Conservation Genetics of High Elevation Five-Needle White Pines

Andrew D. Bower, USDA Forest Service, Olympic National Forest, Olympia, WA; **Sierra C. McLane,** University of British Columbia, Dept. of Forest Sciences, Vancouver, BC; **Andrew Eckert,** University of California Davis, Section of Evolution and Ecology, Davis, CA; **Stacy Jorgensen,** University of Hawaii at Manoa, Department of Geography, Manoa, HI; **Anna Schoettle,** USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO; **Sally Aitken,** University of British Columbia, Dept. of Forest Sciences, Vancouver, BC

Abstract—Conservation genetics examines the biophysical factors influencing genetic processes and uses that information to conserve and maintain the evolutionary potential of species and populations. Here we review published and unpublished literature on the conservation genetics of seven North American high-elevation five-needle pines. Although these species are widely distributed across much of western North America, many face considerable conservation challenges: they are not valued for timber, yet they have high ecological value; they are susceptible to the introduced disease white pine blister rust (caused by the fungus *Cronartium ribicola*) and endemic-turned-epidemic pests; and some are affected by habitat fragmentation and successional replacement by other species. Potential range shifts resulting from global climate change pose additional threats to these high-elevation species, as suitable climates may no longer exist on the mountains where they grow. The combined impacts of these threats have necessitated active management and conservation activities. While several high-elevation five-needle pines have been well studied, large information gaps exist regarding the genetic diversity and population structure of others. This information is crucial for the development of conservation management strategies. In this report, information on genetic diversity, population structure, and strategies for gene conservation is presented and information gaps identified for North America's high-elevation five-needle pines.

Introduction

What Is Conservation Genetics?

Conservation genetics is "the application of genetics to preserve species as dynamic entities capable of coping with environmental change. It encompasses genetic management of small populations, resolution of taxonomic uncertainties, defining management units within species and the use of molecular genetic analyses in forensics and understanding species' biology" (Frankham and others, 2002: p1). Every species, and each population within species, is the product of a unique evolutionary lineage. The genetic diversity within and among populations and individuals is influenced by the dynamics of past, present and future genetic processes. The objective of conservation genetics is to shed light on these factors to develop strategies to conserve and maintain the evolutionary potential of species. Genetic management in biodiversity conservation also aims to maintain sufficient population sizes to avoid inbreeding, and reducing anthropogenic effects on evolutionary processes. This involves investigating current levels of genetic diversity and population structure using molecular markers and quantitative traits and assessing how these measures are affected by ecological changes. Genetic diversity is influenced by the evolutionary forces of mutation, selection, migration, and drift, which impact within- and among-population genetic diversity in differing ways. Discussions of how these forces impact genetic diversity can be found in many genetics texts (for example Frankham and others 2002; Hartl and Clark 1989) and will not be discussed here.

Why Is Genetic Diversity Important?

Genetic diversity and its conservation have become a priority for many taxa. Genetic diversity can be used to identify unique species or populations. For example, these may be populations that have been geographically isolated for a long time and have diverged from each other by adapting to their local environments. Genetic diversity provides the raw materials for adaptation to changing environments. Conserving genetic diversity protects a population's evolutionary potential, which may be especially important given climate change and increasing disease pressures. Maintaining high levels of genetic diversity is also important because it helps offset the generally deleterious fitness effects of inbreeding depression. There is a growing body of evidence that inbred individuals may be more susceptible to diseases (Frankham and others 2002; Altizer and others 2003; Spielman and others 2004), so preventing inbreeding may help reduce the probability of disease epidemics. Maintenance of genetic diversity and knowledge of the distribution of genetic variation in adaptive traits is important in developing guidelines for the movement of seed in reforestation or restoration projects via developing appropriate seed transfer guidelines and will be especially important in predicting the potential effects of climate change.

How Is Genetic Diversity Assessed?

Genetic diversity is generally assessed using molecular markers and/or phenotypic traits measured on individual seedlings or trees growing in the field or in a common garden. Molecular markers include different enzyme products (proteins) resulting in alternate forms of a gene (isozymes and allozymes), or differences in the DNA sequence of the gene itself. Molecular markers in non-coding regions of the DNA sequence are likely to be selectively neutral, reflecting only

the effects of demographic and historical processes and not natural selection, while those within coding sequence may not be. There is a growing body of evidence indicating that these markers may not truly be immune to selection, since they may be very close to or linked to adjacent segments of DNA which are impacted by selection (Hahn 2008). A relatively new branch of genomics research, association genetics, specifically investigates the differences found between single nucleotide polymorphisms, called SNPs, which, when assessed in combination with phenotypic information, can reflect local or lineage-wide adaptation (Eckert and others 2009; Eckert and others 2010; Gonzalez-Martinez and others 2007; Gonzalez-Martinez and others 2008; Hall and others 2010; Holliday and others 2008; Manel and others 2010; Neale and Savolainen 2004).

Any physical trait that can be measured on a plant is a quantitative trait. Examples include height, diameter, leaf area, volume, root:shoot ratio, biomass, stress tolerance (e.g., cold or drought), and phenology (e.g., timing of flowering, growth initiation and cessation). If a trait is associated with an environmental gradient, such as temperature or precipitation, then it may reasonably be inferred that the trait has been affected by natural selection and is considered to be adaptive (Endler 1977). Assessing quantitative traits, whether they are adaptive or not, requires measurement of the traits on individuals from a wide variety of geographic origins that are all growing in a common environment to eliminate differing environmental influences on genotypic expression. The physical expression of a plant's genetic makeup, its phenotype, is a product of its genotype and the environment where it is growing. Mature trees in field test sites or seedlings growing in a common garden study are examples (for example Bower and Aitken 2008; Schoettle and Rochelle 2002; Steinhoff and Andresen 1971; and Wright and others 1971). Both of these tests involve collecting seeds or cuttings from a wide geographic range and growing individual trees. Field test sites are often long term, while common gardens usually only last for a few years.

Conservation Challenges

High elevation five-needle white pines are widely distributed across much of western North and Central America and all face conservation challenges: for example habitat fragmentation, introduced disease and insect pests (for example mountain pine beetle *Dendroctonus ponderosae*), advanced succession and climate change (Gibson and others, 2008b, Tomback and Achuff, 2010) as well as harvesting for firewood and incidental cutting during harvest of other co-occurring species. They have low timber value, yet they have high ecological value; and they are all susceptible to the introduced disease white pine blister rust (caused by the fungus *Cronartium ribicola*) (Schoettle and Sniezko 2007). Potential range shifts resulting from global climate change pose an additional threat to these high elevation species, as suitable climates may only occur above the mountaintops where they are often found (Rehfeldt and others 2006; Warwell and

others 2007; Wang and others in preparation). The impacts of rust differ by species and also within the geographic range of each species (Schoettle and Sniezko 2007). The combined impacts of these threats have necessitated active management and conservation activities for all of these species.

Genetic conservation approaches may be categorized as either *in situ* or *ex situ*. *In situ* conservation means that genetic resources are protected within a species' natural habitat. This type of conservation is relatively inexpensive and simple, and includes areas such as federally designated wildernesses, National Parks, Research Natural Areas, and other parks and preserves where management activities are limited serve to protect standing genetic diversity. The network of currently existing reserves serve *in situ* conservation purposes well; however, there are risks associated with this conservation strategy. Large-scale disturbances, such as fires, disease, and insect outbreaks, could potentially wipe out large areas of protected habitat. In *ex situ* gene conservation, the resources are protected outside their natural environment. This includes seed orchards, clone banks, long-term seed storage, and cryopreservation. While more secure in some respects, *ex situ* gene conservation can be costly and requires sampling, preferably range-wide, in order to capture as much of the standing genetic diversity as possible. This method focuses on long-term storage and contingency usage of the germplasm, and does not explicitly accommodate the ecological processes or linkages among species inherent with *in situ* conservation approaches.

Taxonomy

The high elevation five-needle pines are all in the group of soft or white pines called haploxylon pines. Taxonomically they are all classified as *Pinus* subgenus *Strobus*, which is split into the sections *Parrya* and *Quinquefoliae* (Gernandt and others 2005; Little and Critchfield 1969; Price and others 1998). Within section *Parrya*, Rocky Mountain bristlecone pine (*Pinus aristata*), foxtail pine (*P. balfouriana*), and Great Basin bristlecone pine (*P. longaeva*) are classified in subsection *Balfourianae* (Bailey 1970). Rocky Mountain and Great Basin bristlecone pine were considered a single species (*P. aristata*) until 1970 (Bailey 1970). Within section *Quinquefoliae* (formerly section *Strobus,* Little and Critchfield 1969), limber pine (*P. flexilis*), southwestern white pine (*P. strobiformis*), and Mexican white pine (*P. ayacahuite*) are classified in subsection *Strobus* (formerly subsection *Strobi,* Little and Critchfield 1969; Price and others 1998). While Mexican white pine is not a North American high-elevation five-needle white pine, we have included it here for completeness because of its inclusion in subsection *Strobus* and its close affinity with southwestern white and limber pine. Whitebark pine (*P. albicaulis*) has traditionally been classified in subsection *Cembrae* (Little and Critchfield 1969; Mirov 1967; Price and others 1998; Shaw 1914), the stone pines, which contains four other Eurasian species distinguished by wingless seeds and indehiscent cones (Shaw 1914; Lanner 1982), a character that appears to be an adaptation to seed

dispersal by nutcrackers (genus *Nucifraga*, family Corvidae) (Lanner 1982; Tomback and Linhart 1990). However, a recent treatment by Gernandt and others (2005) using chloroplast DNA sequences collapsed the subsection *Cembrae* into subsection *Strobus*, supporting earlier results that failed to find differences between subsections *Cembrae* and *Strobus* (Strauss and Doerksen 1990; Liston and others 1999; Tomback and others, these proceedings).

Mexican white pine and foxtail pine are the only species with recognized varieties. *P. ayacahuite* var. *veitchii* is found primarily in the northern part of the species' range while var. *ayacahuite* which is found in the southern part of its range (Farjon and Styles 1997). Perry (1991) also recognized var. *brachyptera* which often is synonymous with southwestern white pine in accordance with Farjon and Styles (1997). We have, therefore, included southwestern white pine as a distinct species. Foxtail pine also has two subspecies, defined by their geographic distributions with subspecies delineated by several quantitative, needle, cone and bark characteristics. Subspecies *austrina* is found in the southern Sierra Nevada and subspecies *balfouriana* is found in the Klamath Mountains of northern California (Bailey 1970; Mastrogiuseppe and Mastrogiuseppe 1980). Indirect estimates of divergence times between northern and southern populations are ~10^6 years ago (Eckert and others 2008).

Genetic Diversity and Population Structure

While the genetics of some of these species have been well studied, large information gaps remain regarding the genetic diversity and population structure of others. This information is crucial for the development of management strategies designed to conserve genetic diversity. To date, most molecular assessments of genetic diversity have used isozymes, although the number of DNA marker studies is increasing. Diversity statistics from DNA studies vary depending on marker type and the number of loci assessed. For consistency we have focused on studies using isozymes, as these values are generally comparable across species. We have included results from DNA studies when this is the only information currently available. Genetic diversity (expected heterozygosity, H_e) for these species is generally at or below the mean relative to other widespread western North American conifers (figure 1). However, there is a great deal of variation among species, both in the number and the range of published values. For instance, a value reported (0.327) for Great Basin bristlecone pine is one of the highest
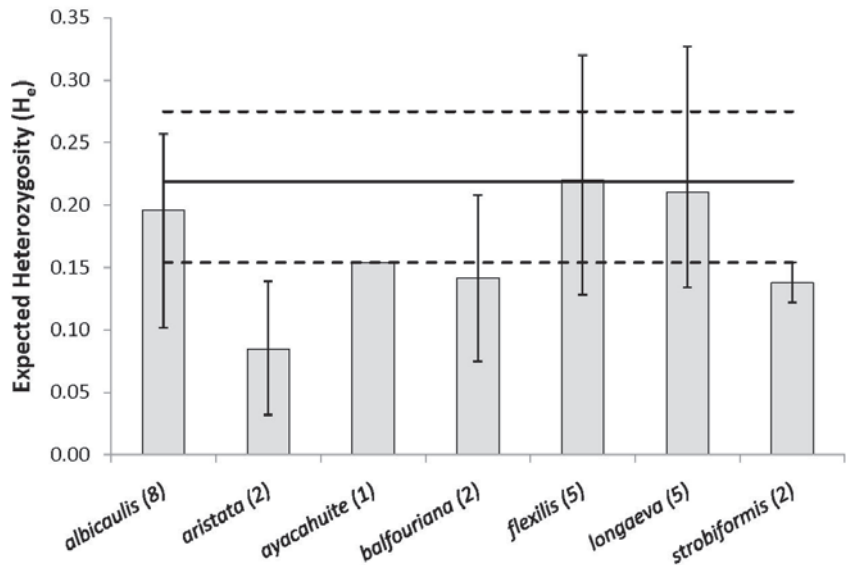

