



# Selection for resistance to white pine blister rust affects the abiotic stress tolerances of limber pine



Patrick J. Vogan<sup>a,b</sup>, Anna W. Schoettle<sup>b,\*</sup>

<sup>a</sup> Mountain Studies Institute, PO Box 426, Silverton, CO 81433, USA

<sup>b</sup> Rocky Mountain Research Station, USDA Forest Service, 240 West Prospect Road, Fort Collins, CO 80256, USA

## ARTICLE INFO

### Article history:

Received 7 November 2014

Received in revised form 28 January 2015

Accepted 29 January 2015

Available online 3 March 2015

### Keywords:

*Cronartium ribicola*

*Pinus flexilis*

Cold hardiness

Drought

Disease resistance

Restoration

## ABSTRACT

Limber pine (*Pinus flexilis*) mortality is increasing across the West as a result of the combined stresses of white pine blister rust (*Cronartium ribicola*; WPBR), mountain pine beetle (*Dendroctonus ponderosae*), and dwarf mistletoe (*Arceuthobium cyanocarpum*) in a changing climate. With the continued spread of WPBR, extensive mortality will continue with strong selection against trees that lack genetic resistance to the disease. Naturally-occurring resistance to the non-native fungal pathogen *C. ribicola* is present in limber pine and is the cornerstone of restoration strategies. Disease resistance to native pathogens can carry a strong fitness cost to the host in the absence of the pathogen. However we suspect this to be unlikely in the case of resistance to a non-native pathogen as the resistance would not have persisted in the pre-invasion population. Genetic resistance to a novel stress which the species has not co-evolved may be neutral or carry a benefit to the host via a function that offers adaptive benefit for environmental factor(s), biotic or abiotic, under which it did evolve. Because plant disease defenses can share physiological activity with those that mediate freezing and drought stress sensitivity, both stresses for which limber pine is responsive, we compared cold and drought tolerances of limber pine seedling families from trees previously determined to have (R families) and not have (S families) the *Cr4* allele for qualitative resistance to WPBR. R families constitutively had (1) greater cold hardiness than S families and (2) lower stomatal conductance than S families during moderate drought, suggesting that R and S families have different abiotic stress responses such that the post-invasion populations may have the potential for modified competitive ability, especially under a warming climate. The presence of different stress tolerances in R families may also inform hypotheses to explain the presence and frequency of a resistance gene against a non-native pathogen to which the species was not previously exposed. We conclude that as the frequency of qualitative resistance to WPBR increases, through natural selection or planting of disease resistant seedling stock, the resultant populations may have a different suite of stress tolerance traits than pre-invasion populations. The shift in the fundamental niche of limber pine in the presence of *C. ribicola* should be considered when selecting seed sources and habitats for restoration and projecting future distributions in a changing climate.

Published by Elsevier B.V.

## 1. Introduction

Since its introduction to western North America in 1910, the invasive fungal pathogen *Cronartium ribicola*, cause of the lethal disease white pine blister rust (WPBR), has penetrated white pine communities across the western United States and Canada and continues to spread, threatening the remaining uninfected communities (Burns et al., 2008). WPBR devastated commercial cultivation of western white pine (*Pinus monticola*) and sugar pine

(*Pinus lambertiana*) (Kinloch et al., 2008) and is a major contributor to substantial declines in other white pine communities across western North America (Tomback and Achuff, 2010). Several of the affected species serve important roles in their native ranges. Among these is limber pine (*Pinus flexilis*), which has a broad range extending from the Rocky Mountains to the eastern Sierra Nevada and eastern Oregon and an elevation range from 870 to 3500 m across its full distribution (Schoettle and Rochelle, 2000; Steele, 1990). Limber pine is an important high elevation species in the Southern Rocky Mountains, often defining the alpine treeline (Schoettle, 2004; Schoettle and Rochelle, 2000). Particularly in these high elevation communities, limber pine constitutes a keystone species through its role in stabilizing otherwise dry, unoccupied

\* Corresponding author. Tel.: +1 970 498 1333; fax: +1 970 498 1212.

