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Search topic: Whitebark pine research, publ. 2000-2012

Databases searched: Web of Science, Scopus, CAB Abstracts, Agricola, FS INFO, Treesearch, Georef, Google, Google Scholar

Anderton, L. K. and M. J. Jenkins (2001). "Cone entomofauna of whitebark pine and alpine larch (Pinaceae): potential impact of *Leptoglossus occidentalis* (Hemiptera : Coreidae) and a new record of *Strobilomyia macalpinei* (Diptera : Anthomyiidae)." Canadian Entomologist 133(3): 399-406.

Laboratory and field feeding tests with *Leptoglossus occidentalis* Heidemann demonstrated that both immature and mature seed bugs can use cones and foliage of whitebark pine, *Pinus albicaulis* Engelmann, as a food source for 1-to 2-week periods. Damage to unprotected **whitebark pine** cones by seed bugs ranged from 0.3 to 2.1% of seeds per cone. Total insect damage ranged from 0.4 to 7.1% of seeds per cone. A seed chalcid, *Megastigmus Dalman. sp.* (Hymenoptera: Torymidae), was documented for the first time on whitebark pine and was found in 4.7% of examined seeds at one site. The larch cone fly, *Strobilomyia macalpinei* Michelsen, was reared from cones of alpine larch, *Larix lyallii* Parl., from the Bitterroot Range of Montana. This is the first record of this species in the United States and the first since its description in 1988. Ninety-four percent of a sample of alpine larch cones were damaged by cone fly larvae and 64% contained larvae or puparia.

Arno, S. F. (2001). Community types and natural disturbance processes. In: *Whitebark Pine Communities: Ecology and restoration*. Tomback, D. F.; Arno, S. F.; Keane, R. E., (Eds.), Washington, DC: Island Press, pp. 74–88.

Asebrook, J. M. L., Joyce, Carolin, Tara (2011) Whitebark and limber pine restoration and monitoring in Glacier National Park. [Extended abstract] In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. *The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium*. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 335-337.

Whitebark pine (*Pinus albicaulis*) and limber pine (*Pinus flexilis*) are keystone species important to watersheds, grizzly and black bears, squirrels, birds, and other wildlife. Both high elevation five-needled pines have dramatically declined in Glacier National Park primarily due to white pine blister rust (*Cronartium ribicola*) and fire exclusion, with mountain pine beetle (*Dendroctonus ponderosae*) as a potential threat. In 1997, we began collecting seed from trees that show phenotypic rust resistance in order to establish a restoration and monitoring program to maintain healthy whitebark and limber pine ecosystems in the park. Most of the seed has been propagated into seedlings through a

cooperative agreement with the US Forest Service (FS) Coeur d'Alene Nursery. From 2000 to 2007, we planted nearly 6,400 whitebark and 4,700 limber pine seedlings. Following monitoring in 2010, 41 percent of all planted whitebark seedlings had survived, while only 6 percent of limber pine survived. In addition to restoration monitoring, we established blister rust monitoring plots as well as a program to monitor individual "plus" trees; trees that potentially have genetic resistance to blister rust. Currently, we are working with a FS regional geneticist to determine if our designated "plus" trees are actually producing blister-rust resistant seedlings.

<http://www.treesearch.fs.fed.us/pubs/38245>

Aubry, C., D. Goheen, et al. (2008). Whitebark pine restoration strategy for the Pacific Northwest 2009-2013. Region 6 Report. US Department of Agriculture, Forest Service, Pacific Northwest Region, Portland, OR. <http://www.fs.fed.us/r6/genetics/documents/publications/pub801.pdf> ; see also: [www.fs.fed.us/r6/genetics/publications/whitebark-pine](http://www.fs.fed.us/r6/genetics/publications/whitebark-pine)

Aubry, C. A. and R. Rochefort (2007). Whitebark Pine in the Pacific Northwest: What's Next? In: Proceedings on the Conference of Whitebark Pine: A Pacific Coast Perspective. USDA Forest Service, Forest Health Protection, R6-NR-FHP-2007-01.

<http://www.fs.fed.us/outernet/r6/nr/fid/wbpine/papers/2007-wbp-impacts-aubry.pdf>

Bansal, S., K. Reinhardt, et al. (2011). "Linking carbon balance to establishment patterns: comparison of whitebark pine and Engelmann spruce seedlings along an herb cover exposure gradient at treeline." Plant Ecology 212(2): 219-228.

There is increasing evidence that landscape vegetation patterns near species' range limits are associated with positive biotic interactions, such as in the alpine-treeline ecotone. In the northern Rocky Mountains, whitebark pine (*Pinus albicaulis*) is considered an early-successional species, able to establish in exposed microsites, while late-successional species such as Engelmann spruce (*Picea engelmannii*) are more dependent on neighboring vegetation to facilitate establishment. We compared ecophysiological traits associated with carbon balance of newly germinated seedlings of whitebark pine and Engelmann spruce along an herb cover gradient to (1) infer which ecophysiological properties explain the establishment success of seedlings, and (2) to assess differences in establishment patterns with respect to distance from neighboring vegetation. We measured survival over 2 years, and concurrently measured gas exchange and water relations (photosynthesis, respiration, and transpiration), morphology [specific leaf area (SLA)], and biochemistry [chlorophyll fluorescence ( $F(v)/F(m)$ ) and nonstructural carbohydrates]. Both species initially established in the most exposed microsites away from vegetation during their first growing season, but only pine persisted in exposed microsites to the end of the second growing season. Pine exhibited phenotypic traits to increase stress tolerance (e.g., higher soluble sugar concentrations, lower SLA) and improve carbon balance (e.g., greater water use efficiency, lower respiration, higher  $F(v)/F(m)$ ) compared to spruce in exposed sites, but had lower carbon balance under herb cover. Superior establishment success of pine in exposed microsites at treeline could thus be attributed to a suite of intrinsic physiological advantages that are apparent at the earliest stage of development.

Barrett, S. W. (2004). "Altered fire intervals and fire cycles in the Northern Rockies." Fire management today 64(3): 25-29.

An empirically-based fire regimes classification for the forests of the Northern Rocky Mountains was developed to support subsequent terrain modelling of fire regimes for land management planning, by mean fire interval, typical tree mortality from fire, and

characteristic location/forest types. . Data are presented on the nonlethal and mixed severity fire regimes in the Northern Rockies. The implications of altered fire were difficult to interpret due to the sparse data available and the highly variable occurrence of forest fires in the area. On the other hand, fire exclusion can affect long interval fire regimes, albeit more subtly than the frequent fire types. Furthermore, at the landscape scale, repeated extinguishing of fires has contributed to the decline of whitebark pine [*Pinus albicaulis*] by favouring successional replacement by shade-tolerant trees. This paper is distilled from a contract final report (Barrett, 2002) prepared for a recent USDA Forest Service landscape modelling project (Jones et al., 2002).

[http://www.fs.fed.us/fire/fmt/fmt\\_pdfs/FMT64-3.pdf#page=25](http://www.fs.fed.us/fire/fmt/fmt_pdfs/FMT64-3.pdf#page=25)

Barringer, L. E. T., Diana F.; Wunder, Michael B. (2011). "The relationship between whitebark pine health, cone production, and nutcracker occurrence across four National Parks. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 45-46."

Whitebark pine (*Pinus albicaulis*) is declining in the central and northern Rocky Mountains from infection by the exotic pathogen *Cronartium ribicola*, which causes white pine blister rust, and from outbreaks of mountain pine beetle (*Dendroctonus ponderosae*). White pine blister rust has been present in Glacier and Waterton Lakes National Parks (NP) about two decades longer than in the Greater Yellowstone Area, but both Grand Teton and Yellowstone NP are currently experiencing major outbreaks of mountain pine beetle. McKinney and Tomback (2007) and McKinney and others (2009) demonstrated that as whitebark pine stands are progressively damaged by blister rust or trees are killed, Clark's nutcrackers (*Nucifraga columbiana*) make fewer stand visits when seeds are ripe. Our goals were to determine what variables best predict the occurrence of nutcrackers in whitebark pine stands in Grand Teton, Yellowstone, Glacier, and Waterton Lakes NP, and to compare the relationship we determine between cone production and nutcracker occurrence to that determined by McKinney and others (2009).

<http://www.treearch.fs.fed.us/pubs/38192>

Bentz, B. J., S. Kegley, et al. (2005). "A test of high-dose verbenone for stand-level protection of lodgepole and whitebark pine from mountain pine beetle (Coleoptera : Curculionidae : Scolytinae) attacks." *Journal of Economic Entomology* 98(5): 1614-1621.

The efficacy of verbenone as a stand-level protectant against mountain pine beetle, *Dendroctonus ponderosae* Hopkins, attacks was tested in lodgepole and whitebark pine stands at five geographically separated sites, including three consecutive years at one site. Forty and 20 high-dose pouches, with a verbenone emission rate up to 50 mg/d per pouch, were spaced in a grid pattern throughout 0.40-ha plots, replicated up to six times at each site. Although the verbenone treatment did not prevent beetles from dispersing through treated stands, attacking large-diameter trees most frequently, the overall number of trees attacked was, on average, reduced significantly compared with nontreated stands. In a few blocks each year, verbenone-treated plots had more attacked trees than controls. These blocks tended to have a large emerging beetle population, exceeding 140 previously attacked trees within the hectare including and surrounding the treated area. Additional research is needed on the behavioral role of verbenone in mountain pine beetle population dynamics and quantification of the infestation level above which treatment efficacy tends to be reduced.

Bentz, B. J. S.-L., Greta (2007). The mountain pine beetle and whitebark pine waltz: Has the music changed?. In Goheen, E. M.; Snieszko, R.A., tech. coords. Proceedings of the Conference Whitebark Pine: A Pacific Coast Perspective; 2006 August 27-31; Ashland, OR. R6-NR-FHP-2007-01. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. p. 43-50.

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae) (MPB), is a bark beetle native to western North American forests, spanning wide latitudinal and elevational gradients. MPB infest and reproduce within the phloem of most *Pinus* species from northern Baja California in Mexico to central British Columbia in Canada, and their geographic range is dictated by the distribution of both suitable host species and favorable climatic regimes (Safranyik 1978, Logan and Bentz 1999).

<http://treesearch.fs.fed.us/pubs/34086>

Bockino, N. K. (2008) Interactions of white pine blister rust, host species, and mountain pine beetle in whitebark pine ecosystems in the Greater Yellowstone. Thesis (M.S.) -- University of Wyoming, Laramie, Wyo. .

The current mountain pine beetle (*Dendroctonus ponderosae* Hopk.) activity in whitebark pine (*Pinus albicaulis* Englem.) ecosystems in the Greater Yellowstone Ecosystem (GYE) is historically unprecedented in extent and severity. In addition, a non-native pathogen, white pine blister rust (*Cronartium ribicola* Fisch.) is widespread and infection rates continue to intensify. Interactions between the beetle and blister rust are placing this species in a precarious state. I recorded stand- and tree-level data on four biogeographically variable sites in the GYE to quantify how four variables; severity of white pine blister rust; the presence of the alternate host lodgepole pine (*Pinus contorta* var. *latifolia* Englem.); whitebark pine density; and diffusion by non-alternate host species influence probability of selection by the mountain pine beetle for individual whitebark pine. Summary data show that 52% of the whitebark pine sampled in this study were dead, 70% attacked by mountain pine beetle, 85% infected with blister rust, and 61% were afflicted with both. Chi-square tests indicated that beetle activity was lower than expected in whitebark pine with light blister rust and increased significantly in whitebark pine with heavy blister rust. Habitat use-availability selection ratios (HSRs) indicated that, on sites with two potential host species, mountain pine beetle preferentially select whitebark pine over lodgepole pine. In addition, HSR analyses indicated that mountain pine beetle preferentially select whitebark pine with heavy blister rust over those with light rust. Whitebark pine diameter, rust severity, and overstory tree species composition were significant, not mutually exclusive predictors in logistic regression models. This work reveals that blister rust increases whitebark pine probability of selection by, and that lodgepole pine are not the preferred host of, the mountain pine beetle. Concurrently, climate change has resulted in the expansion of habitats thermally favorable to bark beetle reproductive success in whitebark pine ecosystems. This research suggests that interactions among these disturbance agents will enhance whitebark pine mortality, widespread population decline, and alter ecological functions and processes to which these trees are critical. However, mountain pine beetle selection preference for whitebark pine with severe blister rust infection accelerates the rate of change in the proportion of whitebark pine with severe rust in the remaining population.

[http://fedgycc.org/documents/WBP\\_bugs\\_rustbocino\\_thesis\\_030508\\_000.pdf](http://fedgycc.org/documents/WBP_bugs_rustbocino_thesis_030508_000.pdf)

Bower, A. D. (2006) Ecological genetics and effects of inbreeding and white pine blister rust on genetic structure of whitebark pine (*Pinus albicaulis* Engelm.). Thesis (Ph.D.)--University of British Columbia, Vancouver.

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

Artificial freeze-testing utilizing the electrolyte-leakage method was used to test the cold hardiness of 2-year-old whitebark pine (*Pinus albicaulis* Engelm.) seedlings growing in a common garden. Testing across all seasons was used to determine the annual pattern of cold hardiness, and more intensive sampling in the fall and spring was used to assess genetic variation in cold injury among geographic regions spanning the range of the species. Mean hardiness varied widely from -9 °C in early summer to below -70 °C in the winter. Trees from interior and northern regions were the most hardy in the fall, while trees from California were the least hardy. Geographic patterns of hardiness in the spring were reversed. Significant differences in cold injury among regions were detected on all dates except during the winter. Heritability was low to moderate for both the spring ( $h^2=0.18$ ) and the fall ( $h^2=0.28$ ), and genetic correlation was weak ( $r(A)=0.18$ ). Only spring cold injury was genetically correlated with date of needle flush ( $r(A)=0.34$ ). Mean cold injury in the fall was most closely correlated with mean temperature of the coldest month in the parental environment ( $r=0.81$ ). Whitebark pine is well adapted to the low temperatures of the harsh environments where it is found; however, regional variation indicates that moving seed for restoration purposes from areas with higher winter temperatures to colder environments may increase the chance of fall cold injury.

Bower, A. D. and S. N. Aitken (2007). Genetic Diversity and Geographic Differentiation in Quantitative Traits, and Seed Transfer Guidelines for Whitebark Pine. In: Proceedings on the Conference of Whitebark Pine: A Pacific Coast Perspective. USDA Forest Service, Forest Health Protection, R6-NR-FHP-2007-01. <http://www.fs.fed.us/outernet/r6/nr/fid/wbpine/papers/2007-wbp-wpbr-resist-bower.pdf>

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

Mating system and inbreeding depression in quantitative traits of whitebark pine (*Pinus albicaulis* Engelm.) was determined using isozymes and a seedling common garden experiment. Simultaneous isozyme analysis of embryo and haploid megagametophytes from progeny arrays of families in three distinct geographic regions (Oregon, Montana, and southern British Columbia) was used to estimate parental and progeny inbreeding coefficients, as well as regional and family mean multilocus outcrossing rates ( $t(m)$ ). Quantitative trait family means of seedlings from the same families growing in two temperature treatments in a common garden experiment were regressed on the estimated inbreeding coefficient to determine the presence and magnitude of inbreeding depression. Regional estimates of  $t(m)$  ranged from 0.73 to 0.93, with a mean over all regions of 0.86. Family mean  $t(m)$  values indicated predominant outcrossing; however, some individuals experienced substantial inbreeding. The Oregon region had a significant excess of heterozygotes in the parental generation relative to Hardy-Weinberg equilibrium, while both the Oregon and southern BC regions had a heterozygote deficiency in progeny, suggesting selection against inbred individuals. Biomass in the ambient temperature treatment for the southern BC region was the only trait significantly related to inbreeding coefficient. The mean inbreeding coefficient for this region was 0.25, and based on this relationship, mean predicted biomass would be reduced by 19.6% in this region if inbred individuals are not removed by selection. The estimated outcrossing rate of whitebark pine is slightly lower than most wind-pollinated conifers, and while most individuals are highly outcrossing, some experience substantial inbreeding.

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

Whitebark pine (*Pinus albicaulis* Engelm.) has greatly declined throughout its range as a result of introduced disease, fire suppression, and other factors, and climate change is predicted to accelerate this decline. Restoration is needed; however, no information regarding the degree of local adaptation is available to guide these efforts. A seedling common-garden experiment was employed to assess genetic diversity and geographic differentiation (Q(ST)) of whitebark pine for traits involved in growth and adaptation to cold and to determine climatic variables revealing local adaptation. Seedlings from 48 populations were grown for two years and measured for height increment, biomass, root to shoot ratio, date of needle flush, fall and spring cold injury, and survival. Significant variation was observed among populations for most traits. The QST was low (0.07-0.14) for growth traits and moderate (0.36-0.47) for cold adaptation related traits, but varied by region. Cold adaptation traits were strongly correlated with mean temperature of the coldest month of population origins, while growth traits were generally correlated with growing season length. We recommend that seed transfer for restoration favor seed movement from milder to colder climates to a maximum of 1.9 degrees C in mean annual temperature in the northern portion of the species range, and 1.0 degrees C in the U. S. Rocky Mountains to avoid maladaptation to current conditions yet facilitate adaptation to future climates.

Bower, A. D. and S. N. Aitken (2011). "Changes in Genetic Diversity of Whitebark Pine (*Pinus albicaulis* Engelm.) Associated with Inbreeding and White Pine Blister Rust Infection." *Silvae Genetica* 60(3-4): 113-123.

We investigated the association of inbreeding and infection by the introduced disease white pine blister rust (caused by the fungus *Cronartium ribicola* J. C. Fisch) with genetic diversity of whitebark pine (*Pinus albicaulis* Engelm.) by genetically comparing cohorts of different ages in natural stands. Isozyme analysis of bud tissue was used to estimate expected and observed heterozygosity ( $H(e)$  and  $H(o)$ ), and Wright's fixation index ( $F(is)$ ) for three age cohorts (seedling, young, and mature), sampled from 14 sites in British Columbia, Oregon, Idaho, and Montana. Comparison of genetic diversity parameters among cohorts within a site was used to assess the extent and persistence of inbreeding with age, while comparisons of parameters among sites within a cohort were used to assess the impact of the disease on genetic diversity. Significant evidence of inbreeding ( $F(is) > 0$ ) was found in all age cohorts. When sites were stratified by level of blister rust infection, differences in  $F(is)$  and  $H(o)$  among cohorts were only significant when level of infection was low. A significant negative association was found between level of blister rust infection and  $H(o)$  in the mature cohort. This suggests that when differential selection due to blister rust is weak, more heterozygous individuals may be favored; however, more homozygous individuals may have higher fitness under higher blister rust levels

Bower, A. D., D. Kolotelo, et al. (2011). "Effects of Length of Storage, and Stratification on Germination of Whitebark Pine Seeds." *Western Journal of Applied Forestry* 26(1): 24-29.

The effects of length of storage and stratification on germination of whitebark pine (*Pinus albicaulis* Engelm.) seeds were determined for 180 open-pollinated families from throughout most of the species range. Seeds came from four geographic regions and were stored from 0 to 10 years at one of four storage facilities. Seeds received a standard 1 month of warm moist treatment and 2 months of cold stratification treatment and germination regime, and germination capacity was determined for 100 viable seeds per family. A subset of families received an additional 6 months of cold stratification. Mean germination was 13.4% after 2 months of cold stratification and 76.6% after an additional 6

months of cold stratification, with a wide range among seedlots for both assessments. The length of storage did not affect germination significantly in the first test, but it was associated with a decline in the second test. Germination capacity of up to 80% was achieved with seeds that had been in storage for 10 years. High viability of stored seeds indicate that ex situ seed storage should provide a viable means of conserving genetic resources; however, we recommend that standard protocols for germination of whitebark pine seeds be modified by extending the cold stratification period.

Bower, A. D. M., Sierra C.; Eckert, Andrew; Jorgensen, Stacy; Schoettle, Anna; Aitken, Sally (2011). "Conservation genetics of high elevation five-needle white pines. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 98-117."

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.

<http://www.treearch.fs.fed.us/pubs/38207>

Bower, A. D. R., Bryce A.; Hipkins, Valerie; Rochefort, Regina; Aubry, Carol (2011). "Comparison of genetic diversity and population structure of Pacific Coast whitebark pine across multiple markers. [Abstract] In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 150."

Analysis of "neutral" molecular markers and "adaptive" quantitative traits are common methods of assessing genetic diversity and population structure. Molecular markers typically reflect the effects of demographic and stochastic processes but are generally assumed to not reflect natural selection. Conversely, quantitative (or "adaptive") traits can be associated with climatic or other environmental variables that drive natural selection, but may not reflect the past demographic processes, such as bottlenecks, post-glacial recolonization, and population isolation. The genetics of whitebark pine has been studied using both molecular markers and adaptive traits, but never from a common set of samples so that the results could be directly compared. In addition, previous studies have not included samples from the Olympic Mountains in northwestern Washington, the westernmost distribution of whitebark pine that is geographically isolated from the rest of the species range. <http://www.treearch.fs.fed.us/pubs/38213>

Brunelle, A., G. E. Rehfeldt, et al. (2008). "Holocene records of *Dendroctonus* bark beetles in high elevation pine forests of Idaho and Montana, USA." Forest Ecology and Management 255(3-4): 836-846.

Paleoecological reconstructions from two lakes in the U.S. northern Rocky Mountain region of Idaho and Montana revealed the presence of bark beetle elytra and head capsules (cf. *Dendroctonus* spp., most likely *D. ponderosae*, mountain pine beetle).

Occurrence of these macrofossils during the period of time associated with the 1920/1930 A.D. mountain pine beetle outbreak at Baker Lake, Montana suggest that when beetle populations reach epidemic levels, beetle remains may be found in the lake sediments. In addition to the beetle remains found at Baker Lake during the 20th century, remains were also identified from ca. 8331, 8410, and 8529 cal yr BP. At Hoodoo Lake, Idaho remains were found at ca. 7954 and 8163 cal yr BP. These Holocene records suggest the infestations occurred during a period when climate changed rapidly to cooler and effectively wetter than present in forests dominated by whitebark pine. These two lake records provide the first preliminary data for understanding the longterm history of climatic influences on *Dendroctonus* bark beetle activity, which may be useful for predicting climate and stand conditions when mountain pine beetle activity occurs.

<http://www.sciencedirect.com/science/article/pii/S037811270700761X>

Bunn, A. G., L. A. Waggoner, et al. (2003). "Spatial variation in distribution and growth patterns of old growth strip-bark pines." *Arctic, Antarctic, and Alpine Research* 35(3): 323-330.

<http://www.jstor.org/stable/1552567>

Burke, S. A. Q., Michael S. (2011) Exploring whitebark pine resilience in the crown of the continent. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 303-311.

Whitebark pine (*Pinus albicaulis*) populations are declining across western North America due to synergies of disturbances, both natural and anthropogenic. Losses at treeline may result in significant changes to the upper subalpine zone, which may result in a regime shift, thus affecting the ecological goods and services whitebark pine systems provide for other species, including humans. Management and restoration should acknowledge the coupled social-ecological dynamics of high-elevation forest systems. Resilience is proposed as an appropriate framework for understanding social-ecological systems because it acknowledges complexity and uncertainty in a changing world. Mismatches of scale (spatial, temporal and functional) are increasingly problematic in management, and can lead to a loss of resilience in connected systems, often years or decades after management strategies have been implemented. Identifying mismatches in whitebark pine systems may inform long-term restoration strategies across jurisdictional boundaries. This paper reviews resilience concepts, with an emphasis on scalar mismatches and the problem of 'fit'. A conceptual framework is proposed to measure the functional fit between institutions in a jurisdictionally diverse, transboundary region and the capacity to manage high-elevation whitebark pine systems. <http://www.treesearch.fs.fed.us/pubs/38242>

Burns, K., J. Blodgett, et al. (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. Forest Health Technology Enterprise Team Ft Collins, CO, pp. 20-24. <http://rap.midco.net/jtb/Abst38.pdf>

Burns, K. S. (2006). White pine blister rust surveys in the Sangre de Cristo and Wet Mountains of southern Colorado. U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Renewable Resources. Biological Evaluation R2-06-05. 22 p.