Figure 1. Expected heterozygosity (H_e) for seven species of high elevation five-needle pines. Bars indicate range of reported values[a]. Lines are the mean (solid) and range (dashed) for pines in the subgenus *Strobus* summarized from Ledig (1998). Error bars are the range of values given in Table 1, numbers in parentheses are the number of values reflected in chart.
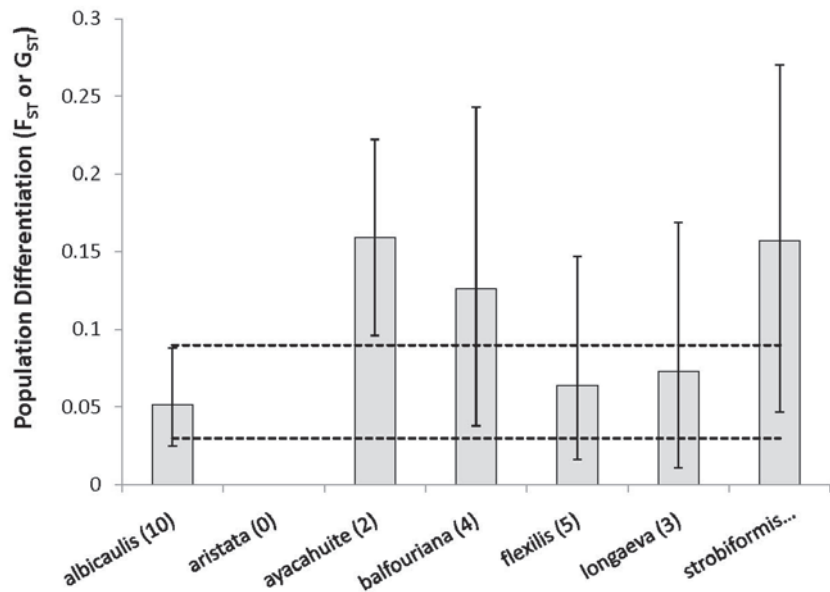

Figure 2. Population differentiation (F_{ST} or G_{ST}) for seven species of high-elevation five-needle pines[a]. Bars indicate the range of reported values. Dashed lines are means for samples of pines with wind- or seed-dispersed seed from (Bruederle et al. 1998). Error bars are the range of values given in Table 1, numbers in parentheses are the number of values reflected in chart

observed in any conifer, while reports for its closest relative, Rocky Mountain bristlecone pine, have been low (figure 1). Population differentiation (F_{ST} or G_{ST}) also varies considerably among species (figure 2). Pines with bird-dispersed seed on average exhibit levels of population differentiation only one third of those with wind-dispersed seed (figure 2),

due to the more efficient mechanism of seed dispersal leading to population homogenization (Bruederle and others 1998; Bruederle and others 2001; Tomback and others, these proceedings). Whitebark and limber pine both rely on the Clark's Nutcracker for seed dispersal, and have relatively low levels of population differentiation. The other species have average or above levels of population differentiation, possibly due to their patchy and discontinuous distributions on mountaintops across large areas. Only a single report of heterozygosity from two populations is available for southwestern white pine, c.f. unpublished data in Ledig (1998).

Genetic Management

Gene conservation strategies have been developed and implemented for whitebark and Rocky Mountain bristlecone pine. The Pacific Northwest Region of the USDA Forest Service developed a restoration strategy for whitebark pine in Oregon and Washington (Aubry and others 2008) and an *ex situ* gene conservation plan (Bower and Aubry 2009), and a range wide restoration strategy is in development (Keane and others in preparation). As noted above, all of these high-elevation five-needle white pine species face a variety of threats. In some instances, the threats are acute (for example, mountain pine beetle, or white pine blister rust), while other threats are more slow acting (for example climate change, habitat fragmentation, land use conversion). Regardless of the threat(s) faced, all of these species are vulnerable to population declines, and active management is necessary to preserve the existing genetic resources and restore degraded populations. Extensive gene conservation efforts are under way for most high elevation five-needle pine species. Development of blister rust resistant planting stock is a crucial part of a restoration plan for any of these species: rust resistance trials are under way for whitebark pine (Mahalovich and Dickerson 2004; Mahalovich and others 2006; Sniezko and others 2007; R. Sniezko personal communication), southwestern white pine (R. Sniezko, personal communication), Great Basin bristlecone pine (D. Vogler, personal communication), limber pine, and Rocky Mountain bristlecone pine (A. Schoettle, personal communication). Blister rust resistance screening has identified some resistance in all of these species (Sniezko and others, these proceedings), including a hypersensitive reaction type of resistance in several species (Kinloch and Dupper 2002).

Whitebark Pine (*Pinus albicaulis* Engelm.)

Occurrence

Whitebark pine occurs in high-elevation treeline ecotones throughout much of northwestern United States and southwestern Canada. The species' range is comprised of two major components: the Sierra Nevada, Cascades, and coastal ranges of British Columbia, Canada, to the west; and the Rocky Mountain ranges to the east, with scattered patches of habitat in between (Arno and Hoff 1989, Tomback and Achuff 2010, Tomback and others, these proceedings). The breadth of temperatures experienced by whitebark pine is relatively consistent throughout its range (Weaver 2001), while the elevation at which it grows drops from 3,600 m in the Sierra Nevada to 900 m in central British Columbia. Whitebark pine is unique among North American pines in that the cones remain closed and affixed to the tree at maturity. The species is almost entirely dependent on Clark's Nutcrackers (*Nucifraga columbiana*) for seed dispersal (Tomback 2001).

Genetic Diversity

Range-wide and regional studies have yielded a range of genetic-diversity estimates for whitebark pine (table 1). In an allozyme study using populations from throughout the species range, Jorgensen and Hamrick (1997) found whitebark pine to have lower within (H_e = 0.092) and among (H_e = 0.102) population genetic diversity than most pines. Bruederle and others (1998) found similar patterns (H_e = 0.152) among whitebark pine populations in the Greater Yellowstone Ecosystem. In a regional study within British Columbia, expected heterozygosity levels were higher (H_e = 0.262), perhaps as a result of founding events from multiple populations within the region (Krakowski and others 2003). There is some evidence of higher genetic diversity in the eastern portion of the species' range than in the west (Jorgensen and Hamrick 1997), and there appears to be lower genetic diversity in the Olympic Peninsula populations than in the Oregon and Washington Cascades (Bower and others unpublished data). Whitebark pine harbors similar levels of genetic diversity relative to other widespread, wind-dispersed pines based on the aggregate of published data (figure 1) (Bruederle and others 1998; Hamrick and others 1992).

Population-level genetic variation and differentiation have been assessed for whitebark pine using both molecular markers (table 1) and quantitative traits (Bower and Aitken 2006; 2008). Neutral marker studies generally reveal little genetic structure among broadly distributed populations (F_{ST} or G_{ST} < 0.09) (table 1 and figure 2). On average, over 95 percent of genetic variation was distributed within populations, and less than 5 percent was among populations.

In a broad-ranging study using microsatellite data from both pollen and seeds, Richardson and others (2002) found relatively homogeneous mtDNA haplotype distributions at both coarse and fine scales within populations, but considerable genetic divergence among populations separated by over 20 km. Pollen-dispersal distances, by contrast, appeared much higher (F_{ST} < 0.007 for cpDNA markers) (Richardson and others 2002). These results concur with expectations of high pollen-mediated gene flow due to wind distribution, but restricted seed-mediated gene flow due to the Clark's Nutcracker, which cache most seeds relatively close to the parent tree, but can fly over a dozen kilometers, thereby mediating long-distance dispersal of genetic material (Tomback 2001). While average genetic diversity is similar among

Table 1. Population genetic information for seven high-elevation five-needle pine species. Data are for isozymes except where noted.

Species	Sample Distribution	# populations	He[a]	Fst or Gst[b]	F[c]	Reference
albicaulis	BC, ID, MT, WY	14		0.075		Bower and others *in press*
	USA range wide and northern AB	30	0.102	0.034	0.084	Jorgensen and Hamrick 1997
	USA Great Basin	14	0.204	0.088	0.06	Yandell 1992
	Canadian Rockies	29	0.224	0.062		Stuart-Smith 1998
	British Columbia	17	0.257	0.061	0.345	Krakowski and others 2003
	range wide	18		0.046[d]		Richardson and others 2002b
	Greater Yellowstone	9	0.152	0.025	0.016	Bruederle and others 1998
	range wide	85	0.194	0.038	0.111	Bower and others these proceedings
	Olympic Peninsula	9	0.163	0.059	0.131	Bower and others these proceedings
	Inland NW	117	0.271	0.026	-0.016	Mahalovich these proceedings
	OR, No. CA, No. NV	13		0.058[e]		Oline unpublished data
flexilis	USA range wide and southern AB	30	0.186	0.101	0.193	Jorgensen and others 2002
	CO	5	0.3	0.035	0.007	Schuster and Mitton 2000
	CO	2	0.32	0.022		Schuster and others 1989
	CO	7		0.016		Latta and Mitton 1997
	n/a[f]	5	0.165	0.147		Hipkins unpublished data
	n/a		0.128			Politov and Krutovsky 2004
strobiformis	Nuevo Leon, MX	2	0.154	0.047		Ledig 1998
	MX	23		0.27[g]		Moreno-Letelier and Pinero 2009
	n/a		0.122			Politov and Krutovsky 2004
ayacahuite	range wide	14	0.154	0.222		Ledig 1998
	MX	7		0.096[h]		Moreno-Letelier and Pinero 2009
balfouriana	range wide	4	0.208			Hiebert and Hamrick unpublished data
	species	16	0.075	0.038	0.267	Oline and others 2000
	subsp. *balfouriana*	5		0.242	0.203	Oline and others 2000
	subsp. *austrina*	11		0.075	0.443	Oline and others 2000
	species	20		0.15[i]		Eckert and others 2008
	between N & S	20		0.17[j]		Eckert and others 2008
aristata	range wide	5	0.139			Hamrick and others 1981
	range wide	4	0.032			Oline unpublished data
longaeva	UT NV	5	0.327	0.0378	0.103	Hiebert and Hamrick 1983
	White Mountains	3	0.134	0.011	0.078	Lee and others 2002
	Great Basin		0.218	0.169		Hamrick and others 1994
	UT		0.237			Hamrick and others 1994
	White Mountains		0.135			Hamrick (cited in Lee and others 2002)

[a] H_e = expected heterozygosity – a measure of genetic diversity;
[b] F_{ST} and G_{ST} are measures of population differentiation;
[c] F is a measure of inbreeding
[d] Φ_{ST} from chloroplast DNA microsatellite data
[e] F_{ST} from chloroplast DNA microsatellite data
[f] n/a = information not available
[g] R_{ST} from chloroplast DNA microsatellite data
[h] R_{ST} from chlorplast DNA microsatellite data
[i] Φ_{SC} from nuclear DNA sequences
[j] Φ_{CT} from nuclear DNA sequences

pines with bird-dispersed and wind-dispersed seed, population differentiation is considerably lower for bird-dispersed species because of the homogenizing effect of birds moving seed among populations (Bruederle and others 1998).

Stand-scale genetic structure is strong for whitebark pine. Stems comprising a "tree cluster" are often half or full-sib relationships, while neighboring clusters in close proximity have the same family structure as those located farther apart (Furnier and others 1987). This was demonstrated by Rogers and others (1999), who found negligible genetic structure among watersheds (F_{ST} = 0.004), but strong differentiation among tree clumps within sites (F_{ST} = 0.334). Again, these trends are directly linked to Clark's Nutcracker seed-caching habits as they can harvest up to 150 seeds at a time, often from a single parent tree, then fly to a caching site and deposit numerous seeds in each cache (Tomback 1982).

Quantitative trait analyses for 48 whitebark pine populations from throughout the species range revealed higher population differentiation (Q_{ST}) for many quantitative traits compared to the differentiation estimates using neutral markers (F_{ST} and G_{ST}) (Bower and Aitken 2006, 2008). Cold adaptation (date of needle flush and fall cold injury) traits showed the strongest geographic differentiation (Q_{ST} = 0.36 – 0.47), while height and biomass growth showed low to moderate differentiation (Q_{ST} = 0.07 – 0.14). In a study using populations from Idaho, Montana and Washington, Mahalovich and others (2006) also found populations differentiated by latitude and climate, with seedlings from milder provenances growing taller but having lower freezing tolerances than those from harsher locations. Using populations from the same region, Warwell (In preparation) found similar trends, with populations from lower elevations and higher latitudes having higher growth potential than their conspecifics. Together, these findings suggest that selection pressures, particularly temperature, are driving local population adaptation.

Mating Systems and Inbreeding Depression

In whitebark pine, high inbreeding rates are attributed to the clustered growth of half and full-sibling individuals caused by Clark's Nutcrackers seed-caching habits (Jorgensen and Hamrick 1997). Numerous studies have quantified inbreeding in whitebark pine at local and regional scales (table 1), indicated by a deficiency of heterozygotes (F_{IS} > 0). In populations from Oregon, Montana and British Columbia, Bower and Aitken (2007) found that outcrossing rates varied among families, with the multilocus outcrossing rate (t_m) averaging 0.86 (range: 0.73 to 0.93). Krakowski and others (2003) found very high inbreeding levels (F_{IS} = 0.345) and outcrossing rates below average for conifers (t_m = 0.73), although only two populations separated by ~100 km were used for these estimates.