E-mail addresses: [voganpj@yahoo.com](mailto:voganpj@yahoo.com) (P.J. Vogan), [aschoettle@fs.fed.us](mailto:aschoettle@fs.fed.us) (A.W. Schoettle).

slopes; as an early colonizer post-fire; as a nurse plant for late-successional tree species; and as habitat and food for animal species, particularly Clark's nutcracker (*Nucifraga columbiana*), an important seed dispersal agent (see Schoettle, 2004).

In the US and Canada, limber pine is under considerable threat of future declines due to the combined impacts of WPBR, mountain pine beetle (*Dendroctonus ponderosae*), dwarf mistletoe (*Arceuthobium cyanocarpum*), and climate change and is therefore of conservation concern. Basal area losses in limber pine are estimated to exceed 40% over the next 15 years (Krist et al., 2014) and the species distribution is expected to contract under climate change in some areas (Monahan et al., 2013). Consequently, limber is listed as a Special Status Species on Bureau of Land Management land in Wyoming (USDI BLM Wyoming, 2013) and as endangered in Alberta (Government of Alberta, 2010); it is recommended for endangered species status nationally in Canada under the Species at Risk Act (Government of Canada, 2014).

Management strategies to reduce the impact of WPBR capitalize on existing genetic resistance to the disease and increasing the frequency of resistance on the landscape to sustain population numbers and restore resilience (Alberta Whitebark and Limber Pine Recovery Team, 2014; Burns et al., 2008; Keane et al., 2012; King et al., 2010; Schoettle and Sniezko, 2007). Despite its being an exotic pathogen, all North American white pine species, including limber pine, exhibit some degree of natural resistance to *C. ribicola* colonization. Breeding efforts have been in place since the 1940s to propagate families of commercial white pine species with heritable resistance mechanisms as a means of restoring devastated communities and plantations (King et al., 2010). Also underway are efforts in several non-commercial species to seed or plant still-extant populations with disease-resistant individuals to stave off potential losses in threatened communities before they occur (Burns et al., 2008; Keane et al., 2012; Keane and Schoettle, 2011; Schoettle and Sniezko, 2007).

Understanding the genetic consequences of management practices and of natural selection by novel stresses is essential for sustaining and conserving forest ecosystems (Alfaro et al., 2014; Ratnam et al., 2014). Possible correlations and trade-offs between disease resistance and plant tolerance to abiotic stress is an important but generally understudied facet of forest management (Sthultz et al., 2009). If present in the WPBR pathosystem, such correlations may influence plant performance and survival across different environments after the selective agency of *C. ribicola* invasion has reduced the frequency of susceptible individuals from the population or after managers have selectively propagated and planted seedlings exhibiting resistance, both of which could inadvertently select for or against associated adaptive traits. Artificial selection for WPBR resistance in western white pine has caused loss of rare alleles as measured with molecular markers assumed to be selectively neutral (Kim et al., 2003), yet the effect of selection on stress tolerance traits is unclear. An understanding of adaptive traits correlated with resistance (or susceptibility) will be necessary to recognize possible WPBR-induced shifts in the fundamental niche of pine species and to inform decisions about seed sources and habitats for restoration planting and how plant performance may change under future climate regimes (Chmura et al., 2011).

Geographic variation in disease resistance among populations suggests possible genetic or physiological correlations between resistance and abiotic stress tolerance. For example, quantitative resistance to WPBR in the interior west tends to increase in whitebark pine (*Pinus albicaulis*) from Montana and Idaho westward (Mahalovich et al., 2006). There is also geographic variation in qualitative resistance to WPBR, which is inherited via a single dominant gene and is characterized by a gene-for-gene hypersensitive-like reaction conditioned by an *R* gene – the *Cr* gene in the