[http://www.fs.usda.gov/Internet/FSE\\_DOCUMENTS/fsbdev3\\_039084.pdf](http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev3_039084.pdf)



Burns, K. S., A. Achoettle, et al. (2007) White pine blister rust in the Rocky Mountain Region and options for management. Biological Evaluation R2-07-04. USDA Forest Service, Rocky Mountain Region, Golden, CO. [http://fedgycc.org/documents/blister-rust\\_R2\\_MGMT.pdf](http://fedgycc.org/documents/blister-rust_R2_MGMT.pdf)

Burns, K. S., A. W. Schoettle, et al. (2008) Options for the management of white pine blister rust in the Rocky Mountain Region. Gen. Tech. Rep. RMRS-GTR-206. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 26 p.

This publication synthesizes current information on the biology, distribution, and management of white pine blister rust (WPBR) in the Rocky Mountain Region. In this Region, WPBR occurs within the range of Rocky Mountain bristlecone pine (*Pinus aristata*), limber pine (*P. flexilis*), and whitebark pine (*P. albicaulis*). This disease threatens white pine species and ecosystems in some of our most treasured public and private lands, including the wildland-urban interface, Wilderness Areas, and National Parks such as Rocky Mountain National Park and Great Sand Dunes National Park and Preserve. Long-term management strategies and management options for sustaining ecosystems and preserving high-value trees are presented. This information provides forest managers with knowledge and resources needed to detect WPBR, evaluate impacted stands, and develop management strategies that are applicable in the Rocky Mountain Region. <http://www.treesearch.fs.fed.us/pubs/29450>

Callaway, R. M., A. Sala, et al. (2000). "Succession may maintain high leaf area: Sapwood ratios and productivity in old subalpine forests." *Ecosystems* 3(3): 254-268.

Old forests are generally believed to exhibit low net primary productivity (NPP) and therefore to be insignificant carbon sinks. This relationship between age and NPP is based, in part, on the hypothesis that the biomass of respiratory tissues such as sapwood increases with age to a point where all photosynthate is required just to maintain existing tissue. However, this theoretical connection between respiration:assimilation ratios and forest productivity is based on age-dependent trends in the sapwood:leaf ratios of individual trees and even-aged stands; it does not take into account such processes in natural forests as disproportional increases in shade-tolerant species over time and multiple-age cohorts. Ignoring succession and structural complexity may lead to large underestimates of the productivity of old forests and inaccurate estimates of the ages at which forest productivity declines. To address this problem, we compared biomass allocation and productivity between **whitebark pine**, a shade-intolerant, early-successional tree species, and subalpine fir, a shade-tolerant, late-successional species, by harvesting 14 whitebark pines and nine subalpine firs that varied widely in dbh and calculating regression models for dbh vs annual productivity and biomass allocation to leaves, sapwood, and heartwood. Late-successional subalpine fir allocated almost twice as much biomass to leaves as early-successional whitebark pine. Subalpine firs also had a much lower allocation to sapwood and higher growth rates across all tree sizes. We then modeled biomass allocation and productivity for 12 natural stands in western Montana that were dominated by subalpine fir and whitebark pine varying in age from 67 to 458 years by applying the regressions to all trees in each stand. Whole-stand sapwood:leaf ratios and stand productivity increased asymptotically with age. Sapwood:leaf ratios and productivity of whitebark pine in these stands increased for approximately 200-300 years and then decreased slowly over the next 200 years. In contrast, sapwood:leaf ratios of all sizes of subalpine fir were lower than those of pine and productivity was higher. As stands shifted in dominance from pine to fir with age, subalpine fir appeared to maintain gradually increasing rates of whole-forest productivity until stands were approximately 400 years old. These results suggest that forests such as these may continue to sequester carbon for centuries. If shade-tolerant species that predominate late in succession maintain high

assimilation-to-respiration ratios in other forests, we may be underestimating production in old forests, and current models may underestimate the importance of mature forests as carbon sinks for atmospheric CO<sub>2</sub> in the global carbon cycle.

Campbell, E. M. and J. A. Antos (2000). "Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia." Canadian Journal of Forest Research 30(7): 1051-1059.

A major decline in the abundance of whitebark pine (*Pinus albicaulis* Engelm.) has recently occurred in the United States, primarily as a result of white pine blister rust (*Cronartium ribicola* J.C. Fisch. ex Raben.). However, no information on the status of whitebark pine in British Columbia, Canada, was available. We sampled 54 subalpine stands in British Columbia, examining all whitebark pine trees within plots for evidence of blister rust and mountain pine beetle (*Dendroctonus ponderosae* Hopk.) damage. About 21% of all whitebark pine stems were dead, and blister rust was the most important agent of mortality. Of all living trees sampled, 27% had obvious blister rust infection (cankers), but actual incidence was suspected of being as high as 44% (using all evidence of blister rust). Blister rust incidence and whitebark pine mortality were significantly related to differences in stand structure and the presence of *Ribes* spp., but relationships with local climate and site variables were absent or weak. The lack of strong relationships with climate suggests favourable conditions for the spread of the disease throughout most of British Columbia. Very little evidence of mountain pine beetle was found. Overall, the prospects for whitebark pine in British Columbia do not appear good; a large reduction in population levels seems imminent.

Campbell, E. M. and J. A. Antos (2003). "Postfire succession in *Pinus albicaulis* - *Abies lasiocarpa* forests of southern British Columbia." Canadian Journal of Botany 81(4): 383-397.

To examine postfire succession in forests where *Pinus albicaulis* Englem. is common, we conducted chronosequence studies in two areas of contrasting climate in southern British Columbia. Tree age and growth data indicated that *Pinus albicaulis* established rapidly following fire disturbance but that trees also continued to establish in late seral stands. Interactions with *Pinus contorta* Dougl. ex Loud., which grows faster, are pivotal in controlling the population dynamics of *Pinus albicaulis*. Where *Pinus contorta* established abundantly after fire, it dominated stands and limited the abundance of *Pinus albicaulis*, even after the postfire *Pinus contorta* had largely died. In contrast, where few or no *Pinus contorta* established, *Pinus albicaulis* dominated stands throughout most of the successional sequence. Although *Pinus albicaulis* decreases in abundance in late seral stands, we found no evidence that it would be completely replaced by more shade-tolerant species in our study areas. Thus, *Pinus albicaulis* is not only a pioneer species like *Pinus contorta*, even though it establishes in abundance after disturbance, but also a stress tolerator, with population dynamics molded by its ability to grow slowly and persist for long periods under adverse conditions and by bird dispersal of its seeds.

Campbell, E. M., R. E. Keane, et al. (2011). Disturbance ecology of high-elevation five-needle pine ecosystems in western North America. [Plenary paper]. p. 154-163. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. The future of high-elevation, five-needle white pines in Western North, America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. [http://www.fs.fed.us/rm/pubs/rmrs\\_p063/rmrs\\_p063\\_154\\_163.pdf](http://www.fs.fed.us/rm/pubs/rmrs_p063/rmrs_p063_154_163.pdf). Notes.

Carey, E. V., A. Sala, et al. (2001). "Are old forests underestimated as global carbon sinks?" Global Change Biology 7(4): 339-344.

Old forests are important carbon pools, but are thought to be insignificant as current atmospheric carbon sinks. This perception is based on the assumption that changes in productivity with age in complex, multiaged, multispecies natural forests can be modelled simply as scaled-up versions of individual trees or even-aged stands. This assumption was tested by measuring the net primary productivity (NPP) of natural subalpine forests (dominated by *Pinus albicaulis* and *Abies lasiocarpa*) in the Northern Rocky Mountains, Montana, USA, where NPP is from 50 to 100% higher than predicted by a model of an even-age forest composed of a single species. If process-based terrestrial carbon models underestimate NPP by 50% in just one quarter of the temperate coniferous forests throughout the world, then global NPP is being underestimated by 145 Tg of carbon annually. This is equivalent to 4.3-7.6% of the missing atmospheric carbon sink. These results emphasize the need to account for multiple-aged, species-diverse, mature forests in models of terrestrial carbon dynamics to approximate the global carbon budget.

<http://onlinelibrary.wiley.com/doi/10.1046/j.1365-2486.2001.00418.x/full>

Clason, A., S.E. Macdonald and S. Haeussler (2010). "Ecosystem change at whitebark pine's northern limits." Nutcracker Notes 18: 12-13.

Clason, A. J. (2010) Overstory and understory dynamics of whitebark pine (*Pinus albicaulis*) ecosystems of northwestern British Columbia. Thesis (M.Sc.)--University of Alberta, 2010.

<http://www.worldcat.org/oclc/696788411>

COSEWIC (2010). COSEWIC assessment and status report on the whitebark pine *Pinus albicaulis* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. x + 44 pp. [http://publications.gc.ca/collections/collection\\_2011/ec/CW69-14-612-2010-eng.pdf](http://publications.gc.ca/collections/collection_2011/ec/CW69-14-612-2010-eng.pdf)

Cottone, N. and G. J. Ettl (2001). "Estimating populations of whitebark pine in Mount Rainier National Park, Washington, using aerial photography." Northwest Science 75(4): 397-406.

Whitebark pine abundance is declining in western North America due to white pine blister rust, fire exclusion, and mountain pine beetle. In this study, natural color aerial photograph (23 x 23 cm) negatives, scales between 1:2,000 and 1:6,000) were used to estimate whitebark pine abundance in Mount Rainier National Park. Ground truth field plots were similar to counts from aerial photographs (80.2% accuracy). Correlation analysis between subpopulation area and abundance was used to supplement incomplete aerial coverage and determine the final whitebark pine abundance in the Park. Whitebark pine density, and vegetation cover type, influenced counts from the aerial photographs. Highly clustered whitebark pine sites demonstrated 7% greater accuracy when compared to sites that exhibited little clustering. Count accuracy was 4-5% more accurate on whitebark pine dominant habitats compared to subalpine fir dominant and subalpine parkland habitat. The total number of living adult whitebark pine within park boundaries was similar to 22,000, with 3,160 adult trees found in the Sunrise region. Aerial photography holds promise as a way to inventory and monitor whitebark pine.

Cripps, C. L. A., Robert K. (2011). Native ectomycorrhizal fungi of limber and whitebark pine: Necessary for forest sustainability? In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 37-44.

Ectomycorrhizal fungi are an important component of northern coniferous forests, including those of *Pinus flexilis* (limber pine) and *P. albicaulis* (whitebark pine) which are being decimated by white pine blister rust and mountain pine beetles. Ectomycorrhizal fungi are known to promote seedling establishment, tree health, and may play a role in forest sustainability. The goal of this research is to discover the native ectomycorrhizal fungi associated with these two pines in the Rocky Mountain region. Here we report 32 species of ectomycorrhizal fungi associated with whitebark pine, 26 with limber pine, with an overlap of 14 species (primarily suilloids). The ectomycorrhizal fungi can be grouped into 1. generalists, 2. western conifer associates, 3. calcareous species (limber pine) and 4. specialists for five-needle pine or stone pines (primarily suilloids). Some of the *Suillus* species occur with stone pines globally, suggesting a long co-evolutionary history and important ecological roles. Their association with limber pines is newly reported. These five-needle pine specialists could confer a competitive advantage over spruce and fir when present. A preliminary study of the physiology of the suilloid fungi reveals intra- and inter-specific variation in pH preference/tolerance in vitro. Strains with limber pines from calcareous sites exhibit a broader pH tolerance than those found with whitebark pine which is restricted to high elevations. It is hoped that these efforts contribute to an understanding of the native ectomycorrhizal fungi with whitebark and limber pine and provide information useful towards sustaining these tree species, including strain selection for inoculation of nursery seedlings. <http://www.treearch.fs.fed.us/pubs/38191>

Cripps, C. L. G., E. (2011) Inoculation and successful colonization of whitebark pine seedlings with native mycorrhizal fungi under greenhouse conditions. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 312-322.

Efforts to maintain and restore whitebark pine (*Pinus albicaulis*) forests in western North America have increased dramatically over the last two decades and now include the planting of nursery-grown rust resistant seedlings in openings and burned areas. Over 200,000 nursery seedlings have been planted in the western U.S. but survival rates are low and in many areas approach zero. One possibility for enhancing seedling survival is application of mycorrhizal fungi in the greenhouse before out-planting. All pines require ectomycorrhizal fungi (ECM) to survive in nature, including whitebark pine.

<http://www.treearch.fs.fed.us/pubs/38243>

Crone, E. E., E. J. B. McIntire, et al. (2011). "What defines mast seeding? Spatio-temporal patterns of cone production by whitebark pine." *Journal of Ecology* 99(2): 438-444.

1. Synchronous, episodic mast seeding is common in plant populations, and is thought to increase plant fitness through economies of scale, such as satiating seed predators, attracting seed dispersers and enhancing pollination success. Although mast seeding is easy to conceptualize, it has been quantified using a number of different metrics that reflect different features of pulsed reproduction. 2. We quantified spatio-temporal patterns of mast seeding across 36 populations of a high-elevation tree, *Pinus albicaulis*, for which perceived declines in cone production are a conservation concern. We tested for trends in mean cone production through space and time, and documented patterns of mast seeding using six different metrics: coefficient of variation, lag-1 autocorrelation, synchrony, average cone production by individual trees, and the frequency of high cone crops on absolute and relative scales. 3. Overall, we did not detect increasing or decreasing trends in cone production during our study period. Average cone production tended to increase from north-east to south-west. Population-level cone production tended to alternate

between high and low years, but overall the coefficient of variation was low for a mast seeding species. 4. Metrics of mast seeding were not concordant across populations. The first principal component describing mast metrics separated populations with frequent high cone crops from those with high coefficients of variation. However, the second principle component was at least somewhat correlated with all metrics of masting, suggesting some ability to separate 'masting' from 'non-masting' populations. 5. In *P. albicaulis*, spatial variation in mast seeding could reflect differences in site productivity, differences in the importance of satiating generalist seed consumers versus attracting specialist seed dispersers, or recent invasion by an introduced pathogen. 6. Synthesis. Our research reinforces the conclusion that populations form a continuum of strategies between 'masting' versus 'non-masting' extremes. However, because different features of masting do not covary in space, understanding where populations fall along this continuum will depend on the features that are most important for mast seeding in a particular context.

Daniels, L. D., S. M. Butler, et al. (2003). Whitebark pine stand dynamics at Morrell Mountain, Montana. In: Speer, J.H. ed. Proceedings of the 13th annual North American dendroecological fieldweek (NADEF): Experiential learning and exploratory research. Pap. 23. Greenough, MT: Indiana State University, Department of Geography, Geology, and Anthropology\_p. 15-29.

We used dendroecological methods to assess disturbance history and population dynamics of whitebark pine and subalpine fir at Morrell Mountain, Lolo National Forest, Montana. Our goal was to test the hypothesis that subalpine fir is replacing whitebark pine due to the cumulative effects of white pine blister rust, mountain pine beetle, and fire suppression during the 20th century. Live canopy dominant white bark pine, up to 567 years old, established between 1436 and 1620. Crossdated samples from snags indicated they died between 1776 and 2002. Blue-stain fungi in the sapwood of many trees showed that mountain pine beetle commonly contributed to tree death. The growth rates of "declining" versus "healthy" whitebark pines (with and without crown dieback, respectively) were not significantly different, although the basal area increment of declining trees decreased significantly during the 20th century, specifically between 1951 and 2000. Interactions between blister rust and mountain pine beetle warrant further investigation. Subalpine fir were 86 to 307 years of age, suggesting that stand-level fires had not burned at the study site for at least 300 years. Prescribed burning at this site may increase the chance of successful establishment of whitebark pine, but it may not restore the historical fire regime. We conclude that dendroecological research can provide important information about disturbance regimes and interactions among disturbance agents needed to successfully meet management and restoration goals. We provide several recommendations for future research of the dynamics of whitebark pine-subalpine fir forests. [http://dendrolab.indstate.edu/nadef/Reports/2003\\_Daniels.pdf](http://dendrolab.indstate.edu/nadef/Reports/2003_Daniels.pdf)

Dumroese, R. K. (2008). "Observations on root disease of container whitebark pine seedlings treated with biological controls." *Native Plants Journal* 9(2): 92-97.

In a greenhouse experiment, whitebark pine (*Pinus albicaulis*) germinants treated with two biological control agents, one commercially available (*Trichoderma harzianum* strain T-22) and the other being studied for potential efficacy (*Fusarium oxysporum* isolate Q12), had less seedling mortality caused by root disease (caused by *Fusarium* and *Cylindrocarpon* spp.) than the non-treated control. Seedlings treated with the biological control agents and non-symptomatic seedlings in the control treatment had similar morphology. The simple use of the biological control agents may be useful to nursery managers to reduce the incidence of root disease in their container crops. <http://treesearch.fs.fed.us/pubs/32845>

Ellison, A. M., W. V. Sobczak, et al. (2005). "Loss of foundation species: consequences for the structure and dynamics of forested ecosystems." Frontiers in ecology and the environment 3(9): 479-486.

In many forested ecosystems, the architecture and functional ecology of certain tree species define forest structure and their species-specific traits control ecosystem dynamics. Such foundation tree species are declining throughout the world due to introductions and outbreaks of pests and pathogens, selective removal of individual taxa, and over-harvesting. Through a series of case studies, we show that the loss of foundation tree species changes the local environment on which a variety of other species depend; how this disrupts fundamental ecosystem processes, including rates of decomposition, nutrient fluxes, carbon sequestration, and energy flow; and dramatically alters the dynamics of associated aquatic ecosystems. Forests in which dynamics are controlled by one or a few foundation species appear to be dominated by a small number of strong interactions and may be highly susceptible to alternating between stable states following even small perturbations. The ongoing decline of many foundation species provides a set of important, albeit unfortunate, opportunities to develop the research tools, models, and metrics needed to identify foundation species, anticipate the cascade of immediate, short- and long-term changes in ecosystem structure and function that will follow from their loss, and provide options for remedial conservation and management.

<http://www.esajournals.org/doi/abs/10.1890/1540-9295%282005%29003%5B0479:LOFSCF%5D2.0.CO%3B2>

Felicetti, L. A., C. C. Schwartz, et al. (2003). "Use of sulfur and nitrogen stable isotopes to determine the importance of whitebark pine nuts to Yellowstone grizzly bears." Canadian Journal of Zoology 81(5): 763-770.

Whitebark pine (*Pinus albicaulis*) is a mast seeding species that produces relatively large, fat- and protein-rich nuts that are consumed by grizzly bears (*Ursus arctos horribilis*). Trees produce abundant nut crops in some years and poor crops in other years. Grizzly bear survival in the Greater Yellowstone Ecosystem is strongly linked to variation in pine-nut availability. Because whitebark pine trees are infected with blister rust (*Cronartium ribicola*), an exotic fungus that has killed the species throughout much of its range in the northern Rocky Mountains, we used stable isotopes to quantify the importance of this food resource to Yellowstone grizzly bears while healthy populations of the trees still exist. Whitebark pine nuts have a sulfur-isotope signature (9.2 +/- 1.3‰ (mean +/- 1 SD)) that is distinctly different from those of all other grizzly bear foods (ranging from 1.9 +/- 1.7‰ per thousand for all other plants to 3.1 +/- 2.6‰ per thousand for ungulates). Feeding trials with captive grizzly bears were used to develop relationships between dietary sulfur-, carbon-, and nitrogen-isotope signatures and those of bear plasma. The sulfur and nitrogen relationships were used to estimate the importance of pine nuts to free-ranging grizzly bears from blood and hair samples collected between 1994 and 2001. During years of poor pine-nut availability, 72% of the bears made minimal use of pine nuts. During years of abundant cone availability, 8 +/- 10% of the bears made minimal use of pine nuts, while 67 +/- 19% derived over 51% of their assimilated sulfur and nitrogen (i.e., protein) from pine nuts. Pine nuts and meat are two critically important food resources for Yellowstone grizzly bears.

Field, S. G., A. W. Schoettle, et al. (2012). "Demographic projection of high-elevation white pines infected with white pine blister rust: a nonlinear disease model." Ecological Applications 22(1): 166-183. <http://www.esajournals.org/doi/pdf/110.1890/1811-0470.1891>.

Fryer, J. L. (2002). *Pinus albicaulis*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.fs.fed.us/database/feis/plants/tree/pinalb/all.html>

Garcia, R., A. M. Siepielski, et al. (2009). "Cone and seed trait variation in whitebark pine (*Pinus albicaulis*; pinaceae) and the potential for phenotypic selection." *American Journal of Botany* 96(5): 1050-1554.

Phenotypic variation among individuals is necessary for natural selection to operate and is therefore essential for adaptive evolution. However, extensive variation within individuals can mask variation among individuals and weaken the potential for selection. Here we quantify variation among and within individuals in female cone and seed traits of whitebark pine (*Pinus albicaulis*). In many plants, the production of numerous reproductive structures creates the potential for considerable variation within a plant, but these same traits should also undergo strong selection because of their direct link to plant fitness. We found about twice as much variation among individuals (overall mean =  $65.3 \pm 4.5\%$  SE) than within individuals (overall mean =  $34.7 \pm 4.5\%$ ). One only needs to sample three to five cones per tree to accurately assess variation among trees in most cone and seed traits. The ease at which trees can be assessed helps account for the strong and consistent patterns of phenotypic selection exerted by seed predators and dispersers of whitebark pine and many other conifers. In contrast, the few traits where variation within trees equaled or exceeded that among trees underwent weak if any phenotypic selection.

Gibson, K. (2004). Mountain pine beetle: conditions and issues in the Western United States, 2003. In: Mountain Pine Beetle Symposium: Challenges and Solutions. October 30-31, 2003, Kelowna, British Columbia. T.L. Shore, J.E. Brooks, and J.E. Stone (editors). Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria, BC, pp. 57-61.

The mountain pine beetle (*Dendroctonus ponderosae*) is by far the most destructive insect pest of pine species in western North America. It is once again at outbreak levels in many parts of the western United States, currently affecting more than 1.5 million acres (0.7 million ha). The infested area in the western US nearly doubled from 2001 to 2002. While infesting most pines within its range, and causing significant concerns in ponderosa [*Pinus ponderosa*], western white [*P. monticola*], and whitebark pines [*P. albicaulis*], lodgepole pine [*P. contorta* var. *latifolia*] is the most frequently infested and most heavily damaged of the beetle's hosts. Nearly 90% of the current mortality is in lodgepole pine. Management strategies and tactics have been developed to better deal with the devastating impact of mountain pine beetle infestations across the western US.

[http://www.for.gov.bc.ca/hfd/library/MPB/gibson\\_2004\\_mount.pdf](http://www.for.gov.bc.ca/hfd/library/MPB/gibson_2004_mount.pdf)

Gibson, K. (2006). Mountain pine beetle conditions in whitebark pine stands in the Greater Yellowstone Ecosystem, 2006. Forest Health Protection Report - Northern Region, USDA Forest Service. Missoula; USA, Northern Region, USDA Forest Service. Numbered Report 06-03.

This paper describes the current status of mountain pine beetle (*Dendroctonus ponderosae*) infestation on whitebark pine (***Pinus albicaulis***) in the Greater Yellowstone Ecosystem (GYE) in the USA. There are a few administrative units in the GYE for which there are no data, but should not be interpreted as areas in which outbreaks do not exist. Rather they are areas not surveyed.

<http://www.for.gov.bc.ca/hfd/library/documents/bib97121.pdf>

Gibson, K., K. Skov, et al. (2008). Mountain pine beetle impacts in high-elevation five-needle pines: current trends and challenges. Forest Health Protection Report - Northern Region, USDA Forest Service. Missoula; USA, Northern Region, USDA Forest Service.