Conservation Status and Action

Whitebark pine is declining throughout its range, primarily due to white pine blister rust and secondarily due to mountain pine beetle and fire suppression (Tomback and

others, these proceedings). Climate change is also predicted to have devastating effects for whitebark populations, particularly throughout southern and central portions of the species' range, where forecasted 21st century temperatures are too warm for whitebark pine to retain a competitive advantage (Warwell and others 2007; Wang and others in preparation). Recognizing that Canada's whitebark pine population is expected to decline by over 50 percent due to all these factors within the next 100 years, Canada's Committee on the Status of Endangered Wildlife in Canada (COSEWIC) formally recommended that whitebark pine be classified as endangered in April, 2010 (Tomback and others, these proceedings). Once it is classified as endangered, the Canadian federal government will be responsible for ensuring that a conservation strategy is put in place for the species. In the United States, the Fish and Wildlife Service is currently conducting a status review for whitebark pine in light of its decline (Tomback and others, these proceedings). Whitebark pine is classified as "vulnerable" according to the IUCN, due to declines attributed to 1) white pine blister rust, 2) mountain pine beetle, and 3) successional replacement by shade tolerant species as a result of fire exclusion (Reuling 2008).

In response to its rapid and widespread decline, numerous governmental and non-governmental organizations are drafting conservation strategies at various scales for whitebark pine. The Pacific Northwest region of the USDA Forest Service has drafted a comprehensive, regional conservation strategy for the species focusing on research, restoration, genetic conservation, and blister rust resistance screening (Aubry and others 2008). Over 500 tagged permanent monitoring plots have been installed at nearly 100 locations in Oregon and Washington to monitor health and status over time. A range-wide conservation strategy is also being developed, focused on providing land management agencies with tools to plan, design and implement fine-scale restoration activities (Keane and others in preparation)

Gene conservation

Much of the range of whitebark pine in the United States is located within protected areas on public lands. In Oregon and Washington, 60 percent of the species' habitat is in congressionally-designated wilderness areas (Aubry and others 2008). Whitebark pine is also found in several national parks, including North Cascades, Mount Rainier, Olympic, Crater Lake, Lassen Volcanic, Yosemite, Glacier, Yellowstone, and Grand Teton in the U.S. and seven National Parks in Canada, including Mount Revelstoke, Glacier, Jasper, Banff, Kootenay, Yoho, and Waterton Lakes. There are also extensive populations in provincial parks and other protected areas throughout southern British Columbia and western Alberta. These lands provide an extensive *in situ* gene conservation resource; however, the integrity of this resource is seriously threatened in many areas by white pine blister rust and mountain pine beetle. Range-wide cone collections have been made for *ex situ* gene conservation, blister rust resistance screening, and restoration (see Sniezko and others these proceedings; Bower and Aubry 2009; Bower

and others 2009). To date, seed has been collected from approximately 700 individuals in the United States for long term *ex situ* gene conservation.

White pine blister rust resistance

White pine blister rust resistance screening initiated at USDA forest genetics centers (Dorena Genetic Resource Center in Cottage Grove, OR; Pacific Southwest Research Station in Placerville, CA; Coeur d'Alene Nursery in Coeur d'Alene, ID) have reported low to moderate levels of natural rust resistance in some populations, as evidenced by the ability of seedlings to survive multiple spore inoculations (Mahalovich and others 2006; Vogler and others 2006; Sniezko and others 2008; Sniezko and others these proceedings). Resistance varies along a geographic cline within the intermountain western U.S., increasing from southeast to northwest (Mahalovich and others 2006). Resistance also appears to be higher among populations from milder climates (Mahalovich these proceedings). In Oregon and Washington, early results show that approximately 25 percent of families field selected for possibly resistance and tested had some level of resistance (R. Sniezko, personal communication). Resistant seedlings have been recommended for immediate use in restoration planting as well as in breeding programs. However, it will be critical to account for other factors—particularly temperature and day length—that may affect survival of planting seedlings. Seed transfer guidelines have been developed based on adaptive traits, in an attempt to minimize maladaptation risks at an acceptable level (Aubry and others 2008; Bower and Aitken 2008; Mahalovich and Dickerson 2004). Exceeding these transfer distances increases the risk of maladaptation under current conditions, and should only be done after weighing this risk against the need for restoration. In the case of white pine blister rust, the risk of disease infection may outweigh the risk of maladaptation, and it may be desirable to move resistant seedlings beyond the recommended limits.

Predicted climate change impacts

Whitebark pine is expected to fare poorly as the climate warms (see also Tomback and others, these proceedings). Within its current range, models predict that faster-growing species such as subalpine fir and Engelmann spruce will encroach from lower elevations (Schrag and others 2008), while ecologically and climatically suitable habitat may not open at higher elevations due to the slow development of adequate soils in alpine environments. Results from growth chamber experiments similarly indicate that lodgepole pine dominates whitebark pine in height growth at virtually all growing season temperatures predicted to occur within whitebark pine's current range within the 21st century (McLane and Aitken in preparation). Moving seed only from south to north has been recommended, as these populations may be "pre-adapted" to a warmer climate. Mixing seed from different populations within the acceptable transfer range would likewise facilitate natural selection among a wider range of genotypes (Bower and Aitken 2008).

Whitebark pine is expected to lose up to 90 percent of its climatic range within Canada by the end of the 21st century (Warwell and others 2007, Wang and others in prep.). However, a large area of northwestern British Columbia that does not currently support this species may be climatically suitable for the species at present, and remain so as the climate warms (Wang and others in preparation). McLane and Aitken (in preparation) established common garden trials at multiple latitudes within the predicted climatic range to assess how climatic and environmental factors impact whitebark pine germination and survival in these areas, and whether populations respond differently across the range of growing conditions. In the first three growing seasons, germination, survival and growth were positively influenced by early-melting snow packs and warmer growing conditions, while population differences were negligible. The common gardens will continue to be monitored at least until the 2030s. McLane and Aitken are also initiating an experiment to evaluate growth and survival of seedlings planted along an altitudinal transect representing a ~3 °C temperature gradient in Whistler, BC. The seedlings were planted in August, 2010, and will be monitored for survival and growth.

Limber Pine (*Pinus flexilis* James)

Occurrence

Occurring from southern Canada to northern New Mexico, limber pine is one of the most widely distributed five-needle pines in North America (Tomback and Achuff 2010; Tomback and others, these proceedings). Mostly occurring in the Rocky Mountain and the Basin and Range regions, populations are also found in the White and Sierra Nevada ranges of California, the Black Hills of South Dakota and as isolates in the Great Plains. Limber pine has a wider elevation al distribution than any of its co-occurring conifers; it grows on sites from 870 m in North Dakota to over 3400 m in Colorado (Steele 1990). While primarily an upper timberline species in relatively dry locations, limber pine is also found at lower timberline in locations such as along the Rocky Mountain Front and in the Great Plains and Black Hills (Steele 1990). Substantial fossil evidence suggests the Pleistocene distribution of the species extended into the Great Plains, Texas and northern Mexico (Wells 1983; Betancourt 1990).

Like whitebark pine, limber pine is partially dependent on Clark's Nutcracker for long distance seed dispersal (Tomback 1978; Tomback and Linhart 1990). Morphologically, it is difficult to distinguish the two species without cones, but the dehiscent and slightly longer and slimmer cones readily identify limber pine, and limber pine usually grows at lower, climatically milder elevations. Despite the similar morphology and reliance on the Clark's Nutcracker for dispersal, limber pine is most closely related to southwestern white pine (*P. strobiformis*) of the southwestern U.S. and northern Mexico, and Mexican white pine (*P. ayacahuite*), which extends into southern Mexico. This group of three species,

which form a seed dispersal cline from wind-dependent in the south to Nutcracker-dependent in the north, has been described as the "world's greatest north-south chain of pine populations…" (Lanner 1996, p. 111). *Pinus flexilis* var. *reflexa* or *P. reflexa* is a taxon of apparently hybrid origin between *P. flexilis* and *P. strobiformis* (Farjon and Styles 1997). There has been speculation that the origin of the hybrid zone is ancient, with most current individuals being later generation backcrosses to *P. strobiformis* (Perry 1991).

Genetic Diversity and Structure

Compared to other North American high elevation five-needle pines, limber pine has relatively high levels of allozyme diversity (table 1 and figure 1). However, there is substantial variation in the amount and distribution of genetic diversity over the species' range (Jorgensen and others 2002). In general, populations from the Basin and Range and central Rocky Mountain regions exhibit higher levels of genetic diversity than northern Rocky Mountain or peripheral isolated populations (Jorgensen and others 2002; Schuster and Mitton 2000).

Genetic variation in quantitative traits has been found among populations and among families within populations. Differences among populations exhibited a gradation with cone size, seed weight, and seedling growth slightly increasing and leaf color darkening from north to south (Steinhoff and Andresen 1971; Wright and others 1971). Quantitative genetic variation in limber pine has been characterized as low (Steinhoff and Andresen 1971).

Contemporary gene flow among populations appears to occur mainly via pollen flow (Latta and Mitton 1997; Schuster and Mitton 2000), despite the Clark's Nutcracker's ability to disperse seeds long distances. Latta and Mitton (1997) examined seven populations of limber pine from Colorado using chloroplast (cpDNA) and mitochondrial (mtDNA) DNA, which are paternally and maternally inherited, respectively. There was virtually no genetic structure among cpDNA haplotypes, representing both pollen and subsequent seed dispersal (F_{ST} = 0.013). In contrast, strong genetic structure was detected among the mtDNA haplotypes, which are dispersed via seeds only (F_{ST} = 0.679). Because of substantial pollen flow, genetic neighborhoods of limber pine populations are quite large (Schuster and Mitton 2000).

Substantial amounts of local pollen flow have not translated to broad-scale patterns of homogeneity, however. Mitochondrial DNA indicates that the current distribution of limber pine was derived from several Pleistocene-era refugial populations (Mitton and others 2000). These ancestral populations, combined with low recent historical seed flow, have resulted in contemporary populations that are substantially differentiated. These patterns are not uniform over the species' range, however. For example, genetic structure among populations in the Basin and Range region, which harbored Pleistocene populations, is substantially higher than among populations from the relatively recently colonized northern Rocky Mountains (G_{ST} of 0.084 and 0.038,

respectively). Studies with a more limited range tended to reveal lower geographic structure than a range-wide study (table 1). Across all of these studies, population differentiation is intermediate between mean values for pines with bird-dispersed and wind-dispersed seed, although there is a substantial range in these values (figure 2).

As a result of the seed foraging and caching behavior of the Clark's nutcracker, limber pine can be found growing as single stems, single genet multi-stemmed trees, and as clusters of genetically distinct individuals. Genetic analysis has shown that approximately 20 percent of these tree groups contain more than one distinct individual. Furthermore, individual stems in these clusters are often related at the level of half to full siblings but were unrelated to stems in nearby clusters (Carsey and Tomback 1994; Schuster and Mitton 1991).

Mating System and Inbreeding Depression

Inbreeding within populations appears to be quite variable over the species' range. The mean F_{IS} for 12 polymorphic allozyme loci analyzed in five populations sampled from northern Colorado was 0.007 (Schuster and Mitton 2000). In contrast, a range-wide survey of 30 populations found a mean F_{IS} = 0.108 using 18 polymorphic allozyme loci (Jorgensen and others 2002). However, there was significant regional variation in the levels of inbreeding within populations, with those from the Basin and Range having significantly more inbreeding on average (F= 0.127) than those from the northern Rocky Mountains (F= 0.025). Given the highly isolated nature of populations in the Basin and Range region, inbreeding there may be of conservation concern, especially since these populations may represent remnants of Pleistocene populations that may harbor genetic diversity or unique alleles not present in other locations within limber pine's range (Jorgensen and others 2002; Mitton and others 2000).

Conservation Status and Action

Populations of limber pine have been severely impacted by pathogens such as white pine blister rust and mountain pine beetle infestations. Among populations in Wyoming and northern Colorado, the mean number of trees infected with blister rust within populations is about 14 percent, although some populations have more than 50 percent rust incidence (Kearns and Jacobi 2007). While the mean infection incidence is lower (5-8 percent) in southern Colorado, local infection pockets also exceed 50 percent rust incidence (Burns 2006). Mountain pine beetle infestations have caused high mortality in limber pine populations. For example, large numbers were killed in the early 1980s in Alberta (Langor 1989). More recently, significant mortality has occurred the northern Rocky Mountains, particularly in the Yellowstone plateau region (Gibson and others 2008) and the southern Rockies (Schoettle and others 2008). As current beetle outbreaks are sustained, increased mortality in limber pine is expected. Other pathogens that have inflicted substantial

mortality in limber pine populations include limber pine dwarf mistletoe (*Arceuthobium cyanocarpum*) (Hawksworth and others 2002). In Canada, *C. ribicola* is known to hybridize with comandra blister rust (*Cronartium comandrae*), a native rust of hard pines, and hybrids have been documented to occur on limber pine (Hamelin and others 2005; Joly and others 2006). What effect this may have on the rust's pathogenicity is currently unknown.

