Associations between Complete Resistance to White Pine Blister Rust and Abiotic Stress Tolerances in Limber Pine (*Pinus flexilis*)

P.J. Vogan[1] and A.W. Schoettle[1, *]

[1] *USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA*

[*] *aschoettle@fs.fed.us*

During the naturalization process of white pine blister rust (WPBR, caused by *Cronartium ribicola*), susceptible pine genotypes will be selected against, along with any traits that are associated with those genotypes, potentially causing a shift in the suite of traits in the post-selection population compared to the native population. Consequently, identifying associated traits with WPBR resistance is critical for effective restoration planning, especially in a changing climate. We sought to determine whether complete resistance to WPBR in limber pine (*Pinus flexilis*) is associated with abiotic stress tolerances, particularly those related to freezing and drought. Previous research has noted that proteins involved in partial resistance to *C. ribicola* also exhibit antifreeze capabilities in vitro and very likely enhance plant frost tolerance in vivo; these proteins are also expressed in response to cold and, occasionally, drought. It is not known if a similar association exists between the major gene in limber pine (*Cr4*) and tolerance of abiotic stress.

We raised 1,020 seedlings of limber pine from 10 rust-resistant (R) and 10 rust-susceptible (S) open-pollinated families (Schoettle et al. 2014), paired as 1 R and 1 S family from each site of origin to filter out potential geographic trait variation. In a series of studies, R families exhibited greater frost tolerance than S families, which may imply a genetic association between *Cr4* and cold tolerance gene(s) or a direct cryoprotective function of the *Cr4* protein product(s) itself. Wintertime freezing tolerance of R and S families was not affected by inoculation with *C. ribicola* the previous fall. This result suggests that differences in frost tolerance between R and S families were not induced by pathogen infection or resistance expression and instead frost tolerance is a constitutive trait of families (Vogan and Schoettle 2015).

We found a tendency for S family seedlings to retain somewhat greater stomatal conductance under modest drought than R families and no significant differences under severe (<–2.0 MPa) drought (Vogan and Schoettle 2015). Drought during the summer resulted in marginally, but not significantly, greater frost tolerance in seedlings the following winter, suggesting that mechanisms induced by drought may have enhanced cold hardiness in the ensuing months. The correlation between cold tolerance and rust resistance may provide an explanation of how *Cr4* resistance exists and persists in limber pine before the arrival of the corresponding pathogen as cold tolerance traits are usually under strong selection in forest trees.

In: Schoettle, Anna W.; Sniezko, Richard A.; Kliejunas, John T., eds. 2018. Proceedings of the IUFRO joint conference: Genetics of five-needle pines, rusts of forest trees, and Strobusphere; 2014 June 15–20; Fort Collins, CO. Proc. RMRS-P-76. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 245 p.

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