case of the WPBR-pine pathosystem. Geographic variation in the frequency of *Cr* alleles has been found in three North American white pines: sugar pine (*Cr1*), western white pine (*Cr2*) and limber pine (*Cr4*). While the average frequency of *Cr2*, *Cr1* and *Cr4* over large areas is 0.1% (range wide), 2.2% (range wide), and 5.0% (in the Southern Rockies), respectively, some populations or entire sections of the distribution of each species lack the allele altogether while others can reach frequencies of 0.8%, 8.9% and 13.8%, respectively (Kinloch, 1992; Kinloch et al., 2003; Schoettle et al., 2014). Specifically, the frequency of *Cr1* in sugar pine and *Cr2* in western white pine is much greater for both species in the high elevations of the southern Sierra Nevada than in the lower elevations of the northern Sierras and the Cascades (Kinloch, 1992; Kinloch et al., 2003; Kitzmiller, 2004), potentially suggesting an association of *Cr* genes with climate and/or abiotic stress tolerance in these species. Recent research suggests that the *Cr4* allele in limber pine also varies geographically, as it has not been detected in bulk lots and families sampled from outside the Southern Rocky Mountains (Kinloch and Dupper, 2002; Schoettle et al., 2014).

*R* genes to native pathogens can carry a strong fitness cost to the host in the absence of the pathogen (Tian et al., 2003); this would be very unlikely in the case of *R* genes to a non-native pathogen or the *R* gene would not have persisted in the pre-invasion population. It is more plausible, we hypothesize, that an *R* gene effective against a novel stress for which it has not co-evolved may be neutral or carry a benefit to the host possibly via a function that offers adaptive advantage to an environmental factor, biotic or abiotic, under which the host did evolve. As a result, a correlation with abiotic stress tolerance may also inform hypotheses about how *Cr* alleles have been maintained in species that have not been exposed previously to the corresponding pathogen.

Some associations between insect or disease resistance and stress tolerance have been shown in other species (Sthultz et al., 2009) and are suspected in white pines. For example, some pathogenesis-related or “PR” proteins that are involved in quantitative resistance to *C. ribicola* are known to be expressed in plants in response to abiotic stresses (Davidson and Ekramoddoullah, 1997; Ekramoddoullah and Tan, 1998). In other plants, PR proteins have exhibited the ability to suppress propagation of ice crystals *in vitro* (Zamani et al., 2003; Cabello et al., 2012) and, when over-expressed *in vivo*, to reduce frost damage and increase thermal hysteresis in whole plants (Griffith and Yaish, 2004; Liu et al., 2013). As well, endogenous induction of PR protein expression during fall cold hardening has been shown to enhance subsequent plant disease resistance and cold tolerance (Cabello et al., 2012) and PR proteins are also expressed in maritime pine (*Pinus pinaster*) (Dubos and Plomion, 2001) and winter wheat (Yeh et al., 2000) in response to drought. The role of PR proteins in both disease resistance and stress tolerance provides a basis to hypothesize an association between qualitative WPBR resistance and cold and drought tolerances in white pine species.

As a species that grows in dry rocky habitats across a range of elevations, shifts in cold and drought tolerances that may result from WPBR resistance selection may affect limber pine performance, especially in a changing climate. Limber pine exhibits conservative water-use traits (Letts et al., 2009) yet seasonal moisture stress still imposes a strong limitation to limber pine survival and is likely to be exacerbated by climate change (Millar et al., 2007; Moyes et al., 2013). Regional warming has already contributed to an increase in western U.S. tree mortality (van Mantgem and Stephenson, 2007) and in the Southern Rocky Mountains, temperatures have risen 0.5–1 °C over the last 30 years, with higher elevations warming more quickly in some areas (McWethy et al., 2010). A projected annual mean temperature increase of 2 °C is expected by 2050 with a decrease in the amount and seasonality of precipitation (Krist et al., 2014; McWethy et al., 2010). Without consideration for WPBR

Download English Version:

<https://daneshyari.com/en/article/86321>

Download Persian Version:

<https://daneshyari.com/article/86321>

[Daneshyari.com](https://daneshyari.com)