Gene conservation

As a result of its wide distribution, limber pine is protected *in situ* in a number of designated wilderness areas, research natural areas, state and provincial parks and preserves, and national parks, including Waterton Lakes, Glacier, Yellowstone, Grand Teton, Rocky Mountain, Great Sand Dunes, Great Basin, Bryce Canyon, Cedar Breaks, and Death Valley National Parks. These lands provide an extensive *in situ* gene conservation resource; however, the value of this resource is seriously threatened in many areas by white pine blister rust and mountain pine beetle. Seed collections have been made for gene conservation, rust resistance screening and research for limber pine in the Rocky Mountains (Schoettle and others these proceedings); more are planned (see Sniezko and others these proceedings). The range of limber pine covers areas where blister rust has been present for almost 100 years to areas where blister rust is not present. This presents a unique opportunity to sample areas for *ex situ* gene conservation both with and without the impacts of blister rust. In 2009 limber pine was recognized as a provincial Endangered Species under the Alberta Wildlife Act.

White pine blister rust resistance

Rust resistance testing for partial and complete resistance mechanisms are underway (Sniezko and others 2008). Early results showed a wide range in rust susceptibility with several families having a large proportion of seedlings developing no stem symptoms following artificial inoculation (Sniezko and others 2008), and final results of this screening are forthcoming. A complete disease resistance phenotype consistent with that found in western white and sugar pines has been detected in a bulk sample from Colorado (Kinloch and Dupper 2002). This resistance mechanism was not found in single bulk populations sampled from Arizona, California or Montana; however, at these locations, seeds were assessed from only a single tree (Kinloch and Dupper 2002). The geographic distribution of this trait will be further defined with more extensive sampling and testing. Preliminary results from ongoing studies suggest evidence for partial resistance mechanisms in limber pine, but results are not yet available (Schoettle and others 2010).

Predicted climate change impacts

Limber pine has broad environmental tolerances (Schoettle and Rochelle 2000); and, because of its adaptation to dry sites, limber pine may be less affected by climate change than other high elevation five-needle pines (Letts and others 2009; Millar and others 2007). It may adjust

to changing climatic conditions via migration or adaption within populations (Schoettle and others 2009). Some climate modeling scenarios have predicted potential range expansion for this species (McKenney and others 2007). For example, an increase in the incidence of fire could benefit limber pine; most populations are sparse with little ground cover, fires typically do not cause extirpation. Furthermore, sites are rapidly re-colonized via seed dispersal by the Clark's Nutcracker (Webster and Johnson 2000). Fire and climate change can also halt or slow succession, which can increase the longevity of limber pine on sites, particularly those at lower timberline and more xeric habitats (Coop and Schoettle 2009; Donnegan and Rebertus 1999; Rebertus and others 1991).

Interactions among threat vectors & other factors

It has been hypothesized that trees weakened by white pine blister rust may be more susceptible to mountain pine beetle attack (Gibson and others 2008). As limber pine is dependent on Clark's Nutcracker for long distance seed dispersal, the status of the two species are interlinked. In 2005, the conservation status of the Clark's Nutcracker was listed as 'sensitive' in Alberta (changed from 'secure') because of its reliance on declining species such as whitebark pine and limber pine. Additionally, the Clark's Nutcracker may also be susceptible to West Nile virus (Blouin 2004).

Southwestern White Pine (*Pinus strobiformis* Engelm.)

Occurrence

Southwestern white pine has a wide but scattered distribution, restricted to very specific environments in high-elevation mixed conifer forests in temperate and humid areas of northern Mexico and the southwestern states of Arizona, New Mexico and a few scattered populations in southwestern Texas (Farjon and Styles 1997; Perry 1991; Tomback and Achuff 2010; Tomback and others, these proceedngs). The taxonomic status of southwestern white pine is ambiguous and it has been classified as a variety of Mexican white pine (var. *brachyptera*, var. *reflexa*, and var. *strobiformis*), as a variety or possibly a hybrid with limber pine (var. *reflexa*); and as distinct species *P. reflexa* and *P. strobiformis* (Andresen and Steinhoff 1971). There is speculation that trees that are morphologically intermediate between limber and southwestern white pine are hybrids between these species (*P. flexilis* var. *reflexa*). These putative hybrids generally occur in the contact zone between these species in Arizona and New Mexico, and possibly on the top of Cerro Potosi in Nuevo Leon, Mexico (Farjon and Styles 1997). The taxonomic ambiguity of southwestern white pine as a possible intermediate between limber pine to the north and Mexican white pine to the south illustrates the hypothesis that these three species are actually a complex of closely related species following a north-south cline of seed wing size, with near-wingless limber pine in the north, to fully winged Mexican white pine in the south (Farjon and Styles 1997; Lanner 1996).

Genetic Diversity

Southwestern white pine is perhaps the least studied of the high elevation five-needle pines in North America. Published population genetic statistics are sparse and of limited use in comparing genetic diversity and population structure of this species to other high elevation five-needle pines. Ledig (1998) presents the only published heterozygosity estimate for the species, but it is based on only two populations (table 1). A more extensive population genetic study covering much of the range of the species is under way but results are not yet available (T. Ledig, personal communication). Moreno-Letelier and Pinero (2009) found significant genetic structure in southwestern white pine; however, their results are not directly comparable with results from other species because they used a different type of genetic marker (chloroplast microsatellite). They reported that genetic diversity was high, especially in western populations, while diversity was less variable in eastern populations and more similar to *P. ayacahuite* of central Mexico.

Genetic variation in quantitative traits has been assessed on a limited number of geographic sources. Seedling traits differed among populations, with populations from northern New Mexico and Arizona generally being shorter, with shorter needles and a shorter period of growth than populations from central and southern Arizona. Seedlings from southern New Mexico and Texas were similar to seedlings from southern Arizona. The differences between northern and southern sources were more pronounced, with a steeper gradient than in limber pine (Steinhoff and Andresen 1971). Compared with limber pine in the same plantings, growth of southwestern white pine was three to four times greater at age two, and was southwestern white pine was five to six times taller at age nine, but was relatively uniform across population sources (Wright and others 1971).

Mating Systems and Inbreeding Depression

No information on mating system or inbreeding depression is currently available for this species.

Conservation Status and Action

Like all five-needle pines, southwestern white pine is susceptible to white pine blister rust. Blister rust was first observed in southwestern white pine in the wild in the Sacramento Mountains in southern New Mexico in 1990 (Hawksworth 1990) and was subsequently traced back to 1970 (Geils and others 1999). Subsequently, blister rust has been found at several sites in northern and western New Mexico and western Arizona (Schwandt 2010 and references therein; Tomback and others, these proceedings) and there is a high risk of the infection spreading to surrounding mountain ranges (Geils and others 1999). In addition to white pine blister rust, this species is the primary host for the dwarf mistletoe *Arceuthobium blumeri*, which extends from southern Arizona south through Durango and east to Cerro Potosí in Nuevo León (Hawksworth and Wiens 1996).

Gene conservation

Seed collections of southwestern white pine have predominantly been made for research purposes; however, this seed may be useful for *ex situ* gene conservation. Recently, seed has been collected specifically for rust testing and gene conservation purposes (see Sniezko and others these proceedings), and further *ex situ* gene conservation collections are planned.

White pine blister rust resistance

Screening for blister rust resistance in southwestern white pine has been limited until recently. The hypersensitive reaction type resistance has been observed in this species (Kinloch and Dupper 2002; Sniezko and others 2008), as have some types of partial resistance in the limited number of families tested (Sniezko and others 2008). Screening of additional families is currently underway (R. Sniezko, personal communication).

Predicted climate change impacts

Climate modeling has not specifically addressed southwestern white pine; however, as in other areas, predictions of future climates under the most common global circulation models and emission scenarios generally predict increased temperatures and aridity (Saenz-Romero and others 2009). This is predicted to lead to a decrease in suitable habitat for other high elevation tree species with which it grows, such as *P. hartwegii* (Saenz-Romero and others 2009) and several Mexican spruces (Ledig and others 2010). It can be inferred that if suitable habitat for sympatric species is predicted to decrease, it is likely that suitable habitat for southwestern white pine therefore may also decrease under predicted global warming scenarios.

Mexican White Pine (*Pinus ayacahuite* Ehren. Ex. Schlecht.)

Occurrence

Mexican white pine is found at 1500-3500 m from central Mexico south to Guatemala, El Salvador, and Honduras, often in mixed conifer stands with other pines, fir, and oak species. It forms a large tree to 45 m tall and 200 cm DBH, with a straight round trunk, conical crown, and regular branch whorls. It is one of the most important and sought-after softwoods native to Central America and Mexico (Farjon and Styles 1997; Wright and others 1996). It has been harvested for use in furniture and finishing carpentry as well as for firewood, leading to depletion of many previously extensive and mature stands (Farjon and Styles 1997). It also occurs in a number of areas where human pressure to expand agricultural land has resulted in a reduction of forest cover (Dvorak and Donahue 1992).

There are three named varieties within this species; however, var. *brachyptera* recognized by Perry (1991), found in central and northern Mexico, is often considered synonymous with southwestern white pine in accordance with Farjon and Styles (1997). Var. *veitchii* is distributed in central

Mexico and is distinguished by its larger cones which are 15-50 cm long with elongated and thickened scales, giving the cone a woody appearance more similar to a hard (diploxylon) pine than a typical five-needle pine (Farjon and Styles 1997) and larger seed size. Var. *ayacahuite* is distributed in the states of southern Mexico as well as Guatemala, El Salvador, and Honduras.

Genetic Diversity

The only published value for genetic diversity indicates that it is about average relative to other pines (table 1 and figure 1). Allozyme studies indicate population differentiation is high (table 1 and figure 2), probably as a result of the patchy, disjunct nature of the distribution. Population differentiation in the central portion of the species' range was lower based on DNA markers (Moreno-Letelier and Pinero 2009).

Studies of genetic variation of adaptive traits are also limited for this species. A provenance test including sources from Honduras, Guatemala, and southern Mexico (Chiapas), areas that ranged in rainfall from 868 to 2367 mm, revealed significant differences in volume per tree, but height growth was relatively low relative to other local pine species (Wright and others 1996).

Mating Systems and Inbreeding Depression

No information on mating system or inbreeding depression is currently available for this species.

Conservation Status and Action

P. ayacahuite var. *ayacahuite* is classified as "least concern" by the IUCN, but var. *veitchii* is classified as "near threatened". The threats identified are pressure from urban development and harvesting for timber. The area where it was formerly described in El Salvador has been intensively exploited for firewood and Mexican white pine may have now been extirpated from El Salvador (Perry 1991).

Gene conservation

In 1983, CAMCORE (Central America and Mexico Coniferous Forest Resources Cooperative) collected seed from 365 trees in 15 provenances in the native range of *P. ayacahuite* for *ex situ* gene conservation and to evaluate its commercial potential. Initial efforts at *ex situ* conservation through plantings in Columbia showed promise (Wright and others 1996). Isolation of many stands makes *in situ* conservation difficult, although it is present in Los Altos de San Miguel Totonicapán Park, Guatemala (ParksWatch 2004). In Mexico the pine is represented in most high elevation national parks within its distribution (for example Parque Nacional Tztacchuatl Popocatepetl, Parque Natural Lagunas de Zempoala, and Parque Natural del Tado de Guerro) (D. Tomback, personal observation)

White pine blister rust resistance

No information on white pine blister rust resistance is currently available for this species. It was ranked last or second to

last of 16 North American and Eurasian white pine species for six resistance mechanisms (Hoff and others 1980). The hypersensitive reaction was not observed in a limited sample of 506 seedlings from four populations (Kinloch and Dupper 2002).

Predicted climate change impacts

Climate modeling for Mexico has not specifically addressed Mexican white pine; however, as in other areas, predictions of future climates under the most common global circulation models and emission scenarios (Hadley, Canadian Centre for Climate Modeling and Analysis, Geophysical Fluid Dynamics Laboratory A2 and B1 scenarios) generally indicate increased temperatures and aridity (Saenz-Romero and others 2009). These will also lead to a decrease in suitable habitat for other pine species such as *P. hartwegii* and *P. pseudostrobus,* (Saenz-Romero and others 2009) which grow with Mexican white pine (Farjon and Styles 1997), and several Mexican spruces (Ledig and others 2010). Suitable habitat for Mexican white pine therefore is also likely to decrease under predicted global warming scenarios.

Foxtail Pine (*Pinus balfouriana* Grev. & Balf.)

Occurrence

Foxtail pine (*Pinus balfouriana* Grev. & Balf.) is distributed within the mountains of California and is divided into two disjunct populations separated by 500 km—the Klamath mountains of northern California and the Sierra Nevada of southern California (Tomback and Achuff 2010; Tomback and others, these proceedings). These regional populations experience dramatically different climate and environmental regimes, as well as ecological conditions (Eckert and Sawyer 2002). Stands in the north are relatively diverse, dense and are located along mountaintops and ridgelines. Within these stands, foxtail pine forms a minor to major ecological component depending on microsite and soil type (Eckert 2006a; Eckert 2006b). Foxtail pine stands in the south form extensive, typically single species subalpine communities throughout most of the southern Sierra Nevada. They are geographically extensive and relatively less diverse and (Rourke 1988; Ryerson 1983). These regional populations have been divided into two subspecies based on needle, cone and bark morphology (Bailey 1970; Mastrogiuseppe 1980)—*P. balfouriana* subsp. *balfouriana* in the north and *P. balfouriana* subsp. *austrina* in the south. Priority was given to the northern population due to John Jeffrey's collection of the first foxtail pine specimen in the Scott Mountains of northern California in 1852 (Colville 1897). The first taxonomic treatment, however, was provided by R. K. Greville and J. Balfour in 1853 (Murray 1853).

Genetic Diversity

Genetic differentiation has been assessed for foxtail pine primarily through molecular markers (Eckert and others 2008; Eckert and others 2010; Hamrick and others 1981;

Oline and others 2000). Although needle, cone and bark morphologies were used to define subspecies (Mastrogiuseppe and Mastrogiuseppe 1980), there has been no published analysis of quantitative characters. Genetic diversity within this species has been assessed with allozymes (Hamrick and others 1981; Oline and others 2000), as well as DNA sequences and nuclear SSRs (Eckert and others 2008; Eckert and others 2010). In general, genetic diversity is low to moderate (table 1). Estimates of F_{ST} between regional populations vary depending on marker type, with allozymes giving the lowest value of 0.038 and mitochondrial DNA sequences (mtDNA) giving the highest value of 0.476 (table 1 and figure 2), both indicating that population structure is greater among stands in the northern population relative to the southern population (allozymes: F_{ST} = 0.242 [north] vs. 0.075 [south]; mtDNA: F_{ST} = 0.321 [north] vs. 0.174 [south]).

There is no information on genetic variation of adaptive traits for this species.

Mating Systems and Inbreeding Depression

Breeding structure and inbreeding depression have not fully been assessed for foxtail pine across its natural range. The allozymes used by Oline and others (2000) tended to have significantly positive values of F_{IS} across various population-level comparisons, which is consistent with substructuring, possibly due to inbreeding. This effect was greater among northern stands. There are, however, pronounced effects of ecological conditions on marker diversities at small spatial scales in the Klamath Mountains. In a study using five nuclear microsatellites, F_{IS} was significantly positive for two stands characterized by high species diversities with low foxtail pine density, and zero for two stands with the opposite patterns (Eckert and others 2010). This pattern was attributed to population bottlenecks followed by spatial expansion within ecologically disparate stand types

Conservation Status and Action

Analysis of size class distributions for foxtail pine in the Klamath region suggests that most stands are stable or growing (Eckert 2006; Eckert and Eckert 2007). This was also confirmed recently for stands located in both regions, with the southern Sierra Nevada having somewhat lower growth rates data (Maloney, unpublished data). These results were attributed to high recruitment in some stands and high survival in most stands, consistent with the pines long lifespan. Downslope expansion within stands in the Klamath Mountains has also been shown by Eckert and Eckert (2007). The magnitude of expansion was correlated to several ecological and environmental variables suggesting that response to climate change in this region will be complex, especially since current estimates of demographic stability or growth are correlated far more with survivorship than recruitment (Maloney, unpublished data).

Gene conservation

Up to 70-90 percent of the range of foxtail pine is protected in federally designated wilderness areas, Research Natural Areas, and in Sequoia-Kings Canyon National Park, providing *in situ* genetic conservation. Cone collections have been made from several stands in both the northern and southern portions of the species distribution (see also Sniezko and others, these proceedings). A portion of these seed will be used for long term *ex situ* gene conservation, and additional cone collections are planned to adequately sample the genetic diversity of the species.

White pine blister rust resistance

Little is known about pathogenic threats to foxtail pine. The hypersensitive response (HR) locus, which confers immunity to white pine blister rust, has not been detected in foxtail pine (Kinloch and Dupper 2002). A recent survey of foxtail pine stands demonstrated that white pine blister rust is present in northern stands but not in southern stands, with considerable variation in frequency among stands (Maloney, unpublished data; see also Duriscoe and Duriscoe 2002; Kliejunas and J. 2007). An opposite pattern was observed for mountain pine beetle, with higher prevalence in the southern Sierra Nevada. A limited blister rust inoculation test (13 families) has been established to adjust the protocols for rust resistance screening at the USDA Forest Service Institute of Forest Genetics in Placerville, CA. Early observations show very high susceptibility to rust infection (A. Delfino-Mix, personal communication).

Predicted climate change impacts

Climate models predict that the distributions of high elevation species will decrease under a variety of climate change scenarios (Parmesan 2006; Rehfeldt and others 2006), therefore foxtail pine is expected to be highly sensitive to climate change. Dendrochronological data and climate modeling, however, suggest that drought stress has been a historical driver of local distribution patterns for many subalpine forest trees, including this species (Bunn and others 2005; Millar and others 2004; Millar and others 2006; Millar and others 2007). Indeed, Maloney (personal communication) postulated that drought stress in combination with mountain pine beetle-induced mortality were the drivers behind low population growth rates in two marginal stands of foxtail pine. Response to climate by this species will be complex, because the effect of climate change on realized drought stress has strong environmental and geographical components, and interactions of climate change with various pathogens affecting this species are unknown.

Rocky Mountain Bristlecone Pine (*Pinus aristata* Engelm.)

Occurrence

Rocky Mountain bristlecone pine is found in montane and subalpine habitats in the Southern Rocky Mountains (Tomback and Achuff 2010; Tomback and others, these proceedings). The core of its range is in south central Colorado, east of the continental divide. The range extends south into New Mexico along the Sangre de Cristo Mountains and north

to just south of Rocky Mountain National Park in northern Colorado. A disjunct population occurs on the San Francisco Peaks in Central Arizona. Rocky Mountain bristlecone pine is a high elevation species occupying dry sites from 2750 to 3670 m elevation (Baker, 1992). Though not common, this species occasionally grows in multi-genet tree clumps. At least 20-25 percent of these clumps are made up of more than one genetically distinct individual (Torick and others 1996; Oline unpublished data). Great Basin bristlecone pine (*Pinus longaeva*) was split from Rocky Mountain bristlecone pine in 1970 by Bailey based on anatomical differences (Bailey 1970).

Genetic Variation

This species contains low levels of genetic variation (expected heterozygosity) as measured by isozymes. Genetic diversity in this species is lower than other high elevation five-needle pine species, and is considerably lower than other pines (Hamrick and others 1992; Ledig 1998; Schoettle and others, these proceedings) (table 1 and figure 1). However, Ledig (1998) cites unpublished data by Hiebert and Hamrick who found much higher than expected heterozygosity compared to the studies mentioned above. Conversely, population differentiation in Rocky Mountain bristlecone pine is much higher than in other pines (Hamrick and others 1992; Schoettle et al, these proceedings) (table 1 and figure 2). Studies of genetic variation in adaptive traits are complete with results forthcoming.

Mating System and Inbreeding Depression

High fixation index (F) values have been observed in Rocky Mountain bristlecone pine, indicating the likely presence of both population substructure and inbreeding. Oline (unpublished data) showed that stands as close as 11 km from one another near the northern extreme of the species range differed from one another in the distribution and presence of certain alleles, suggesting a strong founder effect.

Conservation Status and Action

White pine blister rust was first found on Rocky Mountain bristlecone pine in 2003 in south-central Colorado, and rust incidence is still low (Blodgett and Sullivan 2004). The species is experiencing endemic mountain pine beetle impacts; but, now beetle populations are building and mortality in bristlecone stands in increasing (A. Schoettle and others these proceedings). Several studies have assessed the condition and habitat associations of Rocky Mountain bristlecone pine (Baker 1992; Burns 2006; Cocke and others 2005; Coop and Schoettle 2009; Coop and others 2010; Moir and Ludwig 1979). Evidence of increased stand densities due to fire exclusion is suspected in Arizona (Cocke and others 2005).

Gene conservation

The Rocky Mountain Research Station (RMRS) and Forest Health Protection high elevation five-needle pine program focuses on selection, rust resistance, climate change interactions, and neutral and adaptive genetic variation of Rocky Mountain bristlecone and limber pine (Burns and others 2010; Schoettle and others these proceedings). *Ex situ* gene conservation activities such as long-term performance tests, clone banks, and seed orchards have not yet been established; however, seed collections have been made since 2001 by RMRS and over 340 individual tree collections have been made from over 30 sites thus far (see Schoettle and others, these proceedings). Completion of range wide collections are underway, a portion of which will be archived for long term gene conservation (Sniezko et al, these proceedings). Rocky Mountain bristlecone pine *in situ* genetic resources include several Research Natural Areas as well as national parks and preserves.

White pine blister rust resistance

The distribution of white pine blister rust on bristlecone pine is concentrated within the Mosca Creek drainage in the southern portion of the Sangre de Cristo Mountains within the Great Sand Dunes National Park (Burns 2006). Symptoms of white pine blister rust were more inconspicuous on the bristlecone pines observed in this study than on infected limber pines, making the disease much harder to identify, particularly in the early stages of infection. The latent period between infection and sporulation may be longer on Rocky Mountain bristlecone pine than on other species, possibly as long as 8-16 years (A. Schoettle, this proceedings). Permanent plots have been installed in and around the infection center to provide valuable information on the rate of spread of the rust, disease progression, and mortality on Rocky Mountain bristlecone pine (Burns 2006). A risk analysis showed that 50 percent of the five-needle pine habitat in Colorado has an average climate suitable for white pine blister rust (Kearns 2005; Howell and others 2006). Therefore, we expect the continued spread of blister rust in Rocky Mountain bristlecone pine. Proactive resistance trials of Rocky Mountain bristlecone pine families from the core portion of its range are currently under way (Sniezko and others 2008; Schoettle and others 2010).

Predicted climate change impacts

Maps of predicted future climates show a significant decrease in habitat in the U.S. climatically suitable for Rocky Mountain bristlecone pine under future climate warming scenarios (USDA Forest Service). A related species, Great Basin Bristlecone pine, has shown an increase in radial growth at treeline due to increased temperature in recent years (Salzer and others 2009). Rocky Mountain bristlecone pine may respond similarly. Climate change may also result in range shifts in the frequency of and expansions for mountain pine beetle epidemics, possibly resulting in them becoming more prevalent due to higher survival, or the possibility of supporting a 1-year as opposed to its temperature-restricted 2-year reproductive cycle in the higher elevation forests (Gibson and others 2008; Cudmore and others 2010; Bentz et al these proceedings).

Great Basin Bristlecone Pine
(*Pinus longaeva* Bailey)

Occurrence

Based on morphology, bristlecone pine was split in 1970 into two species, Great Basin and Rocky Mountain bristlecone pines (Bailey 1970). Great Basin bristlecone pine occurs at high altitudes in Utah, Nevada, and in the White Mountains of California (Tomback and Achuff 2010, Tomback and others, these proceedings). In the Great Basin it is found on isolated mountain ranges separated by xeric valleys. It usually inhabits sites with poor soils, but can form extensive stands. It has small, winged seeds typical of wind-dispersed conifers, but on harsh sites at high elevation it regenerates more frequently from seed caches of Clark's Nutcracker (Lanner 1988; Tomback and others, these proceedings). On more mesic sites it has an upright growth form, instead of the twisted, gnarled growth form found on the poorest sites (Hiebert and Hamrick 1984). It is most famous for its extreme longevity, reaching ages of nearly 5000 years (Currey 1965; Schulman 1958).

Genetic Diversity

Across the range of the species, the genetic diversity of *P. longaeva* is about average to above average for pines (figure 1). There is a range of values that have been reported for the species (table 1 and figure 1), and it appears that genetic diversity is highest in the eastern Great Basin (Hiebert and Hamrick 1983) and lower in the White Mountains of California (Hamrick personal communication cited in Lee and others 2002; Lee and others 2002); the reason for the difference is unknown. Expected heterozygosity in the eastern Great Basin is one of the highest ever reported for a conifer (Hiebert and Hamrick 1983).

Population differentiation for *P. longaeva* is slightly lower than for other wind-dispersed pines (table 1 and figure 2). This may be due to dispersal of the seed by birds (Lanner 1988) or may also be explained by continuity among stands during the Pleistocene glacial periods (Hiebert and Hamrick 1983). However, all of the studies have been confined to within one mountain range.

Mating Systems and Inbreeding Depression

Mating system and inbreeding depression in this species have not been explicitly studied, but positive fixation index values (F) indicate a lower level of heterozygosity than would be expected based on allele frequencies, most likely due to some degree of inbreeding (table 1).

Conservation Status and Action

Great Basin bristlecone pine is classified as "vulnerable" by the IUCN. The main threat identified is that it is doubtful whether present rates of regeneration are sufficient to replace the population under present climatic and environmental conditions.

Gene conservation

Portions of Great Basin bristlecone pine's range are protected *in situ* in national parks, including Death Valley, Great Basin, Bryce Canyon, and Cedar Breaks National Parks. Other *in situ* resources include wilderness areas and research natural areas. In 2009, seed was collected from 300 individuals in three widely separated areas of Nevada for *ex situ* gene conservation and rust resistance screening (see Sniezko and others these proceedings), and additional collections are planned from areas in northern Nevada where the range of Great Basin bristlecone pine overlaps with either whitebark or limber pine (D. Vogler, personal communication).

White pine blister rust resistance

Since 2005, 37 families of Great Basin bristlecone pine from groves in the White Mountains have been inoculated with blister rust to screen for resistance at the USDA Forest Service Institute of Forest Genetics in Placerville, CA. These families have shown some resistance in stems, which is being further investigated (D. Vogler, personal communication). Recent collections from the Great Basin and planned collections in northern Nevada will be screened for resistance in the future.

Predicted climate change impacts

Climate change is predicted to have a significant impact on higher elevation ecosystems, resulting in a drastic reduction of suitable habitat for many high elevation plant species (Ledig and others 2010; Tomback and Achuff 2010; Tomback and others, this proceedings; Warwell and others 2007;). Predictions of climate change impacts have not been developed for Great Basin bristlecone pine specifically, but increased radial growth in upper treeline stands of Great Basin bristlecone pine has been linked to warmer temperatures in the last ~50 years (Kipfmueller and Salzer 2010; Salzer and others 2009). Trees at upper treeline sites appear to be sensitive recorders of temperature for several five-needle white pine species, while trees at high elevation sites below treeline appear to be more sensitive to precipitation (Kipfmueller and Salzer 2010). In the Patriarch Grove in the White Mountains of California, anecdotal observations of higher survival of seedlings may be due to warmer temperatures (R. Lanner, personal communication), and while slightly warmer temperature may result in increased radial growth at treeline, the impacts of further warming, especially if there is no increase in moisture, are unknown and may impact survival negatively (Lanner 2007).

Knowledge Gaps

We have identified the following knowledge gaps regarding the conservation genetics of these high elevation five-needle white pine species

- Range wide genetic diversity and population structure of *P. longaeva*, *P. strobiformis*, and *P. ayacahuite*.
- Quantitative trait variation of all species except *P. albi-caulis* (results of several species are forthcoming).
- Potential impacts of climate change.
- Levels, types, durability of white pine blister rust resistance.

Future Research Needs

Understanding the genetics of these species will be helpful in developing and implementing strategies for the conservation and/or restoration of these species to minimize the negative consequences of white pine blister rust and climate change, in particular. The following research and conservation needs have been identified:

- Further investigate the ability of different populations to withstand warming temperatures using *in situ* and *ex situ* common garden experiments
- Continue screening for rust-resistant individuals and/or populations that can be used for restoration planting
- Establish policy frameworks regarding whether and how to assist the migration of species threatened to be extirpated within their current ranges, as may be the case for whitebark pine
- Establish conservation strategies for species where such strategies are not already in place
- Acknowledgements

The authors wish to thank the organizing committee for their invitation to speak about and prepare this review on conservation genetics of high elevation five needle pines, and would like to thank Jodie Krakowski and Nick Wheeler for their helpful and thorough reviews of an earlier version of this manuscript.

References

Altizer, Sonia; Harvell, Drew; Friedle, Elizabeth. 2003. Rapid evolutionary dynamics and disease threats to biodiversity. Trends in Ecology & Evolution. 18(11): 589-596.

Andresen, J. W.; Steinhoff, R. J. 1971. The taxonomy of *Pinus flexilis* and *P. strobiformis*. Phytologia. 22: 57-70.

Arno, Stephen F.; Hoff, Raymond J. 1989. Silvics of whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. INT-GTR-253. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 11 p.

Aubry, Carol; Goheen, Don; Shoal, Robin; Ohlson, Therese; Lorenz, Teresa; Bower, Andrew; Mehmel, Connie; Sniezko, Richard. 2008. Whitebark pine restoration strategy for the Pacific Northwest Region, 2009-2013. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 212 p.

Bailey, D. K. 1970. Phytogeography and taxonomy of *pinus* subsection Balfourianae. Annals of the Missouri Botanical Garden. 57(2): 210-249.

Baker, W. L. 1992. Structure, disturbance, and change in the bristlecone-pine forests of Colorado, U.S.A. Arctic and Alpine Research. 24(1): 17-26.

Betancourt, Julio L. 1990. Late quaternary biogeography of the Colorado Plateau. In: Betancourt, Julio L.; Van Devender, Thomas R.; Martin, Paul S., eds. Packrat middens: the last 40,000 years of biotic change. Tucson, AZ: University of Arizona Press: 259-293.

Blodgett, J. T.; Sullivan, K. F. 2004. First report of white pine blister rust on Rocky Mountain bristlecone pine. Plant Disease. 88(3): 311.

Blouin, François. 2004. Clark's nutcracker (*Nucifraga columbiana*). In: Blouin, François; Taylor, Brad N.; Quinlan, Richard W., eds. The southern headwaters at risk project: a multi-species conservation strategy for the headwaters of the Oldman River. Volume 2: species selection and habitat suitability models. Edmonton, AB: Alberta Sustainable Resource Development, Fish and Wildlife Division; Alberta Species at Risk Report No. 90: 73-81.

Bower, Andrew D.; Aitken, Sally N. 2006. Geographic and seasonal variation in cold hardiness of whitebark pine. Canadian Journal of Forest Research. 36(7): 1842-1850.

Bower, Andrew D.; Aitken, Sally N. 2007. Mating system and inbreeding depression in whitebark pine (*Pinus albicaulis* Engelm.). Tree Genetics & Genomes. 3(4): 379-388.

Bower, Andrew D.; Aitken, Sally N. 2008. Ecological genetics and seed transfer guidelines for *Pinus albicaulis* (Pinaceae). American Journal of Botany. 95(1): 66-76.

Bower, Andrew D.; Aitken, Sally N. [In press]. Changes in genetic diversity of whitebark pine (*Pinus albicaulis* Engelm.) associated with inbreeding and white pine blister rust. Silvae Genetica.

Bower, Andrew D.; Aubry, Carol. 2009. Whitebark pine *ex situ* gene conservation strategy for the Pacific Northwest Region. [Online]. Available: http://fsweb.f9.r6.fs.fed.us/eco/whitebark/index.html

Bower, Andrew D.; Ohlson, Therese; Aubry, Carol. 2009. Whitebark pine restoration program 2009 annual progress report, USDA Forest Service Pacific Northwest Region. [Online]. Available: http://fsweb.f9.r6.fs.fed.us/eco/whitebark/index.html

Bower, Andrew D.; Richardson, Bryce A.; Hipkins, Valerie; Rochefort, Regina; Aubry, Carol. 2008. Unpublished data on file at: U.S. Department of Agriculture, Forest Service, Olympic National Forest, Olympia, WA.

Bruederle, Leo P.; Rogers, Deborah L.; Krutovskii, Konstantin V.; Politov, Dmitri V. 2001. Population genetics and evolutionary implications. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 137-153.

Bruederle, Leo P.; Tomback, Diana F.; Kelly, Kathleen K.; Hardwick, Renea C. 1998. Population genetic structure in a bird-dispersed pine, *Pinus albicaulis* (Pinaceae). Canadian Journal of Botany. 76(1): 83-90.

Bunn, Andrew G.; Waggoner, Lindsey A.; Graumlich, Lisa J. 2005. Topographic mediation of growth in high elevation foxtail pine (*Pinus balfouriana* Grev. et Balf.) forests in the Sierra Nevada, U.S.A. Global Ecology and Biogeography. 14(2): 103-114.

Burns, Kelly; Blodgett, Jim; Conklin, David; Fairweather, Mary Lou; Geils, Brian; Guyon, John; Hoffman, Jim; Jackson, M.; Jacobi, William; Kearns, Holly; Schoettle, Anna. 2010. White pine blister rust in the Interior Mountain West. In: Adams, J. comp. 2010. Proceedings of the 57th Western International Forest Disease Work Conference; 2009 July 20-24; Durango, CO. Fort Collins, CO: Forest Health Technology Enterprise Team: 57-65. [Online]. Available: http://www.cnr.usu.edu/quinney/files/uploads/wifdwc2009.pdf

Burns, Kelly S. 2006. White pine blister rust surveys in the Sangre de Cristo and Wet Mountains of southern Colorado. Biol. Evaluation. R2-06-05. Denver, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region. 22 p.

Carsey, Katherine S.; Tomback, Diana F. 1994. Growth form distribution and genetic relationships in tree cluster of *Pinus flexilis*, a bird-dispersed pine. Oecologia. 98: 402-411.

Cocke, Allison E.; Fule, Peter Z.; Crouse, Joseph E. 2005. Forest change on a steep mountain gradient after extended fire exclusion: San Francisco Peaks, Arizona, U.S.A. Journal of Applied Ecology. 42(5): 814-823.

Colville, Frederick V. 1897. The itinerary of John Jeffrey, an early botanical explorer of western North America. Proceedings of the Biological Society of Washington. 11: 57-60.

Coop, Jonathan D.; Schoettle, Anna 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, Jonathan D.; Massatti, Robert T.; Schoettle, Anna W. 2010. Subalpine vegetation pattern three decades after stand-replacing fire: effects of landscape context and topography on plant community composition, tree regeneration, and diversity. Journal of Vegetation Science. 21(3): 472-487.

Cudmore, Timothy J.; Björklund, Niklas; Carroll, Allan L.; Lindgren, B. Staffan. 2010. Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naive host tree populations. Journal of Applied Ecology. 47(5): 1036-1043.

Currey, Donald R. 1965. An ancient bristlecone pine stand in eastern Nevada. Ecology. 46: 564-566.

Delfino-Mix, Annette. 2010 [Personal communication]. Placerville, CA: U.S. Department of Agriculture, Forest Service, Institute of Forest Genetics.

Donnegan, Joseph A.; Rebertus, Alan J. 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. Ecology. 80: 1370-1384.

Duriscoe, Dan M.; Duriscoe, Cindy S. 2002. Survey and monitoring of white pine blister rust in Sequoia and Kings Canyon National Parks—final report of 1995-1999 survey and monitoring plot network. Science and natural resources management division, Sequoia and Kings Canyon National Parks.

Dvorak, W. S.; Donahue, J. K. 1992. The Central America and Mexico Coniferous Resources Cooperative (CAMCORE) research review, 1980-1992. Raleigh, NC: College of Forest Resources, North Carolina State University. 93 p.

Eckert, Andrew J. 2006a. Influence of substrate type and microsite availability on the persistence of foxtail pine (*Pinus balfouriana*, Pinaceae) in the Klamath Mountains, California. American Journal of Botany. 93(11): 1615-1624.

Eckert, Andrew J. 2006b. The phylogenetic position, historical phylogeographical and population genetics of foxtail pine (*Pinus balfouriana* Grev. & Balf.). Seattle, WA: University of Washington. Dissertation.

Eckert, Andrew J.; Bower, Andrew D.; Gonzalez-Martinez, Santiago C.; Wegrzyn, Jill L.; Coop, Graham; Neale, David B. 2010. Back to nature: ecological genomics of loblolly pine (*Pinus taeda*, Pinaceae). Molecular Ecology. 19(17): 3789-3805.

Eckert, Andrew J.; Bower, Andrew D.; Wegrzyn, Jill L.; Pande, Barnaly; Jermstad, Kathleen D.; Krutovsky, Konstantin V.; St. Clair, J. Bradley; Neale, David B. 2009. Asssociation genetics of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*, Pinaceae). I. Cold-hardiness related traits. Genetics. 182(4): 1289-1302.

Eckert, Andrew J.; Eckert, Melissa L. 2007. Environmental and ecological effects of size class distributions of foxtail pine (*Pinus balfouriana*, Pinaceae) in the Klamath Mountains, California. Madroño. 54: 117-125.

Eckert, Andrew J.; Eckert, Melissa L.; Hall, Benjamin D. 2010. Effects of historical demography and ecological context on spatial patterns of genetic diversity within foxtail pine (*Pinus balfouriana*; Pinaceae) stands located in the Klamath Mountains, California. American Journal of Botany. 97(4): 650-659.

Eckert, Andrew J.; Sawyer, John O. 2002. Foxtail pine importance and conifer diversity in the Klamath Mountains and southern Sierra Nevada, California. Madroño. 49: 33-45.

Eckert, Andrew J.; Tearse, Brandon R.; Hall, Benjamin D. 2008. A phylogeographical analysis of the range disjunction for foxtail pine (*Pinus balfouriana*, Pinaceae): the role of Pleistocene glaciation. Molecular Ecology. 17(8): 1983-1997.

Endler, John A. 1977. Genetic variation, speciation, and clines. Princeton, NJ: Princeton University Press.

Farjon, A.; Styles, B. T. 1997. *Pinus* (Pinaceae). Flora Neotropica Monograph 75. New York: The New York Botanical Garden.

Frankham, Richard; Ballou, Jonathan D.; Briscoe, David A. 2002. Introduction to conservation genetics. New York: Cambridge University Press.

Furnier, Glenn R.; Knowles, Peggy; Clyde, Merlise A.; Dancik, Bruce P. 1987. Effects of avian seed dispersal on the genetic-structure of whitebark-pine populations. Evolution. 41(3): 607-612.

Geils, Brian W.; Conklin, David A.; van Ardsel, Eugene P. 1999. A preliminary hazard model of white pine blister rust for the Sacramento Ranger District, Lincoln National Forest. Res. Note. RMRS-RN-6. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 6 p.

Gernandt, David S.; Lopez, Gretel Geada; Garcia, Sol Ortiz; Liston, Aaron. 2005. Phylogeny and classification of *Pinus*. Taxon. 54(1): 29-42.

Gibson, K.; Skov, K.; Kegley, S.; Jorgensen, C.; Smith, S.; Witcosky, J. 2008. Mountain pine beetle impacts in high-elevation five-needle pines: current trends and challenges. R1-08-020. Missoula, MT: U.S. Department of Agriculture, Forest Service, Forest Health Protection. 32 p.

Gonzalez-Martinez, S. C.; Huber, D.; Ersoz, E.; Davis, J. M.; Neale, D. B. 2008. Association genetics in *Pinus taeda* L. II. Carbon isotope discrimination. Heredity. 101(1): 19-26.

Gonzalez-Martinez, S. C.; Wheeler, N. C.; Ersoz, E.; Nelson, C. D.; Neale, D. B. 2007. Association genetics in *Pinus taeda* l. I. Wood property traits. Genetics. 175(1): 399-409.

Hahn, Matthew W. 2008. Toward a selection theory of molecular evolution. Evolution. 62(2): 255-265.

Hall, David; Tegström, Carolina; Ingvarsson, Pär K. 2010. Using association mapping to dissect the genetic basis of complex traits in plants. Briefings in Functional Genomics. 9(2): 157-165.

Hamelin, R.; Joly, D.; Langor, D. 2005. A hybrid between white pine blister rust and comandra blister rust on limber pine. Phytopathology. 95(6): S39-S40.

Hamrick, James L.; Godt, Mary Jo W.; Sherman-Broyles, Susan L. 1992. Factors influencing levels of genetic diversity in woody plant species. New Forests. 6: 95-124.

Hamrick, James L.; Mitton, Jeffry B.; Linhart, Yan B. 1981. Levels of genetic variation in trees: influence of life history characteristics. In: Conkle, M. Thomas., ed. Proceedings of a symposium on Isozymes of North American Forest Trees and Forest Insects; 1979 July 27; Berkeley, CA. Gen. Tech. Rep. PSW-GTR-48. Berkeley, CA: U.S. Department of Agriculture,

Forest Service, Pacific Southwest Forest and Range Experiment Station: 35-41.

Hamrick, James L.; Schnabel, A. F.; Wells, P. V. 1994. Distribution of genetic diversity within and among populations of Great Basin conifers. In: Harper., K. T.; St. Clair, L. L.; Thorne, K.H.; Hess, W.W., eds. Natural history of the Colorado Plateau and Great Basin. Niwot, CO: University Press of Colorado: 147-161.

Hartl, Daniel L.; Clark, Andrew G. 1989. Principles of population genetics. 2d ed. Sunderland, MA: Sinauer Associates, Inc. 682 p.

Hawksworth, Frank G. 1990. White-pine blister rust in southern New Mexico. Plant Disease. 74(11): 938-938.

Hawksworth, Frank G.; Wiens, Delbert. 1996. Dwarf mistletoes: Biology, pathology and systematics. Agriculture Handbook 709. Washington, DC: U.S. Department of Agriculture, Forest Service. [Online]. Available: http://www.rmrs.nau.edu/publications/ah_709/index.html [2010, September 2].

Hawksworth, Frank G.; Wiens, Delbert; Geils, Brian W. 2002. *Arceuthobium* in North America. In: Geils, Brian W.; Cibrián Tovar, Jose; Moody, Benjamin, tech. coords. Mistletoes of North American conifers. Gen. Tech. Rep. RMRS-GTR-98. Ogden, Utah: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 29-56.

Hiebert, Ronald D.; Hamrick, James L. 1983. Patterns and levels of genetic-variation in Great-Basin bristlecone pine, *Pinus longaeva*. Evolution. 37(2): 302-310.

Hiebert, Ronald D.; Hamrick, James L. 1984. An ecological study of bristlecone pine (*Pinus longaeva*) in Utah and eastern Nevada. Great Basin Naturalist. 44: 487-494.

Hipkins, Valerie. Unpublished data on file at: U.S. Department of Agriculture, Forest Service, National Forest Genetic Electrophoresis Laboratory, Placerville, CA.

Hoff, R.; Bingham, R. T.; McDonald, G. I. 1980. Relative blister rust resistance of white pines. European Journal of Forest Pathology. 10(5): 307-316.

Holliday, Jason A.; Ralph, Steven G.; White, Richard; Bohlmann, Jörg; Aitken, Sally N. 2008. Global monitoring of autumn gene expression within and among phenotypically divergent populations of Sitka spruce (P*icea sitchensis*). New Phytologist. 178(1): 103-122.

Howell, B. E.; Burns, K. S.; Kearns, H. S. J. 2006. Biological evaluation of a model for predicting presence of white pine blister rust in Colorado based on climatic variables and susceptible white pine species distribution. Biol. Eval. R2-06-04. U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Renewable Resources. 15 p. [Online]. Available: http://www.fs.fed.us/r2/fhm/ [2006, March 21].

Joly, D. L.; Langor, D. W.; Hamelin, R. C. 2006. Molecular and morphological evidence for interspecific hybridization between *Cronartium ribicola* and *C. comandrae* on *Pinus flexilis* in southwestern Alberta. Plant Disease. 90: 1552.

Jorgensen, Stacy; Hamrick, James; Wells, P. V. 2002. Regional patterns of genetic diversity in *Pinus flexilis* (Pinaceae) reveal complex species history. American Journal of Botany. 89: 792-800.

Jorgensen, Stacy M.; Hamrick, James L. 1997. Biogeography and population genetics of whitebark pine, *Pinus albicaulis*. Canadian Journal of Forest Research. 27(10): 1574-1585.

Keane, Robert E.; Tomback, Diana; Aubry, Carol; Bower, Andrew; Campbell, Elizabeth; Jenkins, Melissa; Manning, Mary; McKinney, Shawn; Murray, Michael; Perkins, Dana; Reinhart, Dan; Ryan, Chris; Schoettle, Anna; Smith, Cyndi. [In preparation]. A range-wide restoration strategy for whitebark pine (*Pinus albicaulis*). Gen. Tech. Rep. RMRS-GTR-xxx. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 183 p.

Kearns, Holly S. J. 2005. White pine blister rust in the central Rocky Mountains: modeling current status and potential impacts. Fort Collins, CO: Colorado State University. 243 p. Dissertation.

Kearns, Holly S. J.; Jacobi, William R. 2007. The distribution and incidence of white pine blister rust in central and southeastern Wyoming and northern Colorado. Canadian Journal of Forest Research. 37(2): 462-472.

Kinloch, Bohun B.; Dupper, Gayle E. 2002. Genetic specificity in the white pine-blister rust pathosystem. Phytopathology. 92(3): 278-280.

Kipfmueller, Kurt F.; Salzer, Matthew W. 2010. Linear trend and climate response of five-needle pines in the western United States related to treeline proximity. Canadian Journal of Forest Research. 40(1): 134-142.

Kliejunas, John; Dunlap, Joan. 2007. Status of whitebark pine and other high-elevation five-needle pines with emphasis on Pacific Coast ecosystems: What are the issues and concerns? Perspectives from California. In: Goheen, Ellen M.; Sniezko, Richard A., tech. coords. Proceedings of the conference: whitebark pine: a Pacific Coast perspective. 2006 August 27-37; Ashland, OR. R6-NR-FHP-2007-01. Portland, OR: Pacific Northwest Region, Forest Service, U.S. Department of Agriculture: 29-35.

Krakowski, J.; Aitken, S. N.; El-Kassaby, Y. A. 2003. Inbreeding and conservation genetics in whitebark pine. Conservation Genetics. 4(5): 581-593.

Langor, D. W. 1989. Host effects on the phenology, development, and mortality of field populations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Canadian Entomologist. 121: 149-157.

Lanner, R. M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. Canadian Journal of Forest Research. 12(2): 391-402.

Lanner, Ronald M. 1988. Dependence of Great Basin bristlecone pine on Clark's nutcracker for regeneration at high elevations. Arctic and Alpine Research. 20(3): 358-362.

Lanner, Ronald M. 1996. Made for each other: a symbiosis of birds and pines. New York: Oxford University Press. 176 p.

Lanner, R. M. 2007. The bristlecone book: a natural history of the world's oldest trees, Missoula, MT: Mountain Press Publishing Company. 128 p.

Lanner, Ronald M. 2010. [Personal communication]. Placerville, CA: U.S. Department of Agriculture, Forest Service, Institute of Forest Genetics.

Latta, Robert G.; Mitton, Jeffry B. 1997. A comparison of population differentiation across four classes of gene marker in limber pine (*Pinus flexilis* James). Genetics. 146(3): 1153-1163.

Ledig, F. Thomas. 1998. Genetic variation in *Pinus*. In: Richardson, D. M., ed. Ecology and Biogeography of *Pinus*. Cambridge: Cambridge University Press. p. 251-280.

Ledig, F. Thomas; Rehfeldt, Gerald E.; Saenz-Romero, Cuauhtémoc; Flores-Lopez, Celestino. 2010. Projections of suitable habitat for rare species under global warming scenarios. American Journal of Botany. 97(6): 970-987.

Lee, Seok-Woo; Ledig, F. Thomas; Johnson, David R. 2002. Genetic variation at allozyme and RAPD markers in *Pinus longaeva* (Pinaceae) of the White Mountains, California. American Journal of Botany. 89(4): 566-577.

Letts, Matthew G.; Nakonechny, Kevin N.; Van Gaalen, K. Eric; Smith, Cyndi M. 2009. Physiological acclimation of *Pinus flexilis* to drought stress on contrasting slope aspects in Waterton Lakes National Park, Alberta, Canada. Canadian Journal of Forest Research. 39(3): 629-641.

Liston, Aaron; Robinson, William A.; Piñero, Daniel; Alvarez-Buylla, Elena R. 1999. Phylogenetics of *Pinus* (Pinaceae) based on nuclear ribosomal DNA internal transcribed spacer region sequences. Molecular Phylogenetics and Evolution. 11(1): 95-109.

Little, Elbert L., Jr.; Critchfield, William B. 1969. Subdivisions of the genus *Pinus* (pines). Misc. Publ. No. 1144. Washington, DC: U.S. Department of Agriculture, Forest Service.

Mahalovich, Mary F.; Burr, Karen E.; Foushee, David L. 2006. Whitebark pine germination, rust resistance, and cold hardiness among seed sources in the Inland Northwest: planting strategies for restoration. In: Riley, L. E.; Dumroese, R. K.; Landis, T. D., tech. coords. National Proceedings: Forest and Conservation Nursery Association—2005. Proc. RMRS-P-43. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 91-101.

Mahalovich, M. F.; Dickerson, G. A. 2004. Whitebark pine genetic restoration program for the Intermountain West (U.S.A.). In: Sniezko, Richard; Samman, Safiya; Schlarbaum, Scott E.; Kriebel, Howard B., eds. Breeding and genetic resources of five-needle pines: growth, adaptability and pest resistance; 2001 July 23-27; Medford, OR, USA. IUFRO Working Party 2.02.15. Proc. RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Maloney, Patricia E. 2010. [Personal communication]. Davis, CA: University of California.

Maloney, Patricia E. Unpublished data on file at: University of California, Davis, CA.

Manel, Stéphanie; Joost, Stéphane; Epperson, Brian K.; Holderegger, Rolf; Storfer, Andrew; Rosenberg, Michael S.; Scribner, Kim T.; Bonin, Aurélie; Fortin, Marie-Josée. 2010. Perspectives on the use of landscape genetics to detect genetic adaptive variation in the field. Molecular Ecology. 19(17): 3760-3772.

Mastrogiuseppe, R. J.; Mastrogiuseppe, J. D. 1980. A study of *Pinus balfouriana* Grev. and Balf. (Pinaceae). Systematic Botany. 5(1): 86-104.

McKenney, Daniel W.; Pedlar, John H.; Lawrence, Kevin; Campbell, Kathy; Hutchinson, Michael F. 2007. Potential impacts of climate change on the distribution of North American trees. Bioscience. 57(11): 939-948.

McLane, Sierra; Aitken, Sally N. [In preparation]. Whitebark pine assisted migration trial. Centre for Forest Conservation Genetics, University of British Columbia, Vancouver, B.C., Canada.

McLane, Sierra; Aitken, Sally N. [In preparation]. Whitebark pine germination and growth at extreme temperatures. Centre for Forest Conservation Genetics, University of British Columbia, Vancouver, B.C., Canada.

Millar, Constance I.; Westfall, Robert D.; Delaney, Diane L. 2006. Elevational gradients and differential recruitment of limber pine (*Pinus flexilis*) and bristlecone pine (*Pinus longaeva*); White Mountains, California, USA. American Geophysical Union, Fall Meeting, 2006. Poster: C33C-1289. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Sierra Nevada Research Center.

Millar, Constance I.; Westfall, Robert D.; Delany, Diane L. 2007. Response of high-elevation limber pine (*Pinus flexilis*) to multiyear droughts and 20th-century warming, Sierra Nevada, California, USA. Canadian Journal of Forest Research. 37(12): 2508-2520.

Millar, Constance I.; Westfall, Robert D.; Delany, Diane L.; King, John C.; Graumlich, Lisa J. 2004. Response of subalpine conifers in the Sierra Nevada, California, USA, to 20th-century warming and decadal climate variability. Arctic, Antarctic, and Alpine Research. 36(2): 181-200.

Mirov, Nicholas T. 1967. The genus *Pinus*. New York: The Ronald Press Company.

Mitton, J. B.; Kreiser, B. R.; Latta, R. G. 2000. Glacial refugia of limber pine (*Pinus flexilis* James) inferred from the population structure of mitochondrial DNA. Molecular Ecology. 9(1): 91-97.

Moir, W. H.; Ludwig, J. A. 1979. A classification of spruce-fir and mixed conifer habitat types of Arizona and New Mexico. Res. Pap. RM-207. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 47 p.

Moreno-Letelier, Alejandra; Piñero, Daniel. 2009. Phylogeographic structure of *Pinus strobiformis* Engelm. across the Chihuahuan Desert filter-barrier. Journal of Biogeography. 36(1): 121-131.

Murray, Andrew. 1853. Botanical expedition to Oregon. Report No. 8. Edinburgh, UK: Scottish Oregon Association.

Neale, David B.; Savolainen, Outi. 2004. Association genetics of complex traits in conifers. Trends in Plant Science. 9(7): 325-330.

Oline, David K. 2001. Unpublished data on file at: Southern Oregon University, Ashland, OR.

Oline, David K.; Mitton, Jeffry B.; Grant, Michael C. 2000. Population and subspecific genetic differentiation in the foxtail pine (*Pinus balfouriana*). Evolution. 54(5): 1813-1819.

ParksWatch. 2004. Los Altos de San Miguel Totonicapán Regional Park - Park Profile – Biodiversity. [Online]. Available: http://www.parkswatch.org/parkprofile.php?l=eng&country=gua&park=torf&page=bio [2010, August 26].

Parmesan, Camille. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics. 37: 637-669.

Perry, Jesse P. 1991. The pines of Mexico and Central America. Portland, OR: Timber Press.

Politov, D. V.; Krutovsky, K. V. 2004. Phylogenetics, genogeography and hybridization of five-needle pines in Russia and neighboring countries. In: Sniezko, Richard; Samman, Safiya; Schlarbaum, Scott E.; Kriebel, Howard B., eds. Breeding and genetic resources of five-needle pines: growth, adaptability and pest resistance; 2001 July 23-27; Medford, OR, USA. IUFRO Working Party 2.02.15. Proc. RMRS-P-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Price, R. A.; Liston, A.; Strauss, S. H. 1998. Phylogeny and systematics of *Pinus*. In: Richardson, D. M., ed. Ecology and biogeography of *Pinus*. Cambridge, UK: Cambridge University Press: 49-68.

Rebertus, A. J.; Burns, B. R.; Veblen, T. T. 1991. Stand dynamics of *Pinus flexilis*-dominated subalpine forests in the Colorado Front Range. Journal of Vegetation Science. 2: 445-458.

Rehfeldt, Gerald E.; Crookston, Nicholas L.; Warwell, Marcus V.; Evans, Jeffrey S. 2006. Empirical analyses of plant-climate relationships for the western United States. International Journal of Plant Sciences. 167(6): 1123-1150.

Reuling, M. 2008. *Pinus albicaulis*. In: IUCN 2010. IUCN Red List of Threatened Species. Version 2010.2. [Online]. Available: www.iucnredlist.org [2010, August 17].

Richardson, B. A.; Brunsfeld, J.; Klopfenstein, N. B. 2002. DNA from bird-dispersed seed and wind-disseminated pollen provides insights into postglacial colonization and population genetic structure of whitebark pine (*Pinus albicaulis*). Molecular Ecology. 11(2): 215-227.

Richardson, Bryce A.; Klopfenstein, Ned B.; Brunsfeld, Steven J. 2002b. Assessing Clark's nutcracker seed-caching flights using maternally inherited mitochondrial DNA of whitebark pine. Canadian Journal of Forest Research. 32(6): 1103-1107.

Rogers, Deborah L.; Millar, Constance I.; Westfall, Robert D. 1999. Fine-scale genetic structure of whitebark pine (*Pinus albicaulis*): associations with watershed and growth form. Evolution. 53(1): 74-90.

Rourke, M. D. 1988. The biogeography and ecology of *Pinus balfouriana* Grev. & Balf. in the Sierra Nevada of California. Tucson, AZ: University of Arizona. 225 p. Dissertation.

Ryerson, Diane 1983. Population structure of *Pinus balfouriana* Grev. & Balf. Along the margins of its distribution area in the Sierran and Klamath regions of California. Sacramento, CA: Sacramento State University. 198 p. Thesis.

Saenz-Romero, Cuauhtémoc; Rehfeldt, Gerald E.; Crookston, Nicholas L.; Duval, Pierre; St.-Amant, Rémi; Beaulieu, Jean; Richardson, Bryce A. 2009. Spline models of contemporary, 2030, 2060, and 2090 climates for Mexico and their use in understanding climate-change impacts on the vegetation. Climatic Change. 102(3-4): 595-623.

Salzer, Matthew W.; Hughes, Malcolm K.; Bunn, Andrew G.; Kipfmueller, Kurt F. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. Proceedings of the National Academy of Sciences of the United States of America. 106(48): 20348-20353.

Schoettle, Anna. 2010. Unpublished data on file at: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Schoettle, A. W.; Burns, K. S.; Costello, S.; Witcosky, J.; Howell, B.; Connor, J. 2008. A race against beetles: conservation of limber pine. Nutcracker Notes. 14: 11-12.

Schoettle, A. W.; Rochelle, S. G. 2000. Morphological variation of *Pinus flexilis* (Pinaceae), a bird-dispersed pine, across a range of elevations. American Journal of Botany. 87(12): 1797-1806.

Schoettle, Anna W.; Sniezko, Richard A. 2007. Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. Journal of Forest Research. 12(5): 327-336.

Schoettle, Anna W.; Sniezko, Richard A.; Burns, Kelly 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, David; Noh, Eun Woon; King, John; Sniezko, Richard A. eds. Breeding and genetic resources of five-needle pines; Proceedings of the Conference; IUFRO Working Party 2.02.15; 2008 September 22-26; Yangyang, Korea. Seoul: Korea Forest Research Institute: 63-65.

Schoettle, Anna W.; Sniezko, Richard A.; Kegley, Angelia; Hill, Jerry; Burns, Kelly S. 2010. Resistance to white pine blister rust in *Pinus flexilis* and *Pinus aristata* of the Southern Rockies—initial findings. In: Adams, Judy; Jamieson, Carrie; Palacios, Patsy, comps. 2010. Proceedings of the 57th Western International Forest Disease Work Conference; 2009 July 20-24; Durango, CO. Fort Collins, CO: Forest Health Technology Enterprise Team: 109-110. [Online]. Available: http://www.cnr.usu.edu/quinney/files/uploads/WIFDWC2009.pdf

Schrag, Anne M.; Bunn, Andrew G.; Graumlich, Lisa J. 2008. Influence of bioclimatic variables on tree-line conifer distribution in the Greater Yellowstone Ecosystem: implications for species of conservation concern. Journal of Biogeography. 35(4): 698-710.

Schulman, E. 1958. Bristlecone pine, oldest known living thing. National Geographic. 113: 355-372.

Schuster, William S.; Alles, David L.; Mitton, Jeffry B. 1989. Gene flow in limber pine: evidence from pollination phenology and genetic differentiation along an elevational transect. American Journal of Botany. 76(9): 1395-1403.

Schuster, William S. F.; Mitton, Jeffry B. 1991. Relatedness within clusters of a bird-dispersed pine and the potential for kin interactions. Heredity. 67:41-48.

Schuster, William S. F.; Mitton, Jeffry B. 2000. Paternity and gene dispersal in limber pine (*Pinus flexilis* James). Heredity. 84(3): 348-361.

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.

Shaw, George Russell. 1914. The genus *Pinus*. Cambridge: Riverside Press.

Sniezko, Richard. 2010. [Personal communication]. Cottage Grove, OR: U.S. Department of Agriculture, Forest Service.

Sniezko, Richard A.; Kegley, Angelia; Danchok, Robert; Long, Sally. 2007. Variation in resistance to white pine blister rust in 43 whitebark pine families from Oregon and Washington—early results and implications for conservation. In: Goheen, Ellen M.; Sniezko, Richard A., tech. coords. Proceedings of the conference: whitebark pine: a Pacific Coast perspective. 2006 August 27-37; Ashland, OR. R6-NR-FHP-2007-01. Portland, OR: Pacific Northwest Region, Forest Service, U.S. Department of Agriculture: 24-27.

Sniezko, Richard A.; Kegley, Angelia; Danchok, Robert; Schoettle, Anna W.; Burns, Kelly S.; Conklin, Dave. 2008. *Cronartium ribicola* resistance in whitebark pine, southwestern white pine, limber pine and Rocky Mountain bristlecone pine—preliminary screening results from first tests at Dorena GRC. In: McWilliams, Michael; Palacios, Patsy, comps. Proceedings of the 55th Annual Western International Forest Disease Work Conference; 2007 October 15-19; Sedona, AZ. Logan: Utah State University: 84-86.

Spielman, Derek; Brook, Barry W.; Briscoe, David A.; Frankham, Richard. 2004. Does inbreeding and loss of genetic diversity decrease disease resistance? Conservation Genetics. 5(4): 439-448.

Steele, Robert. 1990. *Pinus flexilis* James, limber pine. In: Burns, Russell M.; Honkala, Barbara H., tech. coords. Silvics of North America, Vol. 1, Conifers. Agriculture Handbook 654. Washington, DC: U.S. Department of Agriculture, Forest Service.

Steinhoff, R. J.; Andresen, J. W. 1971. Geographic variation in *Pinus flexilis* and *Pinus strobiformis* and its bearing on their taxonomic status. Silvae Genetica. 20: 159-167.

Strauss, Steven H.; Doerksen, Allan H. 1990. Restriction fragment analysis of pine phylogeny. Evolution. 44(4): 1081-1096.

Stuart-Smith, G. J. 1998. Conservation of whitebark pine in the Canadian Rockies: blister rust and population genetics. Edmonton, Alberta: University of Alberta. Thesis.

Tomback, D. F. 1978. Foraging strategies of Clark's nutcracker. Living Bird. 16: 123-161.

Tomback, Diana F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: a mutualism hypothesis. Journal of Animal Ecology. 51(2): 451-467.

Tomback, D. F. 2001. Clark's nutcracker: agents of regeneration. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 89-104.

Tomback, Diana F.; Linhart, Yan B. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology. 4(3): 185-219.

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

Torick, Lisa L.; Tomaback, Diana F.; Espinoza, Ronald. 1996. Occurrence of multi-genet tree clusters in "wind-dispersed" pines. American Midland Naturalist. 136(2): 262-266.

U.S. Department of Agriculture, Forest Service. 2010. Plant species and climate profile predictions. U.S. Department of Agriculture, Rocky Mountain Research Station, Moscow Forestry Sciences Center. [Online]. Available: http://forest.moscowfsl.wsu.edu/climate/species/ [2010 September].

Vogler, Detlev. 2010. [Personal communication]. Placerville, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station.

Vogler, Detlev R.; Delfino-Mix, Annette; Schoettle, Anna W. 2006. White pine blister rust in high-elevation white pines: screening for simply-inherited, hypersensitive resistance. In: Guyon, J. C., comp. Proceedings of the 53rd Western International Forest Disease Work Conference; 2005 September 26-30; Jackson, WY. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Region: 73-82.

Wang, T. L.; McLane, S. C.; Campbell, E.; Schroeder, T. A. [In preparation]. Whitebark pine may not survive climate change.

Warwell, M. V. [In preparation]. Adaptive variation among whitebark pine populations in the Intermountain West.

Warwell, Marcus V.; Rehfeldt, Gerald E.; Crookston, Nicholas L. 2007. Modeling contemporary climate profiles of whitebark pine (*Pinus albicaulis*) and predicting responses to global warming. In: Goheen, Ellen M.; Sniezko, Richard A., tech. coords. Proceedings of the conference: whitebark pine: a Pacific Coast perspective. 2006 August 27-37; Ashland, OR. R6-NR-FHP-2007-01. Portland, OR: Pacific Northwest Region, Forest Service, U.S. Department of Agriculture: 139-142.

Weaver, T. 2001. Whitebark pine and its environment. In: Tomback, Diana F.; Arno, Stephen F.; Keane, Robert E., eds. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press: 41-73.

Webster, Kara L.; Johnson, Edward A. 2000. The importance of regional dynamics in local populations of limber pine (*Pinus flexilis*). Ecoscience. 7(2): 175-182.

Wells, Phillip V. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. Ecological Monographs. 53(4): 341-382.

Wright, J. A.; Marin, A.; Dvorak, W. 1996. *Ex situ* gene conservation of *Pinus ayacahuite*. FAO Forest Genetic Resources. 24: 48-51.

Wright, J. W.; Kung, F. H.; Read, R. A.; Steinhoff, R. J.; Andresen, J. W. 1971. Nine-year performance of *Pinus flexilis* and *P. strobiformis* progenies in Michigan and Nebraska. Silvae Genetica. 20: 211-214.

Yandell, U. G. 1992. An allozyme analysis of whitebark pine (*Pinus albicaulis* Engelm.). Reno, NV: University of Nevada. Thesis.