A diverse group of five-needle pines native to western North America have captured the imagination of many for being long-lived and thriving in what can be considered harsh environmental conditions. These pines include whitebark pine (*Pinus albicaulis*), limber pine (*P. flexilis*), foxtail pine (*P. balfouriana*), Rocky Mountain bristlecone pine (*P. aristata*) and Great Basin bristlecone pine (*P. longaeva*). In this report, the focus is on these five species and present information on tree mortality trends caused by mountain pine beetles (*Dendroctonus ponderosae*). Also discussed are the challenges and opportunities facing forest managers that, when adequately addressed, will help ensure these pine species remain an integral part of high-elevation landscapes.

Goheen, E. M. and J. Schwandt (2010). "Can whitebark pine be saved?" Phytopathology 100(6): S166-S167.

Goheen, E. M. a. S., R.A., tech. coords. (2007). Proceedings of the conference whitebark pine: a Pacific Coast perspective. 2006 August 27-31. Ashland, OR. R6-NR-FHP-2007-01. Portland, OR: Pacific Northwest Region, Forest Service, U.S. Department of Agriculture. R6-NR-FHP-2007-01. <http://www.fs.fed.us/r6/nr/fid/wbpine/wbp-proceedings-2007.pdf>

Goheen, E. M. G., Donald J.; Marshall, Katy; Danchok, Robert S.; Petrick, John A.; White, Diane E. (2002). The status of whitebark pine along the Pacific Crest National Scenic Trail on the Umpqua National Forest. Gen. Tech. Rep. PNW-GTR-530. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 21 p.

Because of concern over widespread population declines, the distribution, stand conditions, and health of whitebark pine (***Pinus albicaulis*** Englem.) were evaluated along the Pacific Crest National Scenic Trail on the Umpqua National Forest. Whitebark pine occurred on 76 percent of the survey transects. In general, whitebark pine was found in stands with lower overall densities and fewer late-seral species, particularly Shasta red fir (*Abies magnifica* var. *shatensis* A. Murr.) and mountain hemlock (*Tsuga mertensiana* [Bong.] Carr.). Whitebark pine stocking differed widely, from less than 1 up to 24 percent of the trees on transect plots. Most whitebark pines (87 percent) were less than 5 m tall. Of all whitebark pine encountered, 44 percent were alive and healthy, 46 percent were alive but infected by *Cronartium ribicola* (J.C. Fisch) (cause of white pine blister rust), and 10 percent were dead. Two-thirds of the mortality was due to white pine blister rust. Mountain pine beetle (*Dendroctonus ponderosae* Hopkins) alone accounted for 13 percent of the mortality, whereas evidence of mountain pine beetle was found with white pine blister rust on 18 percent of the dead whitebark pines.

<http://www.treearch.fs.fed.us/pubs/29520>

Haeussler, S., A. Woods, et al. (2009). Do whitebark pine–lichen ecosystems of west central British Columbia display tipping point behaviour in response to cumulative stress. Bulkley Valley Centre for Natural Resources Research & Management. Research Report. Smithers, BC. [http://www.bvcentre.ca/files/research\\_reports/09-06WhitebarkPineReportOct29-09.pdf](http://www.bvcentre.ca/files/research_reports/09-06WhitebarkPineReportOct29-09.pdf)

Hamlin, J. K., Angelia; Snieszko, Richard (2011). "Genetic variation of whitebark pine (*Pinus albicaulis*) provenances and families from Oregon and Washington in juvenile height growth and needle color. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort



Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 133-139."

A three year common garden study was conducted on whitebark pine (*Pinus albicaulis*) which included 215 families from the eight provenances or seed zones in Oregon and Washington. Total height and needle color were assessed. Height differed significantly among provenances and families, and was primarily associated with source elevation, longitude, and precipitation. A moderate to high heritability was estimated for total height. Seedling needle color differed among provenances and was associated with temperature:moisture indexes and source elevation. Height growth along the Cascade mountain range (USA), representing four adjoining provenances or seed zones, appeared to be similar and clinal in nature. The four remaining provenances, representing seed zones from a more moderate or extreme environmental settings, differed significantly from the Cascade provenances for one or more traits that were examined. It would seem prudent to restrict seed transfers to within each of these four seed zones respectively. This study also supports the need to plan gene conservation collections within each seed zone for whitebark pine in the Pacific Northwest region.

<http://www.treesearch.fs.fed.us/pubs/38209>

Haroldson, M. A., C. C. Schwartz, et al. (2004). "Possible effects of elk harvest on fall distribution of grizzly bears in the Greater Yellowstone Ecosystem." Journal of Wildlife Management 68(1): 129-137.

The tradition of early elk (*Cervus elaphus*) hunting seasons adjacent to Yellowstone National Park (YNP), USA, provides grizzly bears (*Ursus arctos horribilis*) with ungulate remains left by hunters. We investigated the fall (Aug-Oct) distribution of grizzly bears relative to the boundaries of YNP and the opening of September elk hunting seasons. Based on results from exact tests of conditional independence, we estimated the odds of radiomarked bears being outside YNP during the elk hunt versus before the hunt. Along the northern boundary, bears were 2.40 times more likely to be outside YNP during the hunt in good whitebark pine (***Pinus albicaulis***) seed-crop years and 2.72 times more likely in poor seed-crop years. The level of confidence associated with I-sided confidence intervals with a lower endpoint of 1 was approximately 94% in good seed-crop years and 61% in poor years. Along the southern boundary of YNP, radiomarked bears were 2.32 times more likely to be outside the park during the hunt in good whitebark pine seed-crop years and 4.35 times more likely in poor seed-crop years. The level of confidence associated with I-sided confidence intervals with a lower endpoint of 1 was approximately 93% in both cases. Increased seasonal bear densities and human presence in early hunt units increases potential for conflicts between bears and hunters. Numbers of reported hunting-related grizzly bear mortalities have increased in the Greater Yellowstone Ecosystem (GYE) during the last decade, and nearly half of this increase is due to bear deaths occurring in early hunt units during September. Human-caused grizzly bear mortality thresholds established by the U.S. Fish and Wildlife Service (USFWS) have not been exceeded in recent years. This is because agency actions have reduced other sources of human-caused mortalities, and because population parameters that mortality thresholds are based on have increased. Agencies must continue to monitor and manage hunter-caused grizzly bear mortality at sustainable levels to ensure the long-term health of the GYE population. <http://www.bioone.org/doi/abs/10.2193/0022-541X%282004%29068%5B0129:PEOHO%5D2.0.CO%3B2>

Harvey, A. E. B., James W.; McDonald, GERAL I.; Neuenschwander, Leon F.; Tonn, Jonalea R. (2008). Death of an ecosystem: perspectives on western white pine ecosystems of North America at the end of the twentieth century. Gen. Tech. Rep. RMRS-GTR-208. Fort Collins, CO: U.S.

Department of Agriculture, Forest Service, Rocky Mountain Research Station. 10 p.  
<http://www.treesearch.fs.fed.us/pubs/29617/>

Hatala, J. A., R. L. Crabtree, et al. (2010). "Landscape-scale patterns of forest pest and pathogen damage in the Greater Yellowstone Ecosystem." Remote Sensing of Environment 114(2): 375-384.

Pathogen and pest outbreaks are recognized as key processes in the dynamics of Western forest ecosystems, yet the spatial patterns of stress and mortality are often complex and difficult to describe in an explicit spatial context, especially when considering the concurrent effects of multiple agents. Blister rust, a fungal pathogen, and mountain pine beetle, an insect pest, are two dominant sources of stress and mortality to high-altitude whitebark pine within the Greater Yellowstone Ecosystem (GYE). In whitebark pine populations infested with blister rust or mountain pine beetle, the shift from green to red needles at the outer-most branches is an early sign of stress and infestation. In this analysis, we investigated a method that combines field surveys with a remote sensing classification and spatial analysis to differentiate the effects of these two agents of stress and mortality within whitebark pine. Hyperspectral remotely sensed images from the airborne HyMap sensor were classified to determine the locations of stress and mortality in whitebark pine crowns through sub-pixel mixture-tuned matched-filter analysis in three areas of the GYE in September 2000 and July 2006. Differences in the spatial pattern of blister rust and mountain pine beetle infestation allowed us to separate areas dominated by mountain pine beetle versus blister rust by examining changes in the spatial scale of significant stress and mortality clusters computed by the Ripley's K algorithm. At two field sites the distance between clusters of whitebark pine stress and mortality decreased from 2000 to 2006, indicating domination by the patchy spatial pattern of blister rust infestation. At another site, the distance between significant stress and mortality clusters increased from 2000 to 2006, indicating that the contiguous pattern of mountain pine beetle infestation was the primary source of disturbance. Analysis of these spatial stress and mortality patterns derived from remote sensing yields insight to the relative importance of blister rust and mountain pine beetle dynamics in the landscape.

<http://www.sciencedirect.com/science/article/pii/S0034425709002806>

Hatala, J. A., M. C. Dietze, et al. (2011). "An ecosystem-scale model for the spread of a host-specific forest pathogen in the Greater Yellowstone Ecosystem." Ecological Applications 21(4): 1138-1153.

The introduction of nonnative pathogens is altering the scale, magnitude, and persistence of forest disturbance regimes in the western United States. In the high-altitude whitebark pine (*Pinus albicaulis*) forests of the Greater Yellowstone Ecosystem (GYE), white pine blister rust (*Cronartium ribicola*) is an introduced fungal pathogen that is now the principal cause of tree mortality in many locations. Although blister rust eradication has failed in the past, there is nonetheless substantial interest in monitoring the disease and its rate of progression in order to predict the future impact of forest disturbances within this critical ecosystem. This study integrates data from five different field-monitoring campaigns from 1968 to 2008 to create a blister rust infection model for sites located throughout the GYE. Our model parameterizes the past rates of blister rust spread in order to project its future impact on high-altitude whitebark pine forests. Because the process of blister rust infection and mortality of individuals occurs over the time frame of many years, the model in this paper operates on a yearly time step and defines a series of whitebark pine infection classes: susceptible, slightly infected, moderately infected, and dead. In our analysis, we evaluate four different infection models that compare local vs. global density dependence on the dynamics of blister rust infection. We compare models in which blister rust infection

is: (1) independent of the density of infected trees, (2) locally density-dependent, (3) locally density-dependent with a static global infection rate among all sites, and (4) both locally and globally density-dependent. Model evaluation through the predictive loss criterion for Bayesian analysis supports the model that is both locally and globally density-dependent. Using this best-fit model, we predicted the average residence times for the four stages of blister rust infection in our model, and we found that, on average, whitebark pine trees within the GYE remain susceptible for 6.7 years, take 10.9 years to transition from slightly infected to moderately infected, and take 9.4 years to transition from moderately infected to dead. Using our best-fit model, we project the future levels of blister rust infestation in the GYE at critical sites over the next 20 years.

<http://www.esajournals.org/doi/abs/10.1890/09-2118.1>

Hicke, J. A. and J. Logan (2009). "Mapping whitebark pine mortality caused by a mountain pine beetle outbreak with high spatial resolution satellite imagery." International Journal of Remote Sensing 30(17): 4427-4441.

Insect outbreaks cause significant tree mortality across western North America, including in high-elevation whitebark pine forests. These forests are under several threats, which include attack by insects and white pine blister rust, as well as conversion to other tree species as a result of fire suppression. Mapping tree mortality is critical to determining the status of whitebark pine as a species. Satellite remote sensing builds upon existing aerial surveys by using objective, repeatable methods that can result in high spatial resolution monitoring. Past studies concentrated on level terrain and only forest vegetation type. The objective of this study was to develop a means of classifying whitebark pine mortality caused by a mountain pine beetle infestation in rugged, remote terrain using high spatial resolution satellite imagery. We overcame three challenges of mapping mortality in this mountainous region: (1) separating non-vegetated cover types, green and brown herbaceous cover, green (live) tree cover, and red-attack (dead) tree cover; (2) variations in illumination as a result of variations in slope and aspect related to the mountainous terrain of the study site; and (3) the difficulty of georegistering the imagery for use in comparing field measurements. Quickbird multi-spectral imagery (2.4 m spatial resolution) was used, together with a maximum likelihood classification method, to classify vegetation cover types over a 6400 ha area. To train the classifier, we selected pixels in each cover class from the imagery guided by our knowledge of the study site. Variables used in the maximum likelihood classifier included the ratio of red reflectance to green reflectance as well as green reflectance. These variables were stratified by solar incidence angle to account for illumination variability. We evaluated the results of the classified image using a reserved set of image-derived class members and field measurements of live and dead trees. Classification results yielded high overall accuracy (86% and 91% using image-derived class members and field measurements respectively) and kappa statistics (0.82 and 0.82) and low commission (0.9% and 1.5%) and omission (6.5% and 15.9%) errors for the red-attack tree class. Across the scene, 700 ha or 31% of the forest was identified as in the red-attack stage. Severity (percent mortality by canopy cover) varied from nearly 100% for some areas to regions with little mortality. These results suggest that high spatial resolution satellite imagery can provide valuable information for mapping and monitoring tree mortality even in rugged, mountainous terrain.

Hoff, R. J., D. E. Ferguson, et al. (2001). Strategies for managing whitebark pine in the presence of white pine blister rust. [Chapter 17] pp. 346-366. In: . Whitebark pine communities: Ecology and restoration, Washington, D.C., Island Press.

Hood, S. M., D. R. Cluck, et al. (2008). "Using bark char codes to predict post-fire cambium mortality." *Fire Ecology* 4(1): 57-73.

Cambium injury is an important factor in post-fire tree survival. Measurements that quantify the degree of bark charring on tree stems after fire are often used as surrogates for direct cambium injury because they are relatively easy to assign and are non-destructive. However, bark char codes based on these measurements have been inadequately tested to determine how well they relate to live or dead cambium. Methods for assessing cambium injury through direct sampling have also been questioned as a potential factor for increasing tree mortality. In this study we used data collected from 11 wildfires and 6 prescribed fires in California, Idaho, Montana, and Wyoming to develop a relationship between bark char codes and cambium status for 14 coniferous species. Burned trees were assessed at groundline for bark char severity on each bole quadrant and then sampled at the center of each quadrant to determine cambium status (live or dead). We found that the moderate and deep bark char codes were strongly associated with dead cambium for thin-bark species: lodgepole pine (*Pinus contorta*), whitebark pine (*P. albicaulis*), western white pine (*P. monticola*), western redcedar (*Thuja plicata*), Engelmann spruce (*Picea engelmannii*), western hemlock (*Tsuga heterophylla*), and subalpine fir (*Abies lasiocarpa*). However, bark char codes were somewhat inaccurate in predicting cambium status of the thicker-bark species of white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), and sugar pine (*P. lambertiana*). We also evaluated the effect of direct cambium sampling on ponderosa pine tree mortality in eastern Montana. Mortality rates were equivalent for eastern Montana ponderosa pines with and without cambium sampling. Our results support using bark char codes as surrogates for cambium sampling in tree species with thin bark, but bark char codes for thick-bark species, especially the moderate char code, are often not accurate fire-injury variables, as they do not correlate well with cambium status.

Hudson, L. E. and E. K. Thomas (2010). "Whitebark pine restoration under way at Crater Lake: Preemptive strike against blister rust based on disease-resistant seedlings." *Park Science* 27(2): 6.

Izlar, D. K. (2007) Assessment of whitebark pine seedling survival for Rocky Mountain plantings. Thesis -- University of Montana, Missoula, MT. [http://etd.lib.umt.edu/theses/available/etd-12272007-124748/unrestricted/Izlar\\_WBP\\_thesis\\_12\\_26.pdf](http://etd.lib.umt.edu/theses/available/etd-12272007-124748/unrestricted/Izlar_WBP_thesis_12_26.pdf)

Jackson, S. and E. Campbell (2008) Assessing the threat of mountain pine beetle to whitebark pine in British Columbia. FIA-FSP Project # M08-6048, Final technical report. Research Branch, British Columbia Ministry of Forests and Range. [http://www.for.gov.bc.ca/hfd/library/FIA/2008/FSP\\_M086048a.pdf](http://www.for.gov.bc.ca/hfd/library/FIA/2008/FSP_M086048a.pdf)

Jean, C. S., Erin; Daley, Rob; DeNitto, Gregg; Reinhart, Dan; Schwartz, Chuck (2011) Monitoring white pine blister rust infection and mortality in whitebark pine in the Greater Yellowstone ecosystem. [Extended abstract] In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 218-221.

There is a critical need for information on the status and trend of whitebark pine (*Pinus albicaulis*) in the Greater Yellowstone Ecosystem (GYE). Concerns over the combined

effects of white pine blister rust (WPBR, *Cronartium ribicola*), mountain pine beetle (MPB, *Dendroctonus ponderosae*), and climate change prompted an interagency working group to design and implement a long-term monitoring program in the GYE. Our primary objective was to determine the status and trends in the proportion of trees >1.4 m tall infected with WPBR and to provide information to federal managers, at a regional scale, on estimates of tree survival, taking into account the presence of WPBR and MPB. Long-term monitoring of whitebark pine in the GYE and across its range is vital to understanding the ecological impact of forest insect and disease pathogens on this important high elevation species. <http://www.treesearch.fs.fed.us/pubs/38226>

Jewett, J. T., R. L. Lawrence, et al. (2011). "Spatiotemporal Relationships between Climate and Whitebark Pine Mortality in the Greater Yellowstone Ecosystem." *Forest Science* 57(4): 320-335. Whitebark pine (*Pinus albicaulis*) serves as a subalpine keystone species by regulating snowmelt runoff, reducing soil erosion, facilitating the growth of other plants, and providing food for wildlife. Mountain pine beetle (*Dendroctonus ponderosae*) is an ideal bioindicator of climate change, because its life cycle is temperature-dependent. Western North America is currently experiencing the largest outbreak of mountain pine beetle on record, and evidence suggests that a changing climate has accelerated the life cycle of this bark beetle. This study explored the relationships between climate, mountain pine beetles, and whitebark pine mortality in the Greater Yellowstone Ecosystem. A time series of Landsat satellite imagery (nine images) was used to monitor whitebark pine mortality in the Greater Yellowstone Ecosystem from 1999 to 2008. The patterns of mortality were analyzed with respect to monthly climate variations over the 9-year period. The impacts of topography and autocorrelation (both spatial and temporal) were also analyzed. The most important predictor variables were autocorrelation terms, indicating a strong host-tree depletion effect. Both drier and warmer climatic conditions favored increased whitebark pine mortality. These results show for the first time a statistical link between climate variability and whitebark pine mortality, probably mediated by mountain pine beetles.

Keane, R. E. (2000). The importance of wilderness to whitebark pine research and management. In: McCool, Stephen F.; Cole, David N.; Borrie, William T.; O'Loughlin, Jennifer, comps. 2000. Wilderness science in a time of change conference -- Volume 3: Wilderness as a place for scientific inquiry; 1999 May 23–27; Missoula, MT. Proceedings RMRS-P-15-VOL-3. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Whitebark pine (*Pinus albicaulis*) is a keystone species in upper subalpine forests of the northern Rocky Mountains, Cascades, and Sierra Nevada in the USA and Canada, that has been declining because of recent mountain pine beetle (*Dendroctonus ponderosae*) and exotic blister rust (*Cronartium ribicola*) epidemics, coupled with advancing succession resulting from fire exclusion. Whitebark pine and wilderness have a mutually beneficial relationship because (1) half of whitebark pine's range is in wilderness, (2) many wildlife species depend on whitebark pine ecosystems, (3) whitebark pine forests have high recreation value, and (4) whitebark pine landscapes contain unique ecological processes. Wilderness has not escaped the ravages of beetle, rust and fire exclusion, so restoration of these ecosystems may be warranted in some areas. The best wilderness restoration tool appears to be prescribed fires, especially management-ignited burns. This paper discusses whitebark pine ecology and the importance of the species to wilderness, and presents restoration treatments and management alternatives for these remote settings. [http://www.whitebarkfound.org/publications/rmrs\\_P\\_15\\_v3\\_whitebark.pdf](http://www.whitebarkfound.org/publications/rmrs_P_15_v3_whitebark.pdf)

Keane, R. E. (2001). "Can the fire-dependent whitebark pine be saved?" *Fire management today* 61(3): 17-20.

This paper describes the labour-intensive efforts conducted in the Rocky Mountains to restore the habitat of whitebark pine (*Pinus albicaulis*) by using controlled burning and silvicultural treatments. These measures were used to counteract forest decline due to white pine blister rust, caused by *Cronartium ribicola*, and native mountain pine beetle (*Dendroctonus ponderosae*). [http://www.fs.fed.us/fire/fmt/fmt\\_pdfs/fmn61-3.pdf](http://www.fs.fed.us/fire/fmt/fmt_pdfs/fmn61-3.pdf)

Keane, R. E. (2011) Restoration of whitebark pine forests in the northern Rocky Mountains, USA. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 338-347.

Whitebark pine (*Pinus albicaulis*) has been declining across much of its range in North America because of the combined effects of mountain pine beetle epidemics, fire exclusion policies, and widespread exotic blister rust infections. Whitebark pine seed is dispersed by a bird, the Clark's nutcracker, which caches seed in open, pattern-rich landscapes created by fire. This study was initiated in 1993 to investigate the effects of various restoration treatments on tree populations, fuel dynamics, and vascular plant cover on five sites in the U.S. northern Rocky Mountains. The objective of this study was to restore whitebark pine ecosystems using treatments that emulate the native fire regime - primarily combinations of prescribed fire, silvicultural cuttings, and fuel enhancement cuttings. <http://www.treesearch.fs.fed.us/pubs/38246>

Keane, R. E. and S. Arno (2000). Restoration of whitebark pine ecosystems in western Montana and central Idaho. Pages 324–330. In: Proceedings of the Society of American Foresters 1999 National Convention, Portland OR, September 11–15, 1999. Bethesda MD: Society of American Foresters.

Keane, R. E., S. F. Arno, et al. (2000) Ecosystem-based management in the whitebark pine zone. In: Smith, Helen Y., ed. 2000. The Bitterroot Ecosystem Management Research Project: What we have learned: symposium proceedings; 1999 May 18-20; Missoula, MT. Proc. RMRS-P-17. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 36-40. [http://www.fs.fed.us/rm/pubs/rmrs\\_p017/rmrs\\_p017\\_036\\_040.pdf](http://www.fs.fed.us/rm/pubs/rmrs_p017/rmrs_p017_036_040.pdf)

Keane, R. E., K. L. Gray, et al. (2007) Whitebark pine diameter growth response to removal of competition. Res. Note RMRS-RN-32. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 9 p

Silvicultural cutting treatments may be needed to restore whitebark pine (*Pinus albicaulis*) forests, but little is known of the response of this species to removal of competition through prescribed burning or silvicultural cuttings. We analyzed stem cross-sections from 48 whitebark pine trees in Montana around which most of the competing vegetation was removed by timber harvest treatments. We compared tree ring growth rates before and after the harvest treatment using intervention analysis to determine 1) the potential of release for this little-studied tree species and 2) whether the release is related to tree and stand characteristics. We defined release as a statistically significant increase in radial growth after competing trees were removed. All but one of our 48 sampled trees increased in diameter growth after competition was removed, while 40 trees showed a statistically significant ( $p < 0.05$ ) increase in growth. Diameter release was greatest in stands that were dense prior to tree cutting and greatest in old trees with large diameters.

Recommendations for appropriate silvicultural cutting are included to aid managers in designing effective restoration treatments. <http://www.treesearch.fs.fed.us/pubs/26758>

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

Whitebark pine is declining across much of its range in North America because of the combined effects of mountain pine beetle epidemics, fire exclusion policies, and widespread exotic blister rust infections. This management guide summarizes the extensive data collected at whitebark pine treatment sites for three periods: (1) pre-treatment, (2) 1 year post-treatment, and (3) 5 years post-treatment (one site has a 10 year post-treatment measurement). Study results are organized here so that managers can identify possible effects of a treatment at their own site by matching it to the most similar treatment unit in this study, based on vegetation conditions, fire regime, and geographical area. This guide is based on the Restoring Whitebark Pine Ecosystems study, which was initiated in 1993 to investigate the effects of various restoration treatments on tree mortality, regeneration, and vascular plant response on five sites in the northern Rocky Mountains. The objective was to enhance whitebark pine regeneration and cone production using treatments that emulate the native fire regime. Since data summaries are for individual treatment units, there are no analyses of differences across treatment units or across sites. <http://www.treesearch.fs.fed.us/pubs/34699>

Keane, R. E. and R. A. Parsons (2010). "Restoring whitebark pine forests of the northern Rocky Mountains, USA." *Ecological Restoration* 28(1): 56-70.

Whitebark pine (*Pinus albicaulis*) has been declining across much of its range in North America because of the combined effects of mountain pine beetle (*Dendroctonus ponderosae*) epidemics, fire exclusion policies, and widespread exotic blister rust infections. Whitebark pine seed is dispersed by a bird, the Clark's nutcracker (*Nucifraga columbiana*), which caches in open, pattern-rich landscapes created by fire. This study was initiated in 1993 to investigate the effects of various restoration treatments on tree populations, fuel dynamics, and vascular plant cover on five sites in the U.S. northern Rocky Mountains. The objective of this study was to restore whitebark pine ecosystems using treatments that emulate the native fire regime - primarily combinations of prescribed fire, silvicultural cuttings, and fuel enhancement cuttings. The main effects assessed included tree mortality, fuel consumption, and vegetation response measured just prior to the treatment, one year after the treatment(s), and five years posttreatment. While all treatments that included prescribed fire created suitable nutcracker caching habitat, with many birds observed caching seed in the burned areas, there has yet to be significant regeneration in whitebark pine. All burn treatments resulted in high mortality in both whitebark pine and subalpine fir (> 40%). Fine woody fuel loadings marginally decreased after fire, but coarse woody debris more than doubled because of falling snags. Vascular species decreased in cover by 20% to 80% and remained low for five years. While the treatments were successful in creating conditions that favor whitebark pine regeneration, the high level of blister rust mortality in surrounding seed sources has reduced available seed, which then forced the nutcracker to reclaim most of the cached seed. Manual planting of whitebark pine seedlings is required to adequately restore these sites. A set of management guidelines is presented to guide restoration efforts. [http://www.fs.fed.us/rm/pubs\\_other/rmrs\\_2010\\_keane\\_r002.pdf](http://www.fs.fed.us/rm/pubs_other/rmrs_2010_keane_r002.pdf)

Keane, R. E. A., S. F. (2001). Restoration concepts and techniques. In: Tomback, D. F., Arno, S. F., Keane, R. E. (Eds.), *Whitebark Pine Communities: Ecology and Restoration*. Island Press, Washington, D.C., USA. pp. 367-400.

Keane, R. E. R., Kevin C.; Veblen, Tom T.; Allen, Craig D.; Logan, Jessie; Hawkes, Brad (2002). Cascading effects of fire exclusion in the Rocky Mountain ecosystems: a literature review. General Technical Report. RMRS-GTR-91. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 24 p.  
<http://www.treesearch.fs.fed.us/pubs/5132>

Keane, R. E. T., Diana F.; Murray, Michael P.; Smith, Cyndi M. (2011). "The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 376 p."

High elevation five-needle pines are rapidly declining throughout North America. The six species, whitebark (***Pinus albicaulis*** Engelm.), limber (*P. flexilis* James), southwestern white (*P. strobiformis* Engelm.), foxtail (*P. balfouriana* Grev. & Balf.), Great Basin bristlecone (*P. longaeva* D.K. Bailey), and Rocky Mountain bristlecone pine (*P. aristata* Engelm.), have limited timber value but are of great ecological and symbolic importance to both the U.S. and Canadian West. A comprehensive International symposium, called the High Five symposium, was held June 28-30, 2010, in Missoula, Montana to: (1) bring together scientists, managers, and concerned citizens to exchange information on the ecology, threats, and management of these pines; (2) learn about the threats and current status of pine populations; (3) describe efforts to mitigate threats through restoration techniques and action plans; and, (4) build a foundation for the synthesis of research efforts and management approaches. These proceedings present reports of some of the presentations given at the conference in the form of abstracts, extended abstracts, papers, and plenary papers in the areas of ecology, disturbance dynamics, genetics, climate change, and restoration techniques. <http://www.treesearch.fs.fed.us/pubs/38187>

Kegley, A., R. A. Sniezko, et al. (2004). Influence of inoculum source and density on white pine blister rust infection of **whitebark pine**: early results. In: Geils, B. W. comp. 2004. Proceedings of the 51st Western International Forest Disease Work Conference; 2003 August 18–22; Grants Pass, OR. Flagstaff, AZ: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. pp. 73-78.  
[http://prdp2fs.ess.usda.gov/Internet/FSE\\_DOCUMENTS/stelprdb5280673.pdf](http://prdp2fs.ess.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5280673.pdf)

Kegley, S. and K. Gibson (2004). Protecting whitebark pine trees from mountain pine beetle attack using verbenone. Forest Health Protection Report - Northern Region, USDA Forest Service. Missoula, MT; USA, Northern Region, USDA Forest Service, Report 04-08.

A study was conducted in Montana, USA to determine the effectiveness of verbenone in protecting individual whitebark pine [*Pinus albicaulis*] trees from mountain pine beetle (*Dendroctonus ponderosae*) attack. A thicker membrane pouch (3 mL) formulated to elute verbenone over a longer time period, was compared with the standard pouch (1.5 mL), replaced at mid-season. The treatments used in the study include: (1) control (no verbenone); (2) two standard verbenone pouches per tree, replaced in late July; and (3) 2 new (slow-release) pouches per tree, not replaced. It was observed that treating individual whitebark pine trees with either two standard or two thicker membrane pouches significantly reduced mountain pine beetle attacks compared to the untreated controls. However, there were twice as many pitchouts and strip attacks with the new pouch in comparison with the standard pouch.

Kegley, S. and K. Gibson (2009). Individual-tree tests of verbenone and green-leaf volatiles to protect lodgepole, whitebark and ponderosa pines, 2004-2007. Forest Health Protection Report -



Northern Region, USDA Forest Service. Numbered Report 09-03. Missoula; USA, Northern Region, USDA Forest Service.

Additional verbenone pouch formulations to protect individual trees of *Pinus contorta*, *P. albicaulis* and *P. ponderosa* from mountain pine beetle (*Dendroctonus ponderosae*) were tested in 2004, 2006 and 2007. In 2006 and 2007, the efficacy of verbenone plus green leaf volatile pouch (50:50 blend of z-3-hexenol and 1-hexanol) were also tested. On Corona Ridge, Montana, USA, the treatments include: (1) two 5-gram Pherotech pouches per tree, changed mid-season; (2) two 7.5-gram Biota pouches per tree; and (3) control, no verbenone pouches. On Fisher Peak, the treatments include: (1) two 7.5-gram Biota pouches and; (2) control. The mortality ranged from 32 to 67% in areas surveyed. All areas were at epidemic levels. Results indicated that the verbenone treatments provided the best protection, generally 80% or greater, against mountain pine beetle attack, when compared to untreated controls.

<http://www.msuextension.org/drwanner/MPB/Verbonone%20report%2009-03.pdf>

Kegley, S., K. Gibson, et al. (2003). A test of verbenone to protect individual whitebark pine from mountain pine beetle attack. Forest Health Protection Report - Northern Region, USDA Forest Service, Report 03-9. Missoula; USA, Northern Region, USDA Forest Service.

A study was conducted in the Selkirk Mountains, Idaho, USA, to provide evidence that whitebark pine (*Pinus albicaulis*) individuals can be protected from mountain pine beetle (*Dendroctonus ponderosae*) attack using verbenone. Some 146 whitebark pine trees were randomly assigned one of the following treatments: (1) control (no verbenone); (2) two verbenone (2V) pouches on individual trees; or (3) four verbenone (4V) pouches on individual trees. Significantly ( $P < 0.001$ ) more mass attacks occurred in the control trees than either the 2V or 4V treatment. There was no significant difference between the 2V and 4V treatments.

[http://www.fs.usda.gov/Internet/FSE\\_DOCUMENTS/stelprdb5227166.pdf](http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5227166.pdf)

Kegley, S., J. Schwandt, et al. (2001). Forest health assessment of whitebark pine on Pyramid Pass, Russell Mountain, and Burton Ridge in the Selkirk Mountains on the Idaho Panhandle National Forests. Forest Health Protection Report - Northern Region, USDA Forest Service. Missoula; USA, Northern Region, USDA Forest Service, Report ; 01-8.

Aerial surveys were conducted on the Idaho Panhandle National Forests in the USA, during 1992-2000. Ground surveys in whitebark pine [*Pinus albicaulis*] stands at four different areas in the Selkirk Mountains on the Idaho Panhandle National Forests were also conducted in autumn 2000. Evidence of old as well as recent and current attacks of mountain pine beetle (MPB, *Dendroctonus ponderosae*) was found in all four areas surveyed. Cumulative whitebark pine mortality from current and past MPB activity ranged from 36-74% with 23-44% occurring in the last 2 years. At Pyramid Pass, MPB-caused mortality was recorded in 1995 as well as in 2000. In September 2000, new attacks, eggs, larvae of varying instars, pupae, and new adults were observed in infested whitebark pine. Blister rust (*Cronartium ribicola*) symptoms including top-kill, branch flagging, dead branches, and bole cankers were recorded on live trees with visible crowns. Mature green trees exhibiting blister rust symptoms ranged from 33% on the north side of Russell Ridge to 62% at Pyramid Pass, 82% on Burton Ridge and 87% on the south side of Russell Ridge. At Russell Ridge south and Burton Ridge, there were more MPB attacks in rust-infected trees than uninfected trees. At Pyramid Pass, there were approximately equal numbers of MPB in rust-infected trees as uninfected trees, but MPB populations were so high that most MPB were attacked regardless of blister rust infection. At Russell Mountain north, there were fewer MPB attacks in rust-infected trees than uninfected trees. Removing infested trees prior to beetle emergence could decrease beetle populations and reduce

future beetle-caused tree mortality.

[http://ir.library.oregonstate.edu/xmlui/bitstream/handle/1957/3977/no.%2001-8\\_ocr.pdf?sequence=1](http://ir.library.oregonstate.edu/xmlui/bitstream/handle/1957/3977/no.%2001-8_ocr.pdf?sequence=1)

Kegley, S., J. Schwandt, et al. (2004). Forest health assessment of whitebark pine in selected stands in the Selkirk Mountains of Northern Idaho 2001. Forest Health Protection Report - Northern Region, USDA Forest Service. Missoula; USA, Northern Region, USDA Forest Service, Report ; 04-5.

Results are presented of a study, conducted in 2001, on the assessment of the conditions of whitebark pine (*Pinus albicaulis*) stands in the Selkirk Mountains, Idaho Panhandle National Forests in Idaho, USA due to the occurrence of mountain pine beetles (*Dendroctonus ponderosae*) and pine blister rust (caused by *Cronartium ribicola*).

Kegley, S., N. Sturdevant, et al. (2001). Cone and seed insects and their impact on whitebark pine. Forest Health Protection Report - Northern Region, USDA Forest Service. Missoula; USA, Northern Region, USDA Forest Service, Report 01-6.

Whitebark pine, ***Pinus albicaulis***, is an important but declining high-elevation tree species in western forests. Regeneration of this species has been difficult and the impact of cone and seed insects unknown. Seven sites selected from the geographical range of whitebark pine in Idaho, Montana, Washington, Oregon, and California, USA [date not given] were examined for cone and seed insects and their impact. Ten different insect species (*Polyphylla crinita*, *Frankliniella occidentalis*, *Xyela* spp., *Dichelonyx fulgida*, *Dioryctria* spp., *Dioryctria abietivorella*, *Conophthorus ponderosae*, *Leptoglossus occidentalis*, *Cydia* spp., and *Pineus* spp.) were found affecting various reproductive structures of whitebark pine. Insects having the greatest impact across most sites were fir coneworm (*Dioryctria abietivorella*) and western conifer seed bug (*L. occidentalis*). Coneworms infested up to 68% of cones collected, destroying up to 13% of the seed extracted. Seed bugs damaged up to 27% of the seeds. Pheromone traps for the ponderosa pine cone beetle (*Conophthorus ponderosae*) and coneworms were tested. Ponderosa pine cone beetles were trapped at three of seven sites. Coneworms were trapped at two sites where pheromone traps were deployed. Further studies incorporating different cone crop levels of whitebark pine and other associated tree species are needed to fully determine the effect of cone and seed insects on whitebark pine seed and reproduction.

[http://ir.library.oregonstate.edu/xmlui/bitstream/handle/1957/4021/no.%2001-6\\_ocr.pdf?sequence=1](http://ir.library.oregonstate.edu/xmlui/bitstream/handle/1957/4021/no.%2001-6_ocr.pdf?sequence=1)

Kegley, S. G., Ken (2011). "The use of verbenone to protect whitebark pine from mountain pine beetle. [Abstract] In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 96."

Verbenone is a known anti-aggregation pheromone of mountain pine beetle (*MPB*), *Dendroctonus ponderosae* Hopkins, and has been tested in protecting susceptible host trees from attack since 1988. Inconsistent performance of verbenone during field trials caused formulations and release devices to change through time, resulting in three products currently registered with the Environmental Protection Agency - two pouch formulations containing 7 grams of verbenone that are stapled to tree boles (available from Synergy Semiochemicals Corp. and Contech Enterprises, Inc.), and a flake formulation (available from Hercon Environmental) that can be aerially applied or applied on the ground using fertilizer spreaders. <http://www.treesearch.fs.fed.us/pubs/38206>

Kegley, S. J. and K. E. Gibson (2007). Using verbenone to protect whitebark pine from mountain pine beetle attack. In: Proceedings on the Conference of Whitebark Pine: A Pacific Coast Perspective. USDA Forest Service, Forest Health Protection, R6-NR-FHP-2007-01.  
<http://www.fs.fed.us/outernet/r6/nr/fid/wbpine/papers/2007-wbp-poster-kegley-s.pdf>

Kegley, S. S., John; Gibson, Ken; Perkins, Dana (2011) Health of whitebark pine forests after mountain pine beetle outbreaks. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 85-93.

Whitebark pine (*Pinus albicaulis*), a keystone high-elevation species, is currently at risk due to a combination of white pine blister rust (WPBR) (*Cronartium ribicola*), forest succession, and outbreaks of mountain pine beetle (MPB) (*Dendroctonus ponderosae*). While recent mortality is often quantified by aerial detection surveys (ADS) or ground surveys, little information is presented to describe what stands look like following MPB outbreaks. This information may help prioritize areas for restoration. In 2008 and 2009, the severity of MPB impacts was measured in 42 whitebark pine stands in Idaho, Montana, and Wyoming. WPBR was recorded on remaining live, mature whitebark pine and whitebark pine regeneration. Probable stand trajectory was determined by comparing abundance and health of remaining whitebark pine with other competing tree species. During the recent outbreak, 30 to 97 percent of whitebark pine basal area tallied within each stand was killed by MPB.

[http://www.fs.fed.us/rm/pubs/rmrs\\_p063/rmrs\\_p063\\_085\\_093.pdf](http://www.fs.fed.us/rm/pubs/rmrs_p063/rmrs_p063_085_093.pdf)

Kendall, K. C. and R. E. Keane (2001). Whitebark pine decline: infection, mortality, and population trends. In: Tomback, D.F., S.F. Arno, and R.E. Keane (eds.), Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, D.C., U.S.A., pp. 221-242.

Kinloch Jr, B. B. and G. E. Dupper (2002). "Genetic specificity in the white pine-blister rust pathosystem." *Phytopathology* 92(3): 278-280.

Four of eight white pine species native to western North America surveyed for resistance to white pine blister rust by artificial inoculation showed classical hypersensitive reactions (HR) at frequencies ranging from very low to moderate. Mendelian segregation, indicating a single dominant allele for resistance (Cr3), was observed in southwestern white pine (*Pinus strobiformis*), as it was previously in sugar pine (*P. lambertiana*, Cr1) and western white pine (*P. monticola*, Cr2). HR was present at a relatively high frequency (19%) in one of five bulk seed lot sources of limber pine (*P. flexilis*), and was also presumed to be conditioned by a single gene locus, by analogy with the other three species. HR was not found in whitebark pine (*P. albicaulis*), Mexican white pine (*P. ayacahuite*), foxtail pine (*P. balfouriana*), or Great Basin bristlecone pine (*P. longaeva*), but population and sample sizes in these species may have been below the level of detection of alleles in low frequency. When challenged by (haploid) inocula from specific locations known to harbor virulence to Cr1 or Cr2, genotypes carrying these alleles and Cr3 reacted differentially, such that inoculum virulent to Cr1 was avirulent to Cr2, and inoculum virulent to Cr2 was avirulent to Cr1. Neither of these two inocula was capable of neutralizing Cr3. Although blister rust traditionally is considered an exotic disease in North America, these results, typical of classic gene-for-gene interactions, suggest that genetic memory of similar encounters in past epochs has been retained in this pathosystem.

Kipfmüller, K. F. (2008). "Reconstructed summer temperature in the northern Rocky Mountains wilderness, USA." Quaternary Research 70(2): 173-187.

Ring widths from whitebark pine (*Pinus albicaulis* Englem.) and subalpine larch (*Larix lyallii* Parl.) collected at three high-elevation sites were used to develop tree-growth chronologies to reconstruct summer temperature anomalies. A step-wise multiple regression procedure was used to screen potential predictor variables to generate a transfer function capable of skillfully reconstructing summer temperature. The resulting regression model explained approximately 38% of the adjusted variance in the instrumental temperature record. The fidelity of the reconstruction was verified using product mean and sign tests, both of which suggested significant predictive power in the reconstructions ( $p < 0.05$ ). Reduction of error (RE) and coefficient of efficiency (CE) measures were both positive, indicating the reconstruction contained useful climate information. Cool periods often coincided with reduced solar activity and/or periods of increased volcanic activity. Differences between this reconstruction and others encompassing a broader geographic scale highlight the importance of developing local reconstructions of climate variability, particularly when used in conjunction with ecological data sets that describe the occurrence of fires or insect epidemics. Mixed and divergent climate-response relationships were evident in the whitebark pine chronologies and suggest subalpine larch may be a more useful species than whitebark pine to target for the development of temperature reconstructions in this region. (C) 2008 University of Washington. All rights reserved.

<http://www.sciencedirect.com/science/article/pii/S0033589408000525>

Kipfmüller, K. F. and J. A. Kupfer (2005). "Complexity of successional pathways in subalpine forests of the Selway-Bitterroot Wilderness Area." Annals of the Association of American Geographers 95(3): 495-510.

We examined forest structure and composition in four watersheds in the Selway-Bitterroot Wilderness Area, Idaho and Montana, to better understand the complexity of successional processes following stand-replacing fires in subalpine forest ecosystems. Dendrochronological analyses of more than 1,100 trees were used to identify the timing of establishment of major forest species at sites that had experienced different intervals since the last fire. This was coupled with analyses of forest structure and composition using nonmetric multidimensional scaling. A conceptual model of stand development is presented to highlight our findings. Lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.) dominated most overstories for the first 100-200 years but persisted as a canopy dominant for more than 250 years in some stands. As forests increased in age, Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) became more prominent in the overstory. **Whitebark pine** was present in some young stands and older stands but was most often represented as dead standing trees killed during twentieth-century mountain pine beetle outbreaks. Understory composition was a function of time-since-fire but showed considerable variation that is likely tied to seed arrival, environmental conditions, and establishment. Our results suggest that short fire intervals may limit the development of lodgepole pines capable of producing serotinous cones, leading to young forests dominated by spruce or fir. However, intervals longer than the lifespan of lodgepole pine (as long as 350 years) could also lead to early dominance by spruce or fir following fire. These results refine our understanding of the temporal development of subalpine communities following stand-replacing fires and have implications for the implementation of long-range management goals in these habitats.

Kipfmüller, K. F. and M. W. Salzer (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.

Five-needle pines provide some of the world's longest chronologies of paleoclimate interest. We examined 66 five-needle pine growth chronologies from 1896 to their end years using linear trend, correlation, and cluster analyses. Chronologies were categorized based on the sites' proximity to upper treeline. A significant positive trend in ring width over the post-1896 interval was most common in upper treeline chronologies, but positive linear trend was found in all elevational proximity classes and all species. Cluster analysis of climate response patterns identified four groups exhibiting strong associations with (i) positive response to previous autumn, winter, and spring precipitation, (ii) positive response to spring and (or) summer precipitation coupled with an inverse relationship with summer temperature, (iii) positive response to winter and (or) spring precipitation coupled with an inverse relationship with spring temperature, and (iv) positive associations with temperature in all seasons except spring and no appreciative precipitation response. Most chronologies positively associated with temperatures were from sites located near upper treeline and also contain significant positive linear trend. Our results suggest that some five-needle pine treeline chronologies may be reliable predictors of past temperatures, but careful site selection is required.

Klutsch, J. G., B. A. Goodrich, and W. R. Jacobi (2008). Assessment of Whitebark Pine Regeneration in Burned Areas of the Shoshone and Bridger-Teton National Forests and Wind River Reservation, Wyoming. Final Report For Agreement No. 07-CA-11010000-009. USDA Forest Service, unpublished.

[http://fedgycc.org/documents/WhitebarkPineRegeneration\\_Windriver\\_Apr21008\\_000.doc](http://fedgycc.org/documents/WhitebarkPineRegeneration_Windriver_Apr21008_000.doc)

Kokaly, R. F., D. G. Despain, et al. (2003). "Mapping vegetation in Yellowstone National Park using spectral feature analysis of AVIRIS data." Remote Sensing of Environment 84(3): 437-456.

Knowledge of the distribution of vegetation on the landscape can be used to investigate ecosystem functioning. The sizes and movements of animal populations can be linked to resources provided by different plant species. This paper demonstrates the application of imaging spectroscopy to the study of vegetation in Yellowstone National Park (Yellowstone) using spectral feature analysis of data from the Airborne Visible/Infrared Imaging Spectrometer (AVIRIS). AVIRIS data, acquired on August 7, 1996, were calibrated to surface reflectance using a radiative transfer model and field reflectance measurements of a ground calibration site. A spectral library of canopy reflectance signatures was created by averaging pixels of the calibrated AVIRIS data over areas of known forest and nonforest vegetation cover types in Yellowstone. Using continuum removal and least squares fitting algorithms in the US Geological Survey's Tetracorder expert system, the distributions of these vegetation types were determined by comparing the absorption features of vegetation in the spectral library with the spectra from the AVIRIS data. The 0.68  $\mu\text{m}$  chlorophyll absorption feature and leaf water absorption features, centered near 0.98 and 1.20  $\mu\text{m}$ , were analyzed. Nonforest cover types of sagebrush, grasslands, willows, sedges, and other wetland vegetation were mapped in the Lamar Valley of Yellowstone. Conifer cover types of lodgepole pine, whitebark pine, Douglas fir, and mixed Engelmann spruce/subalpine fir forests were spectrally discriminated and their distributions mapped in the AVIRIS images. In the Mount Washburn area of Yellowstone, a comparison of the AVIRIS map of forest cover types to a map derived from air photos resulted in an overall agreement of 74.1% (kappa statistic = 0.62). Published by Elsevier Science Inc.

Korol, R. L. (2001). Physiological attributes of 11 Northwest conifer species. Gen. Tech. Rep. RMRS-GTR-73. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 9 p.

The quantitative description and simulation of the fundamental processes that characterize forest growth are increasing in importance in forestry research. Predicting future forest growth, however, is compounded by the various combinations of temperature, humidity, precipitation, and atmospheric carbon dioxide concentration that may occur. One method of integrating new management objectives and potential climate scenarios is to model ecosystems mechanistically. General application of ecosystem process models has been difficult. In particular, obtaining initial physiological parameters from current techniques that rely on instantaneous gas exchange measurements can be both expensive and challenging. Frequently, data necessary to parameterize ecosystem process models are not readily available. This report provides model parameters for 11 conifer species (*Pseudotsuga menziesii* var. *glauca*, *Pinus ponderosa*, *P. contorta* subsp. *latifolia*, *Abies lasiocarpa*, *A. grandis*, *Picea engelmannii*, *Thuja plicata*, *Larix occidentalis*, *Pinus monticola*, *P. albicaulis* and *Tsuga heterophylla*) of the Inland Northwest (northern Montana and northern Idaho), USA. Field measurements of photosynthesis (*A*), *A*<sub>max</sub>, conductance (*g*), *g*<sub>max</sub>, internal carbon concentration (*c*<sub>i</sub>), predawn water potentials, analysis of leaf nitrogen concentration, carbon isotope discrimination, and values of *c*<sub>i</sub> and intrinsic water use efficiency inferred from the carbon composition are presented. The relationship of wet leaf weight to dry leaf weight is also presented. The data in this report can be used to calibrate and constrain physiological parameters for modelling physiological processes of 11 conifer species in the Inland Northwest.

<http://www.treearch.fs.fed.us/pubs/4579>

Koteen, L. (2002). Climate change, whitebark pine, and grizzly bears in the Greater Yellowstone Ecosystem. In: Schneider, S.H., and T.L. Root, (eds.), *Wildlife Responses to Climate Change: North American Case Studies*. Island Press, Washington, D.C., U.S.A., pp. 343-414.

Krakowski, J., S. N. Aitken, et al. (2003). "Inbreeding and conservation genetics in whitebark pine." *Conservation Genetics* 4(5): 581-593.

Whitebark pine (*Pinus albicaulis* Engelm.) is threatened across its native range by an exotic fungal pathogen introduced within the last century. Mortality has been extensive, and projected potential range shifts based on impending climate change have revealed further pressures to survival and adaptation for this long-lived, high-elevation conifer. Quantifying genetic variation and the mating system of whitebark pine in its northern range provides a basis for effective conservation measures. Isozyme analysis of vegetative bud tissue revealed high expected heterozygosity (0.262), moderate population differentiation ( $F_{ST} = 0.061$ ) and highly significant correlations between observed heterozygosity and geographic variables ( $R^2 = 0.36$ , latitude;  $R^2 = 0.30$  longitude), supporting the hypothesis that this species recolonized its current northern range following glacial retreat from several refugia in the Washington and Oregon Cascades and in the northern Rockies. Mating system analysis based on simultaneous isozyme analyses of embryo and haploid megagametophyte tissues found relatively high levels of consanguineous mating and selfing for a conifer ( $t(m) = 0.73$ ) within populations. Avian seed distribution by the Clark's nutcracker (*Nucifraga columbiana* Wilson) appears to be the overriding factor influencing genetic patterns: being a mutualistic seed disperser, caches comprised of related seeds develop into clumped stands with strong family substructure. While it is a critical wildlife habitat component, lack of commercial utilization has made in situ adaptation the primary conservation focus. Encouraging regeneration success and nutcracker caching by maintaining natural fire regimes will provide an ecosystem-based

conservation solution; however, in the Rocky Mountains between 52degreesN and 47degreesN, disease-resistant individuals should be located and propagated in order to ensure long-term survival of the species in high pathogen hazard areas.

Kuhn, K. M. and S. B. V. Wall (2007). "Black bears (*Ursus americanus*) harvest Jeffrey pine (*Pinus jeffreyi*) seeds from tree canopies." Western North American Naturalist 67(3): 384-388.  
We documented black bears (*Ursus americanus*) consuming the seeds of Jeffrey pine (*Pinus jeffreyi*) in the eastern Sierra Nevada from late August through September. Shells of pine seeds were the exclusive item in 20 of 27 seat samples collected in September and October and comprised >90% of the remaining 7 samples. Bears obtain seeds of Jeffrey pines by climbing trees, removing ripe, unopened cones from branches, dismantling cones on the ground, and consuming the seeds. Cone harvesting by bears can cause substantial damage to cone-bearing trees and might result in high predispersal mortality of seeds. In other regions, the use of pine seeds by bears has been associated with whitebark pines (*P. albicaulis*) from which bears obtain seeds by exploiting the cone-storing activities of squirrels. Despite the lack of an apparent pine-squirrel-bear interaction, harvesting unopened cones might be a common foraging strategy used by black bears to obtain seeds of Jeffrey pines in the Sierra Nevada.

Landenburger, L., R. L. Lawrence, et al. (2008). "Mapping regional distribution of a single tree species: Whitebark pine in the Greater Yellowstone Ecosystem." Sensors 8(8): 4983-4994.  
Moderate resolution satellite imagery traditionally has been thought to be inadequate for mapping vegetation at the species level. This has made comprehensive mapping of regional distributions of sensitive species, such as whitebark pine, either impractical or extremely time consuming. We sought to determine whether using a combination of moderate resolution satellite imagery (Landsat Enhanced Thematic Mapper Plus), extensive stand data collected by land management agencies for other purposes, and modern statistical classification techniques (boosted classification trees) could result in successful mapping of whitebark pine. Overall classification accuracies exceeded 90%, with similar individual class accuracies. Accuracies on a localized basis varied based on elevation. Accuracies also varied among administrative units, although we were not able to determine whether these differences related to inherent spatial variations or differences in the quality of available reference data. <http://www.mdpi.com/1424-8220/8/8/4983>

Lanner, R. M. (2003). "Made for each other: Clark's nutcracker and the Whitebark Pine." Acta horticulturae(615): 121-125.

Lantz, G. (2002). "Stalwart species." American Forests 108(2): 30-33.  
The ability of whitebark pine to survive and flourish in high-altitude environments that are dominated by long winters and low temperatures is discussed. The species' presence on the high-altitude slopes tends to modify the microclimate, influencing fragile high-altitude life processes just enough to stabilize a number of critical natural functions at a variety of elevations. Whitebarks serve as nurse trees, protecting subalpine fir seedlings as they struggle to survive at the high elevation limits of their range. The multi-trunked shrubby species with broad crowns also act as high-altitude snow fences, regulating spring runoff and reducing erosion. The tree's large, nutritious oil-rich nuts provide an important food source for numerous species.

Lantz, G. (2010). "Imperiled in high places." American Forests 116(1): 33-42.  
Whitebark pine, whose seeds neither drops from the cones, nor require wind to provide dispersal but are planted with the help of bird in subalpine forests, the Clark's nutcracker,

is vital for the subalpine ecosystems. Clark's nutcrackers are adept at prying seeds from the whitebark cones and storing them in a throat pouch with the capacity to hold 80 to 100 of the nutritious nuts. Whitebark pine groves block wind and prevent rapid snowmelt, which prevents erosion and ensures a constant source of cold water to feed mountain streams throughout the summer. While Clark's nutcrackers prepare for the winter by planting whitebark seeds, red squirrels glean cones and gather them into large caches called middens. Grizzlies need the pine nuts both for their food value and for their ability to influence distribution. Trout fishermen are significantly benefited from the roles of high-altitude pines play in preserving the quality midsummer flows that is required by trout.

Larson, E. R. (2005). Spatiotemporal variation in the fire regimes of whitebark pine (*Pinus albicaulis* Englem.) forests, western Montana, USA, and their management implications. M.S. Thesis -- University of Tennessee, Knoxville.  
<http://web.utk.edu/~grissino/downloads/Evan%20Larson%20Thesis.pdf>

Larson, E. R. (2011). "Influences of the biophysical environment on blister rust and mountain pine beetle, and their interactions, in whitebark pine forests." *Journal of Biogeography* 38(3): 453-470. Aim To understand how the biophysical environment influences patterns of infection by non-native blister rust (caused by *Cronartium ribicola*) and mortality caused by native mountain pine beetles (*Dendroctonus ponderosae*) in whitebark pine (*Pinus albicaulis*) communities, to determine how these disturbances interact, and to gain insight into how climate change may influence these patterns in the future. Location High-elevation forests in south-west Montana, central Idaho, eastern and western Oregon, USA. Methods Stand inventory and dendroecological methods were used to assess stand structure and composition and to reconstruct forest history at sixty 0.1-ha plots. Patterns of blister rust infection and mountain pine beetle-caused mortality in whitebark pine trees were examined using nonparametric Kruskal-Wallis ANOVA, Mann-Whitney U-tests, and Kolmogorov-Smirnov two-sample tests. Stepwise regression was used to build models of blister rust infection and mountain pine beetle-related mortality rates based on a suite of biophysical site variables. Results Occurrence of blister rust infections was significantly different among the mountain ranges, with a general gradient of decreasing blister rust occurrence from east to west. Evidence of mountain pine beetle-caused mortality was identified on 83% of all dead whitebark pine trees and was relatively homogenous across the study area. Blister rust infected trees of all ages and sizes uniformly, while mountain pine beetles infested older, larger trees at all sites. Stepwise regressions explained 64% and 58% of the variance in blister rust infection and beetle-caused mortality, respectively, indicating that these processes are strongly influenced by the biophysical environment. More open stand structures produced by beetle outbreaks may increase the exposure of surviving whitebark pine trees to blister rust infection. Main conclusions Variability in the patterns of blister rust infection and mountain pine beetle-caused mortality elucidated the fundamental dynamics of these disturbance agents and suggests that the effects of climate change will be complex in whitebark pine communities and vary across the species' range. Interactions between blister rust and beetle outbreaks may accelerate declines or facilitate the rise of rust resistance in whitebark pine depending on forest conditions at the time of the outbreak.

Larson, E. R. and K. F. Kipfmüller (2010). "Patterns in whitebark pine regeneration and their relationships to biophysical site characteristics in southwest Montana, central Idaho, and Oregon, USA." *Canadian Journal of Forest Research* 40(3): 476-487.

Declines of whitebark pine (*Pinus albicaulis* Engelm.) have occurred across much of the species' range over the last 40 years due to mountain pine beetle outbreaks and white



pine blister rust infection. Management efforts to stem these declines are increasing, yet the long-term success of whitebark pine depends on the species itself adapting to the modern environment. Natural regeneration will be a critical part of this process. We examined patterns in natural whitebark pine regeneration as related to the biophysical environment in sixty 0.1 ha plots in Montana, Idaho, and Oregon. Whitebark pine regeneration was present in 97% of our plots and varied widely in density from 0 to 17 000 seedlings/ha and 0 to 2680 saplings/ha. Using nonparametric correlation analysis and ordination techniques, we found whitebark pine regeneration abundance was unrelated to stand age but significantly related to several biophysical site characteristics, including positive relationships with elevation and canopy tree mortality caused by mountain pine beetle and negative relationships with moisture availability, temperature, and subalpine fir importance. Our findings indicate that whitebark pine is regenerating in many areas and that the widespread mortality from recent mountain pine beetle outbreaks may provide suitable settings for whitebark pine regeneration given sufficient seed sources.

Larson, E. R., S. L. Van De Gevel, et al. (2009). "Variability in fire regimes of high-elevation whitebark pine communities, western Montana, USA." *Ecoscience* 16(3): 282-298.

We investigated the stand history of whitebark pine forests on 3 mountains in the Lolo National Forest, Montana, USA to characterize the fire regimes and other disturbance agents that historically operated at these sites and to explore the potential influences of modern fire suppression on these forests. We used historical fire atlas data and dendroecological data to reconstruct the distinct history of each stand. The fire regimes of each site fit within the general definition of mixed-severity fire regimes, but distinct differences in fire frequency and severity existed between them. All 3 stands contained at least 1 post-disturbance cohort and had experienced at least 1 widespread fire over their histories. We found no consistent fire-climate relationship at these sites. Mountain pine beetles were the primary mortality agent in the current stands at all 3 sites. Subalpine fir began establishing at each site within 2 decades of the most recent widespread fire and well before fire suppression was effective in this region. Fire suppression may have reduced the occurrence of fire during the late 20(th) century at all 3 sites, but only the forest on Point Six has exceeded the mean interval between widespread fires. The differences in fire activity and effects of fire suppression that we observed at these sites are likely the result of different biophysical site characteristics and disturbance legacies and hold important implications for the development of site-specific management strategies for whitebark pine restoration.

Lattin, J. D. (2003). "The Anthocoridae and Miridae (Hemiptera : Heteroptera) on whitebark pine (*Pinus albicaulis*)." *Pan-Pacific Entomologist* 79(2): 79-89.

Three species of Anthocoridae and 13 species of Miridae are reported from whitebark pine (*Pinus albicaulis*) in western North America. The three species of Tetrupleps (Anthocoridae) and species of the mirids *Deraeocapsus*, *Phytocoris*, and *Pilophorus* are predators on insects on the host. Two of the species of Tetrupleps are reported feeding on the introduced balsam woolly aphid. Species of *Dichrooscytus*, *Pinophylus*, and *Platylygus* (Miridae) feed on the host tree. Species of *Pinophylus* and *Platylygus* feed on the developing male cones causing abortion.

Leslie, A. W., Brenda (2011) No free lunch: Observations on seed predation, cone collection, and controlled germination of whitebark pine from the Canadian Rockies. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30

June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 348-354.

Whitebark pine is a keystone species of high elevation forests in western North America that is experiencing rapid decline due to fire exclusion policies, mountain pine beetle, and the introduced pathogen, white pine blister rust. Restoration activities include collecting cones and growing seedlings from individuals that show mechanisms for resistance to blister rust infections. Collecting viable whitebark pine seeds is challenging due to high rates of cone harvest by wildlife prior to seed maturation. This has led to the practice of placing protective coverings over the cones early in the summer, and then collecting them when they fully mature in September. We investigate if the added time, expense, and complications of using protective coverings over cone bearing branches are required for the collection of viable whitebark pine seeds. Aside from anecdotal sources, there appears to be no quantitative information demonstrating this is necessary. We determined the optimal time for cone collection by comparing the timing of seed development and germination rates compared to the timing of seed harvest by wildlife in a stand in Banff National Park, in the northern region of its range. Results clearly indicate that in to collect viable seeds from whitebark pine, protective coverings must be put over unripe cones so that collections can be made at any time from late August to late September.

<http://www.treesearch.fs.fed.us/pubs/38247>

Littell, J. S., E. E. Oneil, et al. (2010). "Forest ecosystems, disturbance, and climatic change in Washington State, USA." Climatic Change 102(1-2): 129-158.

Climatic change is likely to affect Pacific Northwest (PNW) forests in several important ways. In this paper, we address the role of climate in four forest ecosystem processes and project the effects of future climatic change on these processes across Washington State. First, we relate Douglas-fir growth to climatic limitation and suggest that where Douglas-fir is currently water-limited, growth is likely to decline due to increased summer water deficit. Second, we use existing analyses of climatic controls on tree species biogeography to demonstrate that by the mid twenty-first century, climate will be less suitable for key species in some areas of Washington. Third, we examine the relationships between climate and the area burned by fire and project climatically driven regional and sub-regional increases in area burned. Fourth, we suggest that climatic change influences mountain pine beetle (MPB) outbreaks by increasing host-tree vulnerability and by shifting the region of climate suitability upward in elevation. The increased rates of disturbance by fire and mountain pine beetle are likely to be more significant agents of changes in forests in the twenty-first century than species turnover or declines in productivity, suggesting that understanding future disturbance regimes is critical for successful adaptation to climate change.

Lockman, I. B. and G. A. DeNitto (2006). Whitebark–Limber Pine Information System (Version 1.0). Missoula, MT: US Department of Agriculture, Forest Service, Region.

WLIS is a database of summary data of plots established for whitebark and limber pines in the United States and Canada. Data has been assembled from researchers, surveyors, and literature sources and compiled in a standard format. In addition, data from FIA plots with whitebark or limber pine are included. Data can be viewed for any of the plots in the system. The data can also be queried to refine the dataset to meet the user's needs. Plot locations can be spatially depicted through an interactive mapping system. The interactive database provides a user-friendly interface for the addition of new plots or updating data for plots already in the system. A User's Guide is included as part of the download and should be referenced for details on using the system.

<http://www.fs.usda.gov/detailfull/r1/forest-grasslandhealth/?cid=stelprdb5157913&width=full>

Loehman, R. A. C., Allissa; Keane, Robert E. (2011) Modeling climate changes and wildfire interactions: Effects on whitebark pine (*Pinus albicaulis*) and implications for restoration, Glacier National Park, Montana, USA. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 176-189.

Climate changes are projected to profoundly influence vegetation patterns and community compositions, either directly through increased species mortality and shifts in species distributions, or indirectly through disturbance dynamics such as increased wildfire activity and extent, shifting fire regimes, and pathogenesis. High-elevation landscapes have been shown to be particularly sensitive to climatic change and are likely to experience significant impacts under predicted future climate change conditions. Whitebark pine (*Pinus albicaulis*), a keystone and foundation five-needle pine species, is vulnerable to multiple and interacting disturbances that have already caused major changes in species distribution and abundance. We used the mechanistic simulation model FireBGCv2 to assess potential interacting effects of future climate changes and wildfire patterns on the presence and persistence of whitebark pine in a high-elevation watershed in Glacier National Park, Montana, USA. <http://www.treearch.fs.fed.us/pubs/38218>

Logan, J. A., W. W. Macfarlane, et al. (2009). "Effective monitoring as a basis for adaptive management: a case history of mountain pine beetle in Greater Yellowstone Ecosystem whitebark pine." *Iforest-Biogeosciences and Forestry* 2: 19-22.

With reference to massive outbreaks of a variety of bark beetles occurring across the forests of western North America, it is stressed that an accurate assessment of the extent of the problem is the first step toward formulating effective adaptive management strategies. This assessment will only be possible through a coordinated effort that combines all available technologies, that is an approach that builds on satellite image analysis, aerial survey from fixed-wing aircraft, and on the ground observation and measurement. <http://www.sisef.it/iforest/contents/?id=ifor0477-002>

Logan, J. A., W. W. Macfarlane, et al. (2010). "Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem." *Ecological Applications* 20(4): 895-902.

Widespread outbreaks of mountain pine beetles (MPB) are occurring throughout the range of this native insect. Episodic outbreaks are a common occurrence in the beetles' primary host, lodgepole pine. Current outbreaks, however, are occurring in habitats where outbreaks either did not previously occur or were limited in scale. Herein, we address widespread, ongoing outbreaks in high-elevation, whitebark pine forests of the Greater Yellowstone Ecosystem, where, due to an inhospitable climate, past outbreaks were infrequent and short lived. We address the basic question: are these outbreaks truly unprecedented and a threat to ecosystem continuity? In order to evaluate this question we (1) present evidence that the current outbreak is outside the historic range of variability; (2) examine system resiliency to MPB disturbance based on adaptation to disturbance and host defenses to MPB attack; and (3) investigate the potential domain of attraction to large-scale MPB disturbance based on thermal developmental thresholds, spatial structure of forest types, and the confounding influence of an introduced pathogen. We conclude that the loss of dominant whitebark pine forests, and the ecological services they

provide, is likely under continuing climate warming and that new research and strategies are needed to respond to the crisis facing whitebark pine.

Logan, J. A. and J. A. Powell (2008). Ecological consequences of climatic change – altered forest insect disturbance regimes. 33 pp., In: F.H. Wagner (ed.). *Climate Change in western North America: evidence and environmental effects*. Allen Press (in review).

<http://www.usu.edu/beetle/documents/Logan-Powell2005.pdf>

Logan, J. A. P., J. A. (2001). "Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae)." *American Entomologist* 47(3): 160–173.

<http://www.entsoc.org/PDF/Pubs/Periodicals/AE/AE-2001/fall/feature-logan.pdf>

Long, J. N. (2003). "Diversity, complexity and interactions: an overview of Rocky Mountain forest ecosystems." *Tree Physiology* 23(16): 1091-1099.

This overview of Rocky Mountain forest ecosystems characterizes some of the major types, processes and management issues in the region. There are large ranges in edaphic conditions and striking environmental gradients, all interacting to influence the distribution of species, the nature of communities and disturbance regimes. The discussion focuses on the central role of disturbance and how understanding disturbance regimes influences the search for effective approaches to stewardship.

Lorenz, T. J., C. Aubry, et al. (2008) A review of the literature on seed fate in whitebark pine and the life history traits of Clark's nutcracker and pine squirrels. General Technical Report, PNW-GTR-742. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 62 p.

Whitebark pine is a critical component of subalpine ecosystems in western North America, where it contributes to biodiversity and ecosystem function and in some communities is considered a keystone species. Whitebark pine is undergoing rangewide population declines attributed to the combined effects of mountain pine beetle, white pine blister rust, and fire suppression. The restoration and maintenance of whitebark pine populations require an understanding of all aspects of seed fate. In this paper, we review the literature on seed dispersal in whitebark pine. Clark's nutcracker, pine squirrels, and scatter-hoarding rodents are all known to influence whitebark pine seed fate and ultimately affect the ability of whitebark pine populations to regenerate. We also provide a general overview of the natural histories of the most influential species involved with whitebark pine seed fate: Clark's nutcracker and the pine squirrel.

<http://www.treesearch.fs.fed.us/pubs/29647>

Lorenz, T. J. and K. A. Sullivan (2009). "Seasonal Differences in Space Use by Clark'S Nutcrackers in the Cascade Range." *Condor* 111(2): 326-340.

Clark's Nutcrackers (*Nucifraga columbiana*) are important seed dispersers for at least ten species of conifer in western North America and are obligate mutualists for the whitebark pine (*Pinus albicaulis*), a subalpine tree. Despite the important role they play in forest regeneration, space use by nutcrackers has not been formally studied. Several hypotheses exist to explain their year-round patterns of space use. We tested the hypothesis that one population in the Cascade Range, Washington, migrates altitudinally between summer and autumn. In 2006 and 2007, we compared seasonal differences in summer and autumn space use by 26 radio-tagged nutcrackers. Five nutcrackers remained as year-round residents on their home ranges; 21 emigrated from the study area in summer. Among residents we found summer and autumn ranges overlapped and summer ranges were contained within autumn ranges. Residents increased their use of

low-elevation habitats as autumn progressed, but rather than migrating from summer ranges, they used low-elevation forests only for seed harvesting. High-elevation portions of the summer range were used for all other activities including seed storage even though this required residents to transport seeds from source trees up to 29 km in distance and 1007 m in elevation. We were unable to test hypotheses regarding space use by emigrants. However, our results suggest that emigrants in this study did not migrate altitudinally because they showed no seasonal trend in movements either upslope or downslope. <http://www.bioone.org/doi/abs/10.1525/cond.2009.080070>

Lorenz, T. J. and K. A. Sullivan (2010). "Comparison of survey methods for monitoring Clark's Nutcrackers and predicting dispersal of whitebark pine seeds." Journal of Field Ornithology 81(4): 430-441.

Clark's Nutcrackers (*Nucifraga columbiana*) disperse seeds of whitebark pines (*Pinus albicaulis*) in western North America by their scatter-hoarding behavior. Because of declines in whitebark pine, resource managers are seeking an effective means of monitoring nutcracker population trends and the probability of seed dispersal by nutcrackers. We tested the reliability of four survey techniques (standard point counts, playback point counts, line transects, and Breeding Bird Survey routes) for estimating population size by conducting surveys at sites where a portion of the nutcracker population was marked with radio transmitters. The efficacy of distance sampling, based on detection rates from our unadjusted surveys, was also assessed. We conducted counts of whitebark pine cones within stands and related the probability of seed dispersal within stands to cone production and nutcracker abundance. We conducted 70 h of surveys for Clark's Nutcrackers at eight sites from July through November in 2007 and 2009 and estimated cone densities at six of these sites. Detection rates for all survey techniques were low and variable and we detected an average of 5.6 nutcrackers per 30 min of survey time. We also found no difference in detection rates among survey types, although significantly more nutcrackers were detected during surveys conducted during the peak of whitebark pine cone harvest ( $P < 0.0001$ ). Nutcracker abundance was not correlated with cone density ( $P = 0.29$ ) and we observed nutcrackers pouching seeds at all sites. Thus, cone density did not provide reliable information on whether seed dispersal was likely to occur. We suggest that alternate methods be considered for monitoring populations and assessing seed dispersal probability because we did not reliably detect nutcrackers using conventional survey techniques and because nutcracker abundance was not correlated with cone density.

Lorenz, T. J., K. A. Sullivan, et al. (2011). "Cache-Site Selection in Clark's Nutcracker (*Nucifraga columbiana*)." Auk 128(2): 237-247.

Clark's Nutcracker (*Nucifraga columbiana*) is one of the most specialized scatter-hoarding birds, considered a seed disperser for four species of pines (*Pinus* spp.), as well as an obligate coevolved mutualist of Whitebark Pine (*P. albicaulis*). Cache-site selection has not been formally studied in Clark's Nutcrackers, which are considered effective seed dispersers for pines because past studies have found that they harvest and store large quantities of seeds. Although many seeds are placed in sites suitable for germination and establishment, information is lacking on the proportions of seeds placed in suitable versus unsuitable sites. We used radiotelemetry to investigate cache-site selection and evaluate the suitability of selected cache sites for establishment of Whitebark and Ponderosa (*P. ponderosa*) pines. On a landscape scale, Clark's Nutcrackers cached seeds centrally within home ranges, even though this required them to transport seeds up to 32.6 km. They selected low-elevation forests for caching, presumably because these sites accumulated little snow. When caching at high elevations, the birds placed most seeds in

aboveground microsites. Only 15% of Whitebark Pine seed caches (n = 155 caches) were placed below ground and in habitats where seeds could germinate and seedlings grow. For comparative purposes, 42% of Ponderosa Pine seed caches were placed in suitable habitats and below ground. Although Whitebark Pine is an obligate mutualist of Clark's Nutcracker, our study suggests that Clark's Nutcrackers in some populations may be more effective seed dispersers for Ponderosa Pine than for Whitebark Pine.

<http://www.bioone.org/doi/full/10.1525/auk.2011.10101>

Lutz, J. A., J. W. van Wagtenonk, et al. (2009). "Twentieth-century decline of large-diameter trees in Yosemite National Park, California, USA." Forest Ecology and Management 257(11): 2296-2307.

Studies of forest change in western North America often focus on increased densities of small-diameter trees rather than on changes in the large tree component. Large trees generally have lower rates of mortality than small trees and are more resilient to climate change, but these assumptions have rarely been examined in long-term studies. We combined data from 655 historical (1932-1936) and 210 modern (1988-1999) vegetation plots to examine changes in density of large-diameter trees in Yosemite National Park (3027 km<sup>2</sup>). We tested the assumption of stability for large-diameter trees, as both individual species and communities of large-diameter trees. Between the 1930s and 1990s, large-diameter tree density in Yosemite declined 24%. Although the decrease was apparent in all forest types, declines were greatest in subalpine and upper montane forests (57.0% of park area), and least in lower montane forests (15.3% of park area). Large-diameter tree densities of 11 species declined while only 3 species increased. Four general patterns emerged: (1) *Pinus albicaulis*, *Quercus chrysolepis*, and *Quercus kelloggii* had increases in density of large-diameter trees occur throughout their ranges; (2) *Pinus jeffreyi*, *Pinus lambertiana*, and *Pinus ponderosa*, had disproportionately larger decreases in large-diameter tree densities in lower-elevation portions of their ranges; (3) *Abies concolor* and *Pinus contorta*, had approximately uniform decreases in large-diameter trees throughout their elevational ranges; and (4) *Abies magnifica*, *Calocedrus decurrens*, *Juniperus occidentalis*, *Pinus monticola*, *Pseudotsuga menziesii*, and *Tsuga mertensiana* displayed little or no change in large-diameter tree densities. In *Pinus ponderosa*-*Calocedrus decurrens* forests, modern large-diameter tree densities were equivalent whether or not plots had burned since 1936. However, in unburned plots, the large-diameter trees were predominantly *A. concolor*, *C. decurrens*, and *Q. chrysolepis*, whereas *P. ponderosa* dominated the large-diameter component of burned plots. Densities of large-diameter *P. ponderosa* were 8.1 trees ha<sup>-1</sup> in plots that had experienced fire, but only 0.5 trees ha<sup>-1</sup> in plots that remained unburned. (C) 2009

Mahalovich, M. F. a. G. A. D. (2004). Whitebark Pine genetic restoration program for the Intermountain West (United States). In: Snieszko, R.A., S. Salmon, S. Schlarbaum, and H.B. Kriebel (eds.), Proceedings, Breeding and Genetic Resources of Five-needle Pines: Growth, Adaptability and Pest Resistance, July 23-27, 2001. USDA Forest Service Rocky Mountain Research Service, Fort Collins, Colorado. RMRS-P-32, pp. 181-187.

[http://prdp2fs.ess.usda.gov/Internet/FSE\\_DOCUMENTS/stelprdb5341433.pdf](http://prdp2fs.ess.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5341433.pdf)

Mahalovich, M. F. a. R. J. H. (2000). "Whitebark pine operational cone collection instructions and seed transfer guidelines." Nutcracker Notes 11: 10-13.

Mahalovich, M. F. B., 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. 2006.

National Proceedings: Forest and Conservation Nursery Associations - 2005. Proc. RMRS-P-43. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 91-101.

A synthesis of several studies highlights above-average performing seed sources ( $n = 108$ ) of whitebark pine (*Pinus albicaulis*), which practitioners can utilize for restoration, wildlife habitat improvement, and operational planting programs. It is the first report of this magnitude of blister rust resistance for this species. Whitebark pine does have genetic variation and demonstrated resistance to white pine blister rust, increasing from the southeast to the northwest in the Inland Northwest. Early outplanting reports have shown that some seedlings have frost damage or exhibit increased mortality in cold pockets or swales. Cold hardiness, measured in late winter on a smaller sample of sources ( $n = 55$ ), also showed genetic variability increasing from the northwest to the southeast. Seed zones were delineated by Mahalovich and Hoff (2000) based on information on relative rust hazard and demarcation of mountain ranges. These geographic seed zones support conservative seed transfer with a special emphasis on blister rust infection levels. Sufficient variability exists to maintain these seed zone boundaries, because whitebark pine exhibits more of an intermediate adaptive strategy as compared to the generalist adaptive strategy of western white pine (*P. monticola*). Based on this composite information, it is feasible to outplant whitebark pine without the additional delay of waiting until blister rust resistant seedlings are developed from a breeding program. There are sources within each seed zone that have both rust resistance and greater cold hardiness, so those factors should not limit tree planting for restoration or critical wildlife habitat improvement objectives. <http://www.treesearch.fs.fed.us/pubs/26662>

Mahalovich, M. F. H., Valerie D. (2011). "Molecular genetic variation in whitebark pine (*Pinus albicaulis* Engelm.) in the Inland West. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 118-132."

Levels of genetic variation within and among 163 individual- tree collections and one bulk lot of whitebark pine were estimated using isozymes, mitochondrial DNA and chloroplast DNA; 79 of the samples are also part of a common garden study evaluating survival, rust resistance, late winter cold hardiness, and early height-growth. Within the species, 100 percent of the isozyme loci are polymorphic, with the number of alleles per locus ( $N_a$ ) equal to 4.0. Genetic diversity is high ( $H_e = 0.271$ ) relative to other conifers in the same forest cover type and is comparable to quaking aspen (*Populus tremuloides* Michx) and limber pine (*Pinus flexilis* James), two of the most geographically widespread tree species in North America. <http://www.treesearch.fs.fed.us/pubs/38208>

Maher, E. L. and M. J. Germino (2006). "Microsite differentiation among conifer species during seedling establishment at alpine treeline." *Ecoscience* 13(3): 334-341.

Tree establishment is a potentially important factor affecting tree populations in alpine-treeline ecotones. Patterns of seedling establishment of *Abies lasiocarpa*, ***Pinus albicaulis***, and *Picea engelmannii* were evaluated relative to neighbouring trees and herbs over two years and three treelines of the Rocky Mountains, USA. The greatest mortality rates were observed in seedlings that had just emerged from seed and were in their first year of growth and in seedlings that had the least amount of cover provided by trees or other landscape features that block exposure to the sky. Although herb cover promoted survivorship in microsites that were not near trees, no seedlings were detected at or above the upper limit of the treeline ecotone. Microsite tree cover was greatest for A.

lasiocarpa and least for *P. albicaulis* seedlings, which matches predictions based on their relative photosynthetic tolerances to the bright sunlight and frequent frost that occur in exposed microsites. Interspecific differences in seedling requirements for neighbouring plant cover likely contribute to the apparent coexistence and possible interdependency of these conifers along a continuum of colonization and succession within treelines.

<http://www.bioone.org/doi/abs/10.2980/i1195-6860-13-3-334.1>

Maloney, P. E. (2011). "Incidence and distribution of white pine blister rust in the high-elevation forests of California." *Forest Pathology* 41(4): 308-316.

In 2004-2006, a California-wide survey was conducted to evaluate the incidence and distribution of *Cronartium ribicola*, cause of white pine blister rust (WPBR), in the high-elevation white pine forests. WPBR occurrence varied considerably within and between regions, and little to no disease was found in the Basin and Range, eastern Sierra Nevada and Transverse and Peninsular mountain ranges. Field surveys revealed no evidence of rust on Great Basin bristlecone, limber or the southern subspecies of foxtail pine. Rust incidence for western white pine was highest in the North Coast region (42% of trees surveyed), followed by the Klamath (18%) and northern Sierra Nevada (14%). For whitebark pine, WPBR incidence averaged 24% in the northern Sierra Nevada; this was considerably greater than other regions where whitebark pine was found infected. Latitudinal trends in WPBR incidence (i.e. greater in the north) may correspond with earlier introductions of *C. ribicola* into these regions, reflecting the southward spread of the pathogen since its introduction from the north in the early 1900s and environmental conditions favourable for infection. Distance from inoculum sources and potentially host phenology may also be important factors influencing the distribution of *C. ribicola*.

Maloney, P. E. and J. M. Dunlap ([2007]). White pine blister rust and whitebark pine ecosystems in California. In: Proceedings, Whitebark Pine: A Pacific Coast Perspective, Ashland, OR. USDA Forest Service R6-NR-FHP-2007-01. <http://www.fs.fed.us/outernet/r6/nr/fid/wbpine/papers/2007-wbp-wpbr-impacts-maloney.pdf>

Martinson, S. (2003) Whitebark Pine Studies in the Forest Service's Northwest Region. *Nutcracker Notes*. Issue 5: 4-5, 8. <http://www.fs.fed.us/r6/genetics/documents/publications/pub006.pdf>

Mattson, D. J., K.C. Kendall, and D.P. Reinhart. (2001) Whitebark pine, grizzly bears, and red squirrels. pp. 121-136, In: D.F. Tomback., S.F. Arno, and R.E. Keane (eds.). Whitebark pine communities: ecology and restoration. Island Press. Washington, DC, USA

Mattson, D. J. (2002). "Consumption of wasps and bees by Yellowstone grizzly bears." *Northwest Science* 76(2): 166-172.

I investigated the consumption of wasps and bees by grizzly bears in the Yellowstone region, 1977-1992, using data collected during a study of radio-marked bears. Although wasp, and bees are not a major source of energy, Yellowstone grizzly bears are among only a few populations of their species in North America known to consume these insects in sometimes noteworthy amount. Consumption of wasps and bees was greatest during the driest months of the study and during years when abundant ungulate carrion and few whitebark pine seeds were available. Peak Consumption during dry years probably reflected increases in wasp and bee populations, whereas little consumption during years when pine seeds were abundant probably reflected a relative preference for pine seeds. The odds that bears should consume wasps and bees were greatest when they were in forest stands with abundant coarse woody debris and considerable live basal area.



Excavation of ground nests also was most extensive in dense forest stands. All detected exploitation involved excavation of nests, almost all of which were located in or under logs and stumps or in duff near the base of trees. It is not clear if this pattern of exploitation reflected the distribution of wasps and bees, and, if so, why wasps and bees were concentrated in dense forests with abundant coarse woody debris. In short, Yellowstone grizzly bears apparently consumed wasps and bees most often when and where these insects were most abundant as well as when known high-quality bear foods were scarce. <http://research.wsulibs.wsu.edu/jspui/handle/2376/951>

Mattson, D. J. and T. Merrill (2002). "Extirpations of grizzly bears in the contiguous United States, 1850-2000." *Conservation Biology* 16(4): 1123-1136.

We investigated factors associated with the distribution of grizzly bears (*Ursus arctos horribilis*) in 1850 and their extirpation during 1850-1920 and 1920-1970 in the contiguous United States. We used autologistic regression to describe relations between grizzly bear range in 1850, 1920, and 1970 and potential explanatory factors specified for a comprehensive grid of cells, each 900 km<sup>2</sup> in size. We also related persistence, 1920-1970, to range size and shape. Grizzly bear range in 1850 was positively related to occurrence in mountainous ecoregions and the ranges of oaks (*Quercus* spp.), pinon pines (*Pinus edulis* and *P. monophylla*), whitebark pine (*P. albicaulis*), and bison (*Bos bison*) and negatively related to occurrence in prairie and hot desert ecoregions. Relations with salmon (*Oncorhynchus* spp.) range and human factors were complex. Persistence of grizzly bear range, 1850-1970, was positively related to occurrence in the Rocky Mountains, whitebark pine range, and local size of grizzly bear range at the beginning of each period, and negatively related to number of humans and the ranges of bison, salmon, and pinon pines. We speculate that foods affected persistence primarily by influencing the frequency of contact between humans and bears. With respect to current conservation, grizzly bears survived from 1920 to 1970 most often where ranges at the beginning of this period were either larger than 20,000 km<sup>2</sup> or larger than 7,000 km<sup>2</sup> but with a ratio of perimeter to area of < 2. Without reductions in human lethality after 1970, there would have been no chance that core grizzly bear range would be as extensive as it is now. Although grizzly bear range in the Yellowstone region is currently the most robust of any to potential future increases in human lethality, bears in this region are threatened by the loss of whitebark pine.

Mattson, D. J., S. R. Podruzny, et al. (2002). "Consumption of fungal sporocarps by Yellowstone grizzly bears." *Ursus* 13: 95-103.

Sign of grizzly bears (*Ursus arctos horribilis*) consuming fungal sporocarps (mushrooms and truffles) was observed on 68 occasions during a study of radiomarked bears in the Yellowstone region, 1977-96. Sporocarps also were detected in 96 grizzly bear feces. Most fungi consumed by Yellowstone's grizzly bears were members of the Boletaceae (*Suillus* spp.), Russulaceae (*Russula* spp. and *Lactarius* sp.), Morchellaceae (*Morchella elata*), and Rhizopogonaceae. Consumption of false truffles (*Rhizopogon* spp.) was indicated by excavations that were deeper, on average (1.1 dm), than excavations for mushrooms (0.6 dm). Consumption of sporocarps was most frequent during September (7% of all activity), although median numbers of sporocarps excavated at feeding sites peaked during both August and September (22-23 excavations/site). Almost all consumption (75%) occurred on edaphically harsh sites typically dominated by lodgepole pine (*Pinus contorta*). At broad scales, consumption of sporocarps was most likely where these types of lodgepole pine-dominated sites were extensive or where high-elevation sites supporting mature whitebark pine (*P. albicaulis*) were rare. The number of sporocarps excavated at a feeding site was greatest when cone crops of whitebark pine were small and in stands with abundant

lodgepole pine. At finescales, consumption of fungi was positively associated with lodgepole pine basal area and negatively associated with total ground vegetation cover. Because of the strong association of sporocarp consumption with lodgepole pine and its disassociation at broad scales with availability of whitebark pine seeds, consumption of mushrooms and truffles by grizzly bears will likely increase in the Yellowstone ecosystem with global warming. Lodgepole pine is predicted to increase and **whitebark pine** to decline with global warming. <http://www.jstor.org/stable/pdfplus/3873191.pdf>

McCaughey, W. W., G. L. Scott, et al. (2009). "Whitebark pine planting guidelines." Western Journal of Applied Forestry 24(3): 163-166.

This article incorporates new information into previous whitebark pine guidelines for planting prescriptions. Earlier 2006 guidelines were developed based on review of general literature, research studies, field observations, and standard US Forest Service survival surveys of high-elevation whitebark pine plantations. A recent study of biotic and abiotic factors affecting survival in whitebark pine plantations was conducted to determine survival rates over time and over a wide range of geographic locations. In these revised guidelines, we recommend reducing or avoiding overstory and understory competition, avoiding swales or frost pockets, providing shade and wind protection, protecting seedlings from heavy snow loads and soil movement, providing adequate growing space, avoiding sites with lodgepole or mixing with other tree species, and avoiding planting next to snags.

McDermid, G. J. and I. U. Smith (2008). "Mapping the distribution of whitebark pine (*Pinus albicaulis*) in Waterton Lakes National Park using logistic regression and classification tree analysis." Canadian Journal of Remote Sensing 34(4): 356-366.

Accurate spatial information on the distribution of whitebark pine, a keystone species in alpine environments across western Canada, is critical for the planning of conservation activities designed to ameliorate the damaging effects of blister rust, mountain pine beetle, and interspecific competition. We compared classification tree analysis and logistic regression analysis to explore their relative abilities to model whitebark pine presence and absence with medium-spatial-resolution satellite and topographic variables across a complex study site in Waterton Lakes National Park, Alberta. Both techniques were found to be effective, generating map products of roughly equal thematic quality (91% overall accuracy; kappa = 0.76). However, the logistic model was valuable in its ability to predict ratio-level probability surfaces, whereas the classification tree approach was simpler, faster, and found to generate a slightly more balanced model from an individual class accuracy perspective. End users selecting between the two techniques should make choices that balance flexibility with simplicity while always taking care to exercise sound modeling practices.

McKinney, S. T. (2007) Ecological process and the blister rust epidemic: Cone production, cone predation, and seed dispersal in whitebark pine (*Pinus albicaulis*). Thesis (Ph. D.) -- University of Montana, 2007. <http://etd.lib.umt.edu/theses/available/etd-01042008-111653/unrestricted/umi-umt-1054.pdf>

McKinney, S. T. and C. E. Fiedler (2010). "Tree squirrel habitat selection and predispersal seed predation in a declining subalpine conifer." Oecologia 162(3): 697-707.

Differential responses by species to modern perturbations in forest ecosystems may have undesirable impacts on plant-animal interactions. If such disruptions cause declines in a plant species without corresponding declines in a primary seed predator, the effects on the plant could be exacerbated. We examined one such interaction between *Pinus albicaulis*

(whitebark pine), a bird-dispersed, subalpine forest species experiencing severe population declines in the northern part of its range, and *Tamiasciurus hudsonicus* (red squirrel), an efficient conifer seed predator, at 20 sites in two distinct ecosystems. Hypotheses about squirrel habitat preferences were tested to determine how changes in forest conditions influence habitat use and subsequent levels of predispersal cone predation. We performed habitat selection modeling and variable ranking based on Akaike's information criterion; compared the level and variance of habitat use between two forest types (*P. albicaulis* dominant and mixed conifer); and modeled the relationship between *P. albicaulis* relative abundance and predispersal cone predation. *T. hudsonicus* did not demonstrate strong habitat preference for *P. albicaulis*, and thus, declines in the pine were not met with proportional declines in squirrel habitat use. *P. albicaulis* habitat variables were the least important in squirrel habitat selection. Squirrel habitat use was lower and varied more in *P. albicaulis*-dominant forests, and predispersal cone predation decreased linearly with increasing *P. albicaulis* relative abundance. In Northern Rocky Mountain sites, where *P. albicaulis* mortality was higher and abundance lower, squirrel predation was greater than in Central Rocky Mountain sites. In ecosystems with reduced *P. albicaulis* abundance, altered interactions between the squirrel and pine may lead to a lower proportion of *P. albicaulis* contributing to population recruitment because of reduced seed availability. Reducing the abundance of competing conifers will create suboptimal squirrel habitat, thus lowering cone predation in *P. albicaulis* and ensuring more seeds are available for avian dispersal.

McKinney, S. T., C. E. Fiedler, et al. (2009). "Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem." *Ecological Applications* 19(3): 597-607.

Human-caused disruptions to seed-dispersal mutualisms increase the extinction risk for both plant and animal species. Large-seeded plants can be particularly vulnerable due to highly specialized dispersal systems and no compensatory regeneration mechanisms. Whitebark pine (***Pinus albicaulis***), a keystone subalpine species, obligately depends upon the Clark's Nutcracker (*Nucifraga columbiana*) for dispersal of its large, wingless seeds. Clark's Nutcracker, a facultative mutualist with whitebark pine, is sensitive to rates of energy gain, and emigrates from subalpine forests during periods of cone shortages. The invasive fungal pathogen *Cronartium ribicola*, which causes white pine blister rust, reduces whitebark pine cone production by killing cone-bearing branches and trees. Mortality from blister rust reaches 90% or higher in some whitebark pine forests in the Northern Rocky Mountains, USA, and the rust now occurs nearly rangewide in whitebark pine. Our objectives were to identify the minimum level of cone production necessary to elicit seed dispersal by nutcrackers and to determine how cone production is influenced by forest structure and health. We quantified forest conditions and ecological interactions between nutcrackers and whitebark pine in three Rocky Mountain ecosystems that differ in levels of rust infection and mortality. Both the frequency of nutcracker occurrence and probability of seed dispersal were strongly related to annual whitebark pine cone production, which had a positive linear association with live whitebark pine basal area, and negative linear association with whitebark pine tree mortality and rust infection. From our data, we estimated that a threshold level of similar to 1000 cones/ha is needed for a high likelihood of seed dispersal by nutcrackers (probability  $\geq 0.7$ ), and that this level of cone production can be met by forests with live whitebark pine basal area  $>5.0 \text{ m}^2/\text{ha}$ . The risk of mutualism disruption is greatest in northernmost Montana (USA), where three-year mean cone production and live basal area fell below predicted threshold levels. There, nutcracker occurrence, seed dispersal, and whitebark pine regeneration were the lowest of the three ecosystems. Managers can use these threshold values to differentiate

between restoration sites requiring planting of rust-resistant seedlings and sites where nutcracker seed dispersal can be expected.

McKinney, S. T. and D. F. Tomback (2007). "The influence of white pine blister rust on seed dispersal in whitebark pine." Canadian Journal of Forest Research 37(6): 1044-1057.

We tested the hypotheses that white pine blister rust (*Cronartium ribicola* J.C. Fisch.) damage in whitebark pine (*Pinus albicaulis* Engelm.) stands leads to reduced (1) seed cone density, (2) predispersal seed survival, and (3) likelihood of Clark's Nutcracker (*Nucifraga columbiana* (Wilson, 1811)) seed dispersal. We gathered data from two sets of paired forest sites in the Bitterroot Mountains of eastern Idaho and western Montana that were similar in topography, canopy structure, tree species composition, and successional stage, but differed in rust infection level, crown kill, and tree mortality. We counted initial (mid-July) and final (late August) seed cones, observed vertebrate seed predator activity, and documented nutcracker seed dispersal in study sites in 2001 and 2002. High-rust sites had higher rates of seed predation relative to cone abundance, lower predispersal seed survival, and fewer observations of nutcracker seed dispersal than paired low-rust sites. These findings suggest that as blister-rust-induced damage increases within stands in the Bitterroot Mountains, the likelihood of nutcracker seed dispersal decreases. We propose that whitebark pine in heavily rust-damaged forests may not self-regenerate and would therefore require planting of seeds or seedlings from genetically rust-resistant trees.

McKinney, S. T. T., Diana F.; Fiedler, Carl E. (2011) Altered species interactions and implications for natural regeneration in whitebark pine communities. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 56-60.

Whitebark pine (*Pinus albicaulis*) decline has altered trophic interactions and led to changes in community dynamics in many Rocky Mountain subalpine forests (McKinney and Tomback 2007). Here we discuss how altered species interactions, driven by disproportionate whitebark pine mortality, constrain the capability of whitebark pine forests to contribute genetic material to subsequent generations. The degree to which whitebark pine forests are reproductively limited, however, depends in large part on tree species composition and forest structure. The results of these changed dynamics have several important implications for restoration decisions.

<http://www.treesearch.fs.fed.us/pubs/38195>

McLane, S. C. A., Sally N. (2011) Whitebark pine (*Pinus albicaulis*) assisted migration trial. [Abstract] In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 205.

Assisted migration - the translocation of a species into a climatically-suitable location outside of its current range - has been proposed as a means of saving vulnerable species from extinction as temperatures rise due to climate change. We explore this controversial technique using the keystone wildlife symbiote and ecosystem engineer, whitebark pine (*Pinus albicaulis*). Species distribution models (SDMs) predict that whitebark pine will be extirpated from most of its current range over the next 70 years. However, the same models indicate that a large quadrant of northwestern British Columbia is climatically

suitable for the species under current conditions, and will remain so beyond the 21st century. <http://www.treesearch.fs.fed.us/pubs/38222>

Mellmann-Brown, S. (2005). Regeneration of whitebark pine in the timberline ecotone of the Beartooth Plateau, U.S.A.: spatial distribution and responsible agents. In: Mountain Ecosystems: Studies in Treeline Ecology (eds Broll, G. and B. Keplin), pp. 97-115. Springer Berlin Heidelberg.

Millar, C. I., J. C. King, et al. (2006). "Late Holocene forest dynamics, volcanism, and climate change at Whitewing Mountain and San Joaquin Ridge, Mono County, Sierra Nevada, CA, USA." Quaternary Research 66(2): 273-287.

Deadwood tree stems scattered above treeline on tephra-covered slopes of Whitewing Mtn (3051 in) and San Joaquin Ridge (3122 in) show evidence of being killed in an eruption from adjacent Glass Creek Vent, Inyo Craters. Using tree-ring methods, we dated deadwood to AD 8151350 and infer from death dates that the eruption occurred in late summer AD 1350. Based on wood anatomy, we identified deadwood species as *Pinus albicaulis*, *R. monticola*, *P. lambertiana*, *R. contorta*, *R. jeffreyi*, and *Tsuga mertensiana*. Only *P. albicaulis* grows at these elevations currently; *P. lambertiana* is not locally native. Using contemporary distributions of the species, we modeled paleoclimate during the time of sympatry to be significantly warmer (+3.2 degrees C annual minimum temperature) and slightly drier (-24 mm annual precipitation) than present, resembling values projected for California in the next 70-100 yr. <http://treesearch.fs.fed.us/pubs/31776>

Millar, C. I., R. D. Wesfall, et al. (2004). "Response of subalpine conifers in the Sierra Nevada, California, U.S.A., to 20th-century warming and decadal climate variability." Arctic Antarctic and Alpine Research 36(2): 181-200.

Four independent studies of conifer growth between 1880 and 2002 in upper elevation forests of the central Sierra Nevada, California, U.S.A., showed correlated multidecadal and century-long responses associated with climate. Using tree-ring and ecological plot analysis, we studied annual branch growth of krummholz *Pinus albicaulis*; invasion by *P. albicaulis* and *Pinus monticola* into formerly persistent snowfields; dates of vertical branch emergence in krummholz *P. albicaulis*; and invasion by *Pinus contorta* into subalpine meadows. Mean annual branch growth at six treeline sites increased significantly over the 20th century (range 130-400%), with significant accelerations in rate from 1920 to 1945 and after 1980. Growth stabilized from 1945 to 1980. Similarly, invasion of six snowfield slopes began in the early 1900s and continued into snowfield centers throughout the 20th century, with significantly accelerated mean invasion from 1925 to 1940 and after 1980. Rate of snowfield invasion decreased between 1950 and 1975. Meadow invasion and vertical leader emergence showed synchronous, episodic responses. *Pinus contorta* invaded each of ten subalpine meadows in a distinct multidecadal pulse between 1945 and 1976 (87% of all trees) and vertical release in five krummholz *P. albicaulis* sites also occurred in one pulse between 1945 and 1976 (86% of all branches). These synchronies and lack of effect of local environments implicate regional climate control. Composite weather records indicated significant century-long increases in minimum monthly temperature and multidecadal variability in minimum temperature and precipitation. All ecological responses were significantly correlated with minimum temperature. Significant interactions among temperature, precipitation, Pacific Decadal Oscillation (PDO) indices, and multiyear variability in moisture availability further explained episodic ecological responses. Four multidecadal periods of the 20th century that are defined by ecological response ( 1925; 1925-1944; 1945-1976; > 1976) correlate with positive and negative PDO phases, as well as with steps in the rate of temperature increase. These diverse factors in spatially distributed upper-montane and treeline ecosystems respond

directionally to century-long climate trends, and also exhibit abrupt and reversible effects as a consequence of interdecadal climate variability and complex interactions of temperature and moisture.

Mohatt, K. R., C. L. Cripps, et al. (2008). "Ectomycorrhizal fungi of whitebark pine (a tree in peril) revealed by sporocarps and molecular analysis of mycorrhizae from treeline forests in the Greater Yellowstone Ecosystem." Botany 86(1): 14-25.

Whitebark pine (*Pinus albicaulis* Engelm.) is unique as the only stone pine in North America. This species has declined 40%-90% throughout its range owing to blister rust infection, mountain pine beetle, fire suppression, and global climate change. However, intact mature and old growth forests still exist in the Greater Yellowstone Ecosystem (GYE) at high timberline elevations. This study addresses the urgent need to discover the ectomycorrhizal (ECM) fungi critical to this tree species before forests are further reduced. A study of mature whitebark pine forests across five mountain ranges in the Northern GYE confirmed 32 ECM species of fungi with the pine by sporocarp occurrence in pure stands or by identification of mycorrhizae with ITS-matching. Boletales and Cortinariales (*Cortinarius*) comprise 50% of the species diversity discovered. In Boletales, *Suillus subalpinus* M.M. Moser (with stone pines), *Suillus sibericus* Singer (stone pines), *Rhizopogon evadens* A.H. Sm. (five-needle pines), *Rhizopogon* spp. (pines) and a semi-secotioid *Chroogomphus* sp. (pines) are restricted to the hosts listed and are not likely to occur with other high elevation conifers in the GYE. The ascomycete generalist, *Cenococcum geophilum* Fr., was the most frequent (64%) and abundant (51%) ECM fungus on seedling roots, as previously reported for high elevation spruce-fir and lower elevation lodgepole pine forests in the GYE. The relative importance of the basidiomycete specialists and the ascomycete generalist to whitebark pine (and for seedling establishment) is not known, however this study is the first step in delineating the ECM fungi associated with this pine in peril.

Moody, R. and J. Vinnedge (2008). "Whitebark pine: initiating restoration efforts in British Columbia." BC Journal of Ecosystems and Management 9(3): 156-158.

Whitebark pine (*Pinus albicaulis*) is a 5-needle stone pine found at high elevations throughout western North America. The distribution of whitebark pine across the landscape is almost exclusively due to the seed-caching activities of Clarks nutcrackers (*Nucifraga columbiana*). The seeds are also a very important source of food for red squirrels and grizzly bears. Whitebark pine is blue-listed (vulnerable) in British Columbia due to a combination of threats including white pine blister rust, mountain pine beetle, climate change, and forest succession. White pine blister rust (*Cronartium ribicola*) is an exotic fungal disease that kills cone-bearing branches and eventually kills the tree. Mountain pine beetles also kill trees, including some that exhibit rust resistance. Climate change may reduce suitable habitat for whitebark pine. Fire suppression has allowed for successional replacement of whitebark pine by more shade-tolerant species. This poster reports on two recent restoration efforts, both directed at collecting seed for the purpose of gene conservation and restoration. In the Fort St. James Forest District, 145 000 seeds were collected, helping to markedly increase the provincial seed bank numbers. The project also provided a valuable opportunity to increase awareness and understanding about a threatened species. Further south in Manning Park, 18 500 seeds were collected with 10 500 sown directly into local restoration areas, and the remaining seeds directed to seedling production projects. The locations of seeds planted in restoration areas were mapped for future monitoring.

Moody, R. J. (2006). Post-fire regeneration and survival of whitebark pine (*Pinus albicaulis*). Thesis -- University of British Columbia.  
[https://circle.ubc.ca/bitstream/handle/2429/18081/ubc\\_2006\\_fall\\_moody\\_randy.pdf?sequence=4](https://circle.ubc.ca/bitstream/handle/2429/18081/ubc_2006_fall_moody_randy.pdf?sequence=4)

Mulvey, R. and E. Hansen (2009). "White pine blister rust on new telial hosts (*Castilleja* and *Pedicularis*) in whitebark pine ecosystems at Mt. Rainier and Crater Lake National Parks." *Phytopathology* 99(6): S90-S91.

Mulvey, R. L. and E. M. Hansen (2011). "Castilleja and Pedicularis confirmed as telial hosts for *Cronartium ribicola* in whitebark pine ecosystems of Oregon and Washington." *Forest Pathology* 41(6): 453-463.

The primary objective of this research was to determine whether native species of *Castilleja* and *Pedicularis* are naturally infected by *Cronartium ribicola* in whitebark pine ecosystems of the Oregon and Washington Cascade Range, USA. Secondary objectives were to monitor the phenology of aecial and telial hosts to determine whether there is sufficient time for *C. ribicola* to complete its life cycle within high-elevation stands and to evaluate the variety of susceptible native host species within these genera through field and growth chamber inoculation. These objectives were approached through fieldwork in 2008 and 2009 in whitebark pine ecosystems at Mt. Rainier, Mt. Adams, Mt. Hood, Mt. Bachelor, Tumalo Mtn. and Crater Lake. Forty-nine observational study plots were established and monitored. Natural *C. ribicola* infection was detected on 84 *Pedicularis racemosa* plants and five *Castilleja* plants (*C. applegatei*, *C. miniata* and *C. parviflora*). Field observation provided evidence that there is sufficient time for *C. ribicola* to complete its life cycle on hosts within high-elevation whitebark pine stands. In 2009, 18 field inoculation plots were established at Mt. Rainier and Crater Lake. Field inoculation confirmed the susceptibility of two additional species within these genera, *C. arachnoidea* and *P. bracteosa*. All four *Castilleja* species inoculated in the growth chamber developed infection, with an overall infection incidence of 62% (167 out of 270 plants). The identity of the rust species on field specimens as *C. ribicola* was verified through PCR and sequencing of the ITS1-5.8S-ITS2 region of DNA. Improved understanding of the role of these newly recognized hosts in white pine blister rust epidemiology should be used to prioritize sites for the restoration of ecologically valuable whitebark pine.

Murray, M. (2008). Fires in the high cascades: new findings for managing whitebark pine. *Fire management today*. Washington; USA, United States Department of Agriculture, Forest Service. 68: 26-29.

The early physical fitness studies and work capacity tests for firefighters conducted by the Missoula Technology and Development Center (MTDC), in Montana, USA, are briefly described. MTDC works in cooperation with universities, private firms and research groups to solve firefighter safety, health and welfare programmes; to advance existing technology; and to build and test prototype fire fighting equipment for safety standards. It is emphasized that fatigue management and adequate nutrition are important components of the health, welfare and performance of the firefighter.

Murray, M. (2010). "Will whitebark pine not fade away?: Insight from crater lake national park (2003-2009)." *Park Science* 27(2): 5.

Populations of whitebark pine (*Pinus albicaulis*) are under threat from nonnative blister rust disease (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*), and climatic change throughout most of its range. Whitebark pine provides habitat for dozens of high-mountain plant and animal species and is a uniquely picturesque tree for thousands of visitors in the Pacific Northwest and Rocky Mountains every year. Crater

Lake National Park, Oregon, supports the most extensive lakeside population of this species known. Findings acquired through annual monitoring indicate that healthy whitebark pine trees are declining by about 1% annually since 2003. Combined with a nearly one-third reduction in whitebark pine since the estimated spread of blister rust to Crater Lake in the 1930s, a continued downward trajectory indicates a significant loss of the species. Measures to protect and restore whitebark pine can include developing blister rust resistance, outplanting disease-resistant seedlings, and applying beetle deterrents.

Murray, M. P. (2001). "Annual observations of conspicuous canker activity on whitebark pine (2003 to 2007). [Extended abstract] In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 235-237."

Whitebark pine's (*Pinus albicaulis*) notable ecological values, combined with its precarious state, underscore the need for monitoring its health and dynamics. Populations of whitebark pine are in decline throughout most of its range. White pine blister rust, caused by the fungus *Cronartium ribicola*, has denuded stands since introduction during the early 1900s (Tomback and Achuff 2010). The exclusion of fire, which historically promoted whitebark pine over its competitors, has further lessened its proportional abundance with competitors (Murray 2007; Murray and others 2000). Mountain pine beetle epidemics have killed vast acreages since 2003 (Haeussler 2008; Kegley and others, these proceedings; Logan and others 2010). Due to one or more of these threats, whitebark pine has declined in areal cover up to 98 percent in places (Schwandt 2006).

<http://www.treesearch.fs.fed.us/pubs/38229>

Murray, M. P. (2007). "Cone collecting techniques for whitebark pine." Western Journal of Applied Forestry 22(3): 153-155.

Whitebark pine (*Pinus albicaulis* Engelm.), a common long-lived tree of high elevation and timberline forests in much of western North America, is declining because of insect infestation, fire exclusion, and the introduced white pine blister rust disease. Restoration treatments relying on nursery production of seedlings for artificial regeneration are quickly developing. (one collecting techniques are a critical step in this process. The aim of this study was to describe common and emerging techniques for cone collection used at Crater Lake National Park in 2005. Recommendations are offered to guide managers and fieldworkers in efficient, safe, and effective cone collection.

Murray, M. P. (2007). Fire and Pacific coast whitebark pine. pp. 51-60. In: Proceedings of the Conference Whitebark Pine: A Pacific Coast Perspective, USDA Forest Service R6-NR-FHP-2007-01.

<http://www.whitebarkfound.org/Am2009/Murray%20Fire%20and%20Pac%20Coast%20WBP.pdf>

Murray, M. P., S. C. Bunting, et al. (2000). "Landscape trends (1753-1993) of whitebark pine (*Pinus albicaulis*) forests in the west big hole range of Idaho/Montana, USA." Arctic Antarctic and Alpine Research 32(4): 412-418.

*Pinus albicaulis* (whitebark pine) is an important tree species in subalpine forests of the Northern Rocky Mountains. Populations have been declining at unprecedented rates due to the introduction of an exotic pathogen and fire suppression. We initiated this study to evaluate historical trends in *Pinus albicaulis* abundance along with associated subalpine conifers within a small biogeographically disjunct mountain range. The central objective was to estimate historic trends in subalpine forest: composition and structure at the



species and community scales. Reconstruction of forest stands reveals an 85% increase in tree volume among all species since the 1870s. *Pinus albicaulis* has historically dominated most stands associated with *Abies bifolia* (subalpine fir) and *Picea engelmannii* (Engelmann spruce) but dominance has shifted to these late-seral species for most of the study area since the early 1900s. We estimate, that since 1753, nearly 50% of the study area has shifted to later successional stages while only 3% has receded to earlier stages. We discuss the implications for *Pinus albicaulis* and suggest that careful reintroduction of fire can aid in the maintenance of ecological integrity at the community and landscape scales.

Murray, M. P. and M. C. Rasmussen (2003). "Non-native blister rust disease on whitebark pine at Crater Lake National Park." Northwest Science 77(1): 87-91.

Crater Lake National Park supports one of the largest aggregations of whitebark pine in the southern Cascades. The pine is valued by Park visitors and is considered a keystone species in local ecosystems. Although white pine blister rust has been in the region since the early 1900s, no formal survey of whitebark pine infection in the Park has been conducted to date. We sampled 1,200 whitebark pine trees with 24 transects to measure incidence of disease and other damaging agents in the Park. Blister rust is currently the most ubiquitous source of mortality for the Park's pines, outweighing all other biotic agents combined. The National Park Service is initiating actions to conserve whitebark pine.

Newcomb, M. (2003). White pine blister rust, whitebark pine, and *Ribes* species in the Greater Yellowstone area. Thesis -- University of Montana

Owens, J. N., T. Kittirat, et al. (2008). "Whitebark pine (*Pinus albicaulis* Engelm.) seed production in natural stands." Forest Ecology and Management 255(3-4): 803-809.

The mature cones of whitebark pine from two high-elevation natural stands in central Idaho and western Nevada were analyzed in 2004 to determine the seed numbers and quality. It has the typical 2-year pine reproductive cycle. Cones are indehiscent and deciduous at maturity and the seeds lack seed wings. Cones averaged 62 scales, 75% of which were fertile with a seed potential of 96 seeds per cone. Total seeds per cone averaged 66 of which 46 were filled. Other potentially filled seeds were lost for different causes including abortion before pollination, abortion soon after pollination due to a lack of pollination or self-pollination, abortion about the time of fertilization due to self-fertilization, abortion during early and late-embryo development, and damage by insects or disease during development. About 70% of total seeds were filled and likely viable, which is high for conifers in natural stands especially at high elevations.

Perkins, D. L. (2001) Ecology of treeline whitebark pine (*Pinus albicaulis*) populations in central Idaho: successional status, recruitment and mortality, and a spring temperature reconstruction from **whitebark pine** tree rings. PhD thesis. Utah State University, Dept. of Forest Resources, Logan, UT. <http://www.cnr.usu.edu/quinney/htm/collections/theses-dissertations/publication=10597>

Perkins, D. L. and D. W. Roberts (2003). "Predictive models of whitebark pine mortality from mountain pine beetle." Forest Ecology and Management 174(1-3): 495-510.

Stand-level and tree-level data collected from whitebark pine (*Pinus albicaulis* Engelm.) stands in central Idaho were used to estimate the probability of attack and mortality of whitebark pine caused by mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Coleoptera: Scolytidae). Logistic regression models were calibrated from reconstructed pre-epidemic stand conditions and post-epidemic mortality levels resulting from a

widespread mountain pine beetle outbreak that occurred from 1909 to 1940. Basal area ( $m^2/ha$ ) and stand density index (SDI) were stand-level variables that completely differentiated stands into attacked or non-attacked categories. Whitebark pine stands with basal areas above  $10 m^2/ha$  ( $44 ft^2/acre$ ) or with an SDI above 80 had a 100% probability of being attacked. Tree diameter, basal area per 0.04 ha, trees per 0.04 ha, and number of stems in a tree cluster were significant predictors of individual tree attack ( $p$  less than or equal to 0.001) in logistic regression. The tree-level model may be used to estimate anticipated cumulative mortality in currently or potentially infested whitebark pine stands. Stand susceptibility to mountain pine beetle infestation may be identified from density (basal area) or relative density (SDI) thresholds. Predictor variables selected by the models corroborate the susceptible host characteristics identified in other mountain pine beetle-pine systems. This work presents evidence of the generality of host susceptibility characteristics across pine species and over elevation gradients.

Perkins, D. L. J., Carl L.; Rinella, Matt (2011) Protecting whitebark pines through a mountain pine beetle epidemic with verbenone-is it working?. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 94-95.

We initiated a multi-year project to protect individual cone-bearing whitebark pines (*Pinus albicaulis*) from mountain pine beetle (MPB), *Dendroctonus ponderosae* (Hopkins), attack with the anti-aggregating pheromone, verbenone (4,5,5-trimethylbicyclo [3.1.1] hept-3-en-2-one). Our objective was to protect trees through the course of the epidemic that began ca. 2000 in central Idaho. The study population was a subalpine stand of whitebark pine at 9,400 feet elevation near Clayton, ID. Associated conifer species included lodgepole pine, Douglas-fir and subalpine fir. <http://www.treesearch.fs.fed.us/pubs/38205>

Piñol, J. and A. Sala (2000). "Ecological implications of xylem cavitation for several Pinaceae in the Pacific Northern USA." *Functional Ecology* 14(5): 538-545.

1. Xylem hydraulic properties and vulnerability to cavitation (determined using the air-injection method) were studied in six Pinaceae of the northern Rocky Mountains: *Pinus ponderosa*, *Pseudotsuga menziesii*, *Larix occidentalis*, *Pinus contorta*, *Pinus albicaulis* and *Abies lasiocarpa*. We tested whether species extending into drier habitats exhibited increased resistance to water stress-induced cavitation, and whether there is a trade-off between xylem transport capacity and resistance to cavitation. 2. At lower elevations the more drought-tolerant *P. ponderosa* was much less resistant to cavitation than the codominant *P. menziesii*. Greater vulnerability to cavitation in *P. ponderosa* was compensated for, at least in part, by increased stomatal control of water loss (inferred from carbon isotope discrimination) and by increased sapwood to leaf area ratios. Similar differences, but less pronounced, were found in codominant species at higher elevations. 3. Leaf specific hydraulic conductivity was negatively correlated with mean cavitation pressure. When species were separated into pines and non-pines, sapwood specific conductivity and mean cavitation pressure were also negatively correlated within each of the two groups. 4. Our results indicate that within the evergreen conifers examined, greater resistance to water stress-induced cavitation is not required for survival in more xeric habitats, and that there is a trade-off between

xylem conductance and resistance to cavitation.

<http://onlinelibrary.wiley.com/doi/10.1046/j.1365-2435.2000.t01-1-00451.x/abstract>

Powell, J. A. and N. E. Zimmermann (2004). "Multiscale analysis of active seed dispersal contributes to resolving Reid's paradox." *Ecology* 85(2): 490-506.

"Reid's paradox" is the mismatch between theoretical estimates of invasion rates for plants and "observed" rates of plant migration, particularly in the Holocene postglacial migration northwards. While Reid couched his paradox in terms of the migration of oaks in Great Britain, observers have documented the same problem in a wide variety of species. In almost all cases, these authors suggest that occasional, long-distance events, probably mitigated by active dispersal factors (ants, birds, rodents) are responsible. Clark and co-workers have shown that order statistics can bridge the gap between theory and predictions, essentially using "fat-tailed" dispersal kernels raised to high powers corresponding to rare, distant dispersal events. However, the spatial caching structure induced by most active dispersers has not been specifically examined. In this paper we develop a complementary approach to order statistics, based on the theory of homogenization, to describe the long-distance dispersal probabilities of seeds. The homogenization approach includes the spatial structure of active dispersal explicitly, and generates a corrective factor to current estimates of migration rates. This corrective factor is the "caching scale ratio," the ratio of mean scatter-hoard size to mean separation between cache sites, and is, in principle, directly observable. The methodology is not limited to animal dispersers and can be used to address any set of dispersal agencies operating at differing scales, in one or more spatial dimensions. This approach is tested for three dispersal mutualisms where Reid's paradox is known to operate: harvester ant/wild ginger, Blue Jay/ oaks, and nutcracker/stone pine. Migration rates predicted using the homogenized approach compare favorably with estimates for tree species based on the paleo-ecological record. However, these rates do not seem to explain the Holocene migration of wild ginger. <http://www.esajournals.org/doi/full/10.1890/02-0535>

Rehfeldt, G. E., D. E. Ferguson, et al. (2008). "Quantifying the abundance of co-occurring conifers along inland northwest (USA) climate gradients." *Ecology (Washington D C)* 89(8): 2127-2139.

The occurrence and abundance of conifers along climate gradients in the Inland Northwest (USA) was assessed using data from 5082 field plots, 81% of which were forested. Analyses using the Random Forests classification tree revealed that the sequential distribution of species along an altitudinal gradient could be predicted with reasonable accuracy from a single climate variable, a growing-season dryness index, calculated from the ratio of degree-days > 5 degrees C that accumulate in the frost-free season to the summer precipitation. While the appearance and departure of species in an ascending altitudinal sequence were closely related to the dryness index, the departure was most easily visualized in relation to negative degree-days (degree-days < 0 degrees C). The results were in close agreement with the works of descriptive ecologists. A Weibull response function was used to predict from climate variables the abundance and occurrence probabilities of each species, using binned data. The fit of the models was excellent, generally accounting for > 90% of the variance among 100 classes.

Reinhart, D. P., M. A. Haroldson, et al. (2001). "Effects of exotic species on Yellowstone's grizzly bears." *Western North American Naturalist* 61(3): 277-288.

Humans have affected grizzly bears (*Ursus arctos horribilis*) by direct mortality, competition for space and resources, and introduction of exotic species. Exotic organisms that have affected grizzly bears in the Greater Yellowstone Area include common

dandelion (*Taraxacum officinale*), nonnative clovers (*Trifolium* spp.), domesticated livestock, bovine brucellosis (*Brucella abortus*), lake trout *Salvelinus namaycush*, and white pine blister rust (*Cronartium ribicola*). Some bears consume substantial amounts of dandelion and clover. However, these exotic foods provide little digested energy compared to higher-quality bear foods. Domestic livestock are of greater energetic value, but use of this food by bears often leads to conflicts with humans and subsequent increases in bear mortality. Lake trout, blister rust, and brucellosis diminish grizzly bear foods. Lake trout prey on native cutthroat trout (*Oncorhynchus clarkii*) in Yellowstone Lake; white pine blister rust has the potential to destroy native whitebark pine (*Pinus albicaulis*) stands; and management response to bovine brucellosis, a disease found in the Yellowstone bison (*Bison bison*) and elk (*Cervus elaphus*), could reduce populations of these 2 species. Exotic species will likely cause more harm than good for Yellowstone grizzly bears. Managers have few options to mitigate or contain the impacts of exotics on Yellowstone's grizzly bears. Moreover, their potential negative impacts have only begun to unfold. Exotic species may lead to the loss of substantial high-quality grizzly bear foods, including touch of the bison, trout, and pine seeds that Yellowstone grizzly bears currently depend upon. <https://ojs.lib.byu.edu/ojs/index.php/wnan/article/view/1006/867>

Resler, L. M. and M. A. Fonstad (2008). A Markov Analysis of Tree Islands at Alpine Treeline. In: The Changing Alpine Treeline in Glacier National Park Montana, USA (Butler, D.R., G.P. Malanson, S.J. Walsh, and D.B. Fagre, eds). Elsevier, The Netherlands: 151-165.

The pattern of conifer establishment and the potential role of positive plant interactions in tree islands at alpine treeline are examined at three treeline locations in Glacier National Park. Tree island development is often initiated by the establishment of a conifer near a microtopographic shelter source, and subsequent establishment creates a linear, series-like pattern in the lee of previously established trees. First-order Markov analysis of series pattern of established individuals in tree islands demonstrates relative stability or self-perpetuation of many of the early-established individuals, lowering the number of predominant vegetation classes. Embedded Markov analysis, however, suggests that the establishment of conifers within a patch does not follow a predictable spatial sequence; however, *Pinus albicaulis*, a foundation and keystone species, occupies sites immediately behind shelters more than other species and therefore may facilitate subsequent conifer establishment. The spatial patterns of these treeline series are highly variable with study sites, as would be expected from the highly variable local environments of these sites and a largely structural facilitation regime. Where species richness and patch dynamism is high, there may be greater potential for treeline advance on a coarse scale than there is at sites with low species richness. Low richness sites may be more susceptible to stochastic disturbance events that would disrupt conifer establishment and survival.

<http://www.sciencedirect.com/science/article/pii/S0928202508002083>

Resler, L. M. and D. F. Tomback (2008). "Blister rust prevalence in krummholz whitebark pine: Implications for treeline dynamics, northern Rocky Mountains, Montana, USA." Arctic Antarctic and Alpine Research 40(1): 161-170.

Whitebark pine (*Pinus albicaulis*), an important treeline conifer in northern Montana, is considered both a keystone and foundation species in high-elevation ecosystems. The introduced fungal pathogen *Cronartium ribicola*, which causes white pine blister rust, has resulted in severe declines in whitebark pine in subalpine forest communities throughout the northern Rockies during past decades. However, the prevalence of blister rust in whitebark pine within the alpine treeline community and its impact remain to be determined. We gathered field data on blister rust infection incidence in the treeline ecotone at two locations east of the Continental Divide in the northern Rocky Mountains,

Montana, U.S.A. Our objectives were (1) to examine the potential importance of whitebark pine in tree island formation, (2) to determine if blister rust is present in whitebark pine within the alpine treeline community, and (3) to characterize the incidence and intensity of blister rust in krummholz tree islands. We found that whitebark pine is the primary initial colonizer in tree island formation, indicating that the species is important in generating vegetation pattern in these communities. Thirty-five percent of all sampled whitebark pine were infected with blister rust. Although more cankers were found in solitary whitebark pine trees, highest infection incidence per tree occurred in trees that were part of multitree islands. Finally, we found a significant correlation between tree island length and infection incidence. These results have important implications with respect to alpine treeline dynamics on a landscape scale, especially in the context of climate change.

Richardson, B. A., S. J. Brunfeld, et al. (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.

Uniparentally inherited mitochondrial (mt)DNA and chloroplast (cp)DNA microsatellites (cpSSRs) were used to examine population genetic structure and biogeographic patterns of bird-dispersed seed and wind-disseminated pollen of whitebark pine (*Pinus albicaulis* Engelm.). Sampling was conducted from 41 populations throughout the range of the species. Analyses provide evidence for an ancestral haplotype and two derived mtDNA haplotypes with distinct regional distributions. An abrupt contact zone between mtDNA haplotypes in the Cascade Range suggests postglacial biogeographic movements. Among three cpSSR loci, 42 haplotypes were detected within 28 cpSSR sample populations that were aggregated into six regions. Analysis of molecular variance (AMOVA) was used to determine the hierarchical genetic structure of cpSSRs. AMOVA and population pairwise comparisons ( $F_{ST}$ ) of cpSSR, and geographical distribution of mtDNA haplotypes provide insights into historical changes in biogeography. The genetic data suggest that whitebark pine has been intimately tied to climatic change and associated glaciation, which has led to range movements facilitated by seed dispersal by Clark's nutcracker (*Nucifraga columbiana* Wilson). The two hypotheses proposed to explain the genetic structure are: (I) a northward expansion into Canada and the northern Cascades in the early Holocene; and (II) historical gene flow between Idaho and the Oregon Cascades when more continuous habitat existed in Central Oregon during the late Pleistocene. Genetic structure and insights gained from historical seed movements provide a basis on which to develop recovery plans for a species that is at risk from multiple threats.

Richardson, B. A., N. B. Klopfenstein, et al. (2002). "Assessing Clark's nutcracker seed-caching flights using maternally inherited mitochondrial DNA of whitebark pine." Canadian Journal of Forest Research 32(6): 1103-1107.

Maternally inherited mitochondrial DNA haplotypes in whitebark pine (*Pinus albicaulis* Engelm.) were used to examine the maternal genetic structure at three hierarchical spatial scales: fine scale, coarse scale, and inter population. These data were used to draw inferences into Clark's nutcracker (*Nucifraga columbiana* Wilson) seed-caching flight distances. Statistical analyses of fine-scale and coarse-scale distribution of haplotypes showed no apparent signs of deviation from a random pattern. This suggests nutcrackers are effective in dispersal of seed within populations, which is consistent with data gathered on nutcracker seed-caching behavior. However, the lack of homogeneity in haplotype frequencies among populations indicates nutcrackers rarely disperse seeds across large gaps (>20 km) in subalpine habitat.

Richardson, B. A. W., Marcus V.; Kim, Mee-Sook; Klopfenstein, Ned B.; McDonald, GERAL I. (2010) Integration of population genetic structure and plant response to climate change: sustaining genetic resources through evaluation of projected threats. In: Pye, John M.; Rauscher, H. Michael; Sands, Yasmeen; Lee, Danny C.; Beatty, Jerome S., tech. eds. 2010. Advances in threat assessment and their application to forest and rangeland management. Gen. Tech. Rep. PNW-GTR-802. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest and Southern Research Stations: 123-131.

To assess threats or predict responses to disturbances, or both, it is essential to recognize and characterize the population structures of forest species in relation to changing environments. Appropriate management of these genetic resources in the future will require (1) understanding the existing genetic diversity/variation and population structure of forest trees, (2) understanding climatic change and its potential impacts on forest species and populations, and (3) development and use of new tools to identify populations at risk and geographic areas that will provide suitable habitat in the future. Forest trees exist within distinct geographic populations created by climatic shifts, evolutionary processes, the availability of suitable habitats, and other environmental factors. These processes have occurred over millennia and continue to shape the biogeography and genetic structure of these species. Forest trees in Western North America are being defined on the basis of molecular markers and quantitative traits. For example, studies of whitebark pine (***Pinus albicaulis***) and western white pine (*P. monticola*) demonstrate the existence of several distinct populations that likely developed via the long-term processes described above. These studies and others have shown that distinct populations exist within western conifer species and further indicate that the biogeographies of forest species are quite dynamic over time and space. Here, we present a case study using genetic data from whitebark pine and western white pine coupled with landscape-based, plant-climate modeling. Suitable contemporary habitat is accurately predicted for both species based on presence/absence of field observations. General circulation models were used to predict areas of suitable habitat for both species under the current climate and the projected climate around the year 2030. These models predict that these species will respond differently to projected climate change. Suitable habitat (i.e., climate space) for whitebark pine is predicted to decline dramatically by ca. 2030. Populations in the lower latitudes (below 45° N) and those persisting at the low elevation limits show the greatest threat to extinction from climate change. Predictions also indicate that suitable habitat for western white pine will be reduced in some southern latitudes, whereas the suitable habitat will be increased in the northern latitudes of its distribution. For whitebark and western white pine, both molecular markers and quantitative traits frequently reveal congruent genetic structure for species conservation. The combination of genetic studies with climate modeling can provide base-line tools that will enable managers to focus genetic conservation efforts on populations at highest risk while restoring areas that have the lowest risk for predicted climatic extirpation. The ability to define forest populations and predict landscape-level effects of climate change is critical for sustaining future forest health. <http://www.treearch.fs.fed.us/pubs/37031>

Rocheffort, R. M. (2008). "The influence of white pine blister rust (*Cronartium ribicola*) on whitebark pine (*Pinus albicaulis*) in Mount Rainier National Park and North Cascades National Park Service Complex, Washington." Natural Areas Journal 28(3): 290-298.

Surveys to assess the status of whitebark pine (*Pinus albicaulis* Engelm.) populations, with respect to white pine blister rust (*Cronartium ribicola* J.C. Fisch.), were conducted in Mount Rainier National Park and North Cascades National Park Service Complex between 1994 and 1999. A total of 2173 whitebark pine trees and 1029 saplings were surveyed. Blister rust was documented in every stand, but rates of blister rust infections

were highly variable (0% to 70%). Overall, 22% of trees were infected, 3 1% were dead, and 47% of all trees showed no signs of infection. Surveys of saplings (< 2.54 cm dbh) documented infection rates of 28%, mortality rates of 10%, and uninfected rates of 62%. Generally, the percent of trees that were infected increased from west to east and with increasing elevation. Mortality rates decreased with elevation, which may be a result of shorter growing seasons at higher elevations and a longer time period for the infection to spread within the tree. A long-term monitoring program, with permanent plots, has been established to track population status and to inform restoration programs.

Sala, A. (2006). "Hydraulic compensation in northern Rocky Mountain conifers: does successional position and life history matter?" *Oecologia* 149(1): 1-11.

As trees grow tall and the resistance of the hydraulic pathway increases, water supply to foliage may decrease forcing stomata to close and CO<sub>2</sub> uptake to decline. Several structural (e.g. biomass allocation) and physiological adjustments, however, may partially or fully compensate for such hydraulic constraints and prevent limitations on CO<sub>2</sub> uptake and growth. The degree to which trees compensate for hydraulic constraints as they grow tall may depend on the costs and benefits associated with hydraulic compensation according to their ecology and life history. Because later successional Rocky Mountain conifers are more shade tolerant, optimization Of CO<sub>2</sub> uptake as trees grow tall and shade increases may confer greater benefits than in earlier successional species. If so, higher compensation for hydraulic constraints is expected in later successional species relative to co-occurring earlier successional species. I have examined height-related changes of crown stomata conductance on a leaf area basis (G(LA)) and leaf to sapwood ratios (A(L):A(s)) for five conifer species in the northern Rocky Mountains. Species were arranged in pairs, each pair consisting of an early and late successional species. For high elevations I used, respectively, whitebark pine (**Pinus albicaulis**) and subalpine fir (*Abies lasiocarpa*); for mid-elevations, western larch (*Larix occidentalis*) and Douglas-fir (*Pseudotsuga menziesii*); for lower elevations, ponderosa pine (*Pinus ponderosa*) and Douglas-fir. A(L):A(s) either decreased (subalpine fir, ponderosa pine), remained constant (Douglas-fir, western larch) or increased (whitebark pine) with tree height. As hypothesized, earlier successional species (ponderosa pine, whitebark pine and western larch) exhibited significantly stronger decreases of G(LA) with tree height relative to their later successional pairs (Douglas-fir and subalpine fir), which fully compensated for height-related hydraulic constraints on G(LA). A life history approach that takes into account the optimization of size- and species-specific ecological functions may also help researchers better understand biomass allocation and hydraulic function in trees.

<http://www.springerlink.com/content/y4301v7p63362284/fulltext.pdf>

Sala, A., E. V. Carey, et al. (2001). "Water use by whitebark pine and subalpine fir: potential consequences of fire exclusion in the northern Rocky Mountains." *Tree Physiology* 21(11): 717-725.

In subalpine forests of the northern Rocky Mountains, fire exclusion has contributed to large-scale shifts from early-successional whitebark pine (*Pinus albicaulis* Engelm.) to late-successional subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), a species assumed to be more shade tolerant than whitebark pine and with leaf to sapwood area ratios (ALAS) over twice as high. Potential consequences of high ALAS for subalpine fir include reduced light availability and, if hydraulic sufficiency is maintained, increased whole-tree water use. We measured instantaneous gas exchange, carbon isotope ratios and sap flow of whitebark pine and subalpine fir trees of different sizes in the Sapphire Mountains of western Montana to determine: (1) whether species-specific differences in gas exchange are related to their assumed relative shade tolerance and (2) how differences in AL:As affect

leaf- and whole-tree water use. Whitebark pine exhibited higher photosynthetic rates ( $A = 10.9 \mu\text{mol m}^{-2} \text{s}^{-1} \pm 1.1 \text{ SE}$ ), transpiration rates ( $E = 3.8 \text{ mmol m}^{-2} \text{s}^{-1} \pm 0.7 \text{ SE}$ ), stomatal conductance ( $g(s) = 166.4 \text{ mmol m}^{-2} \text{s}^{-1} \pm 5.3 \text{ SE}$ ) and carbon isotope ratios ( $\delta C-13 = -25.5 \text{ parts per thousand} \pm 0.2 \text{ SE}$ ) than subalpine fir ( $A = 5.7 \mu\text{mol m}^{-2} \text{s}^{-1} \pm 0.9 \text{ SE}$ ;  $E = 1.4 \text{ mmol m}^{-2} \text{s}^{-1} \pm 0.3 \text{ SE}$ ;  $g(s) = 63.4 \text{ mmol m}^{-2} \text{s}^{-1} \pm 1.2 \text{ SE}$ ,  $\delta C-13 = -26.2 \text{ parts per thousand} \pm 0.2 \text{ SE}$ ;  $P < 0.01$  in all cases). Because subalpine fir had lower leaf-area-based sap flow than whitebark pine ( $Q(L) = 0.33 \text{ kg m}^{-2} \text{ day}^{-1} \pm 0.03 \text{ SE}$  and  $0.76 \text{ kg m}^{-2} \text{ day}^{-1} \pm 0.06 \text{ SE}$ , respectively;  $P < 0.001$ ), the higher  $A(L):A(S)$  in subalpine fir did not result in direct proportional increases in whole-tree water use, although large subalpine firs used more water than large whitebark pines. The linear relationships between tree size and daily water use ( $r^2 = 0.94$  and  $0.97$  for whitebark pine and subalpine fir, respectively) developed at the Sapphire Mountains site were applied to trees of known size classes measured in 12 natural subalpine stands in the Bob Marshall Wilderness Complex (western Montana) ranging from 67 to 458 years old. Results indicated that the potential for subalpine forests to lose water by transpiration increases as succession proceeds and subalpine fir recruits into whitebark pine stands.

Samman, S., J. W. Schwandt, et al. (2003) Managing for healthy white pine ecosystems in the United States to reduce the impacts of white pine blister rust. USDA Forest Service, Report R1-03-118, Missoula, Montana. September 2003.

[http://ir.library.oregonstate.edu/xmlui/bitstream/handle/1957/11408/Man\\_for\\_Hea\\_Whi\\_Pin\\_Eco.pdf?sequence=1](http://ir.library.oregonstate.edu/xmlui/bitstream/handle/1957/11408/Man_for_Hea_Whi_Pin_Eco.pdf?sequence=1)

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

Only recently have efforts begun to address how management might prepare currently healthy forests to affect the outcome of invasion by established non-native pests. *Cronartium ribicola*, the fungus that causes the disease white pine blister rust (WPBR), is among the introductions into North America where containment and eradication have failed; the disease continues to spread. Ecosystem function is impaired by high rust-caused mortality in mature five-needle white pine forests. This paper evaluates five proactive management options to mitigate the development of impacts caused by white pine blister rust in threatened remote high-elevation five-needle pine ecosystems of western North America. They are: reducing pest populations; managing forest composition; improving host vigor; introducing resistant stock with artificial regeneration; and diversifying age class structure to affect the natural selection process for resistance. Proactive intervention to manage and facilitate evolutionary change in the host species may sustain host populations and ecosystem function during pathogen naturalization.

Schoettle, A. W. K., J. G.; Antolin, M. F.; Field, S. (2011). "A population genetic model for high-elevation five-needle pines: Projecting population outcomes in the presence of white pine blister rust. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 145-146."

The slow growth and long generation time of the five-needle pines have historically enabled these trees to persist on the landscape for centuries, but without sufficient regeneration opportunities these same traits hinder the species' ability to adapt to novel stresses such as the non-native disease white pine blister rust (WPBR). Increasing the frequency of resistance to WPBR is the foundation for options to sustain five-needle pine



species in the presence of the pathogen. Depending on the condition of the ecosystems, increasing resistance can be achieved via outplanting resistant seedling stock and/or stimulating natural regeneration (Schoettle and Sniezko 2007). As the objective of management intervention in the high elevation ecosystems is often to promote multiple generations of sustainability, greater understanding of the regeneration cycle and the potential for increasing the frequency of resistance are needed. This is especially critical for the WPBR pathosystem as WPBR kills trees of all ages and therefore impacts multiple stages of the regeneration cycle of five-needle pines.

<http://www.treesearch.fs.fed.us/pubs/38211>

Schrag, A. M., A. G. Bunn, et al. (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.

Aim: Tree-line conifers are believed to be limited by temperature worldwide, and thus may serve as important indicators of climate change. The purpose of this study was to examine the potential shifts in spatial distribution of three tree-line conifer species in the Greater Yellowstone Ecosystem under three future climate-change scenarios and to assess their potential sensitivity to changes in both temperature and precipitation. Location: This study was performed using data from 275 sites within the boundaries of Yellowstone and Grand Teton national parks, primarily located in Wyoming, USA. Methods: We used data on tree-line conifer presence from the US Forest Service Forest Inventory and Analysis Program. Climatic and edaphic variables were derived from spatially interpolated maps and approximated for each of the sites. We used the random-forest prediction method to build a model of predicted current and future distributions of each of the species under various climate-change scenarios. Results: We had good success in predicting the distribution of tree-line conifer species currently and under future climate scenarios. Temperature and temperature-related variables appeared to be most influential in the distribution of whitebark pine (**Pinus albicaulis**), whereas precipitation and soil variables dominated the models for subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). The model for whitebark pine substantially overpredicted absences (as compared with the other models), which is probably a result of the importance of biological factors in the distribution of this species. Main conclusions: These models demonstrate the complex response of conifer distributions to changing climate scenarios. Whitebark pine is considered a 'keystone' species in the subalpine forests of western North America; however, it is believed to be nearly extinct throughout a substantial portion of its range owing to the combined effects of an introduced pathogen, outbreaks of the native mountain pine beetle (*Dendroctonus ponderosae*), and changing fire regimes. Given predicted changes in climate, it is reasonable to predict an overall decrease in pine-dominated subalpine forests in the Greater Yellowstone Ecosystem. In order to manage these forests effectively with respect to future climate, it may be important to focus attention on monitoring dry mid- and high-elevation forests as harbingers of long-term change. <http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2699.2007.01815.x/full>

Schwandt, J. and S. Kegley (2004). Mountain pine beetle, blister rust, and their interaction on whitebark pine at Trout Lake and Fisher Peak in northern Idaho from 2001-2003. Forest Health Protection Report - Northern Region, USDA Forest Service. Missoula; USA, Northern Region, USDA Forest Service, Report ; 04-9.

In August 2003, whitebark pine [*Pinus albicaulis*] was re-examined for mountain pine beetle (MPB; *Dendroctonus ponderosae*) attack and pine blister rust (BR; *Cronartium ribicola*) infection at Trout Lake and Fisher Peak, Idaho Panhandle National Forests, northern Idaho, USA. Data recorded for each tree included diameter at breast height (dbh)

and a description of any bark beetle activity or BR infection. In 2001, MPB appeared to prefer trees infected with BR at relatively low beetle population levels at Fisher Peak (27% MPB-killed trees) and Trout Lake (14% MPB-killed trees). Two years later, MPB-caused tree mortality doubled at Fisher Peak, and more than tripled at Trout Lake and beetles appeared to prefer trees with little or no BR. No relationships were found between MPB and dbh at Trout Lake, while a negative relationship was observed at Fisher Peak in 2003.

Schwandt, J. C., Kristen; Kearns, Holly; Jensen, Chris (2011) Whitebark pine direct seeding trials in the Pacific Northwest. [Extended abstract] In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 357-361.

Whitebark pine (*Pinus albicaulis*) is a critical species in many high elevation ecosystems and is currently in serious decline due to white pine blister rust (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*), and competition from other species (Schwandt 2006; Tomback and Achuff 2010; Tomback and others 2001). Many areas needing restoration are very remote or in areas where the planting of seedlings may not be logistically or politically feasible. Consequently, it is important to determine if direct planting of seeds is practicable and which treatments enhance germination and chances of survival. <http://www.treesearch.fs.fed.us/pubs/38249>

Schwandt, J. W. (2001). Evaluation of blister rust in whitebark pine. Forest Health Protection Report - Northern Region, USDA Forest Service. Missoula; USA, Northern Region, USDA Forest Service, Report 01-7.

This paper presents the observations of a group during the trip near Pyramid Pass and Roman Nose Lakes, Bonners Ferry Ranger District and Idaho Panhandle National Forests, USA on the impacts of white pine rust [*Cronartium ribicola*] and mountain pine beetle [*Dendroctonus ponderosae*] on whitebark pine [*Pinus albicaulis*]. A discussion on management options and related research needs is provided.

[http://ir.library.oregonstate.edu/xmlui/bitstream/handle/1957/3827/no.%2001-7\\_ocr.pdf?sequence=1](http://ir.library.oregonstate.edu/xmlui/bitstream/handle/1957/3827/no.%2001-7_ocr.pdf?sequence=1)

Schwandt, J. W. (2006) Whitebark pine in peril: a case for restoration. Coeur d'Alene, ID: USDA Forest Service, Forest Health Protection R1-06-28, August 2006. [http://www.fs.usda.gov/Internet/FSE\\_DOCUMENTS/stelprdb5341409.pdf](http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5341409.pdf)

Schwandt, J. W. (2007) Whitebