearns, H.S.; Witcosky, J.J.; Cross, F. 2006. Biological evaluation of a model for predicting presence of white pine blister rust in Colorado based on climatic variable and susceptible white pine species distribution. Biological Evaluation. R2-06-04. Lakewood, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Renewable Resources. 15 p.

Keane, R.E.; Parsons, R.A. 2010. A management guide to ecosystem restoration treatments: the whitebark pine forests of the northern Rocky Mountains. Gen. Tech. Rep. RMRS-GTR-232. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 133 p.

Keane, R.E.; Schoettle, A.W. 2011. Plenary paper: Strategies, tools, and challenges for sustaining and restoring high elevation five-needle white pine forests in western North America. In: Keane, R.E.; Tomback, D.F.; Murray, M.P.; Smith, C.M., eds. The future of high-elevation, five-needle white pines in western North America: proceedings of the high five symposium. Proc. RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 276–294. http://www.fs.fed.us/rm/pubs/rmrs_p063/rmrs_p063_276_294.pdf. (03 May 2012).

Kearns, H.S.J.; Ferguson, B.A.; Schwandt, J.W. 2012. Performance of rust-resistant western white pine in operational plantations in northern Idaho: 1995-2006. Report 12-03. Missoula, MT: U.S. Department of Agriculture, Forest Service, Forest Health Protection, Northern Region.

Kegley, A.J.; Sniezko, R.A. 2004. Variation in blister rust resistance among 226 *Pinus monticola* and 217 *P. lambertiana* seedling families in the Pacific Northwest. In: Sniezko, RA; Samman, S.; Schlarbaum, S.E.; Kriebel, H.B., eds. Breeding and genetic resources of five-needle pines: growth, adaptability and pest resistance. Proceedings RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 209–226. http://www.fs.fed.us/rm/pubs/rmrs_p032.html. (05 May 2012).

Kinloch, B.B., Jr.; Davis, D.A. 1996. Mechanisms and inheritance of resistance to blister rust in sugar pine. In: Kinloch, B.B., Jr.; Marosy, M.; Huddleston, M.E., eds. Sugar pine: status, values, and roles in ecosystems. Davis, CA: University of California, Division of Agriculture and Natural Resources: 125–132.

Kinloch, B.B., Jr.; Dupper, G.E. 2002. Genetic specificity in the white pine-blister rust pathosystem. Phytopathology. 92**:** 278–280.

Kinloch, B.B., Jr.; Sniezko, R.A.; Dupper, G.E. 2003. Origin and distribution of Cr2, a gene for resistance to white pine blister rust in natural populations of western white pine. Phytopathology. 93: 691–694.

McDonald, G.I.; Zambino, P.J.; Klopfenstein, N.B. 2005. Naturalization of host-dependent microbes after introduction into terrestrial ecosystems: Evolutionary epidemiology of white pine blister rust. In: Lundquist, J.E.; Hamelin, R.C., eds. From molecules to ecosystems - forest pathology in the era of genes and landscapes. St. Paul, MN: American Phytopathological Society Press: 41–57.

Schoettle, A.W. 2004. Ecological roles of five-needle pines in Colorado: potential consequences of their loss. In: Sniezko, R.A.; Samman, A.S.; Schlarbaum, S.E.; Kriebel, H.B., eds. Breeding and genetic resources of five-needle pines: growth, adaptability, and pest resistance. RMRS-P-32. Ft. Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 124–135. http://www.fs.fed.us/rm/pubs/rmrs_p032/rmrs_p032_124_135.pdf. (05 May 2012).

Schoettle, A.W.; Goodrich, B.A.; Klutsch, J.G.; Burns, K.S.; Costello, S.; Sniezko, R.A.; Connor, J. 2011a. The proactive strategy for sustaining five-needle pine populations: an example of its implementation in the southern Rocky Mountains. In: Keane, R.E.; Tomback, D.F.; Murray, M.P.; Smith, C.M., eds. The future of high-elevation, five-needle white pines in western North America: Proceedings of the high five symposium. RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 323-334. http://www.fs.fed.us/rm/pubs/rmrs_p063/rmrs_p063_323_334.pdf. (05 May 2012).

Schoettle, A.W.; Sniezko, R.A. 2007. Preparing the landscape for invasion – proactive intervention to mitigate impacts of a non-native pathogen. Journal of Forest Research. 12: 327–336. http://www.springerlink.com/content/9v91t44278w74430/. (05 May 2012).

Schoettle, A.W.; Sniezko, R.A.; Burns, K.S. 2009. Sustaining *Pinus flexilis* ecosystems of the southern Rocky Mountains (USA) in the presence of *Cronartium ribicola* and *Dendroctonus ponderosae* in a changing climate. In: Noshad, D.; Noh, E.; King, J.; Sniezko, R., eds. Breeding and genetic resources of five-needle pines conference, iufro working party 2.02.15. Yangyang, Republic of Korea: Korea Forest Research Institute: 63–65. http://www.iufro.org/publications/proceedings/proceedings-meetings-2008/. (05 May 2012).

Schoettle, A.W.; Sniezko, R.A.; Kegley, A.; Burns, K.S. 2011b. Preliminary overview of the first extensive rust resistance screening tests of *Pinus flexilis* and *Pinus aristata*. In: Keane, R.E.; Tomback, D.F.; Murray, M.P.; Smith, C.M., eds. The future of high-elevation, five-needle white pines in western North America: proceedings of the high five symposium. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 265–269. http://www.fs.fed.us/rm/pubs/rmrs_p063/rmrs_p063_265_269.pdf. (05 May 2012).

Sniezko, R.A.; Kegley, A.J. 2003. Blister rust resistance experience in Oregon/Washington: evolving perspectives. In: Stone, J.; Maffei, H., comps. 50th Annual Western International Forest Disease Work Conference. Bend, OR: U.S. Department of Agriculture, Forest Service, Central Oregon Forest Insect and Disease Service Center: 111–119.

Sniezko, R.A.; Kegley, A.J.; Danchok, R.S.; Long, S. 2007. Variation in resistance to white pine blister rust among 43 whitebark pine families from Oregon and Washington—early results and implications for conservation. In: Goheen, E.M.; Sniezko, R.A., tech. coords. Whitebark pine: a Pacific Coast perspective. R6-NR-FHP-2007-01. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region: 82–97. http://www.fs.fed.us/r6/nr/fid/wbpine/papers/2007-wbp-wpbr-resist-sniezko.pdf. (05 May 2012).

Sniezko, R.A.; Kegley, A.J.; Danchok, R. 2008. White pine blister rust resistance in North American, Asian, and European species – results from artificial inoculation trials in Oregon. Annals of Forest Research. 51: 53–66. http://www.e-afr.org. (05 May 2012).

Sniezko, R.A.; Mahalovich, M.F.; Schoettle, A.W.; Vogler, D.R. 2011a. Plenary paper: Past and current investigations of the genetic resistance to *Cronartium ribicola* in high-elevation five-needle pines. In: Keane, R.E.; Tomback, D.F.; Murray, M.P.; Smith, C.M., eds. The future of high-elevation, five-needle white pines in western North America: Proceedings of the high five symposium. RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 246–264. http://www.fs.fed.us/rm/pubs/rmrs_p063/rmrs_p063_246_264.pdf. (05 May 2012).

Sniezko, R.A.; Schoettle, A.W.; Dunlap, J.; Vogler, D.; Conklin, D.; Bower, A.; Jensen, C.; Mangold, R.; Daoust, D.; Man, G. 2011b. *Ex situ* gene conservation in high elevation white pine species in the United States-a beginning. In: Keane, R.E.; Tomback, D.F.; Murray, M.P.; Smith, C.M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the high five symposium. RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 147–149. http://www.fs.fed.us/rm/pubs/rmrs_p063/rmrs_p063_147_149.pdf. (05 May 2012).

Schwandt, J.W.; Lockman, I.B.; Kliejunas, J.T.; Muir, J.A. 2010. Current health issues and management strategies for white pines in the western United States and Canada. Forest Pathology. 40: 226–250.

Tomback, D.F.; Achuff, P. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. Forest Pathology. 40: 186–225.

Tomback, D.F.; Achuff, P.; Schoettle, A.W.; Schwandt, J.W.; Mastrogiuseppe, R.J. 2011. Plenary paper: The magnificent high-elevation five-needle white pines: ecological roles and future outlook. In: Keane, R.E.; Tomback, D.F.; Murray, M.P.; Smith, C.M., eds. The future of high-elevation, five-needle white pines in western North America: Proceedings of the high five symposium. RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 228. http://www.fs.fed.us/rm/pubs/rmrs_p063/rmrs_p063_002_028.pdf. (05 May 2012).

U.S. Department of Agriculture, Forest Service. 2011. National forest system invasive species management policy. Federal Register. Vol. 76 (233): 75860-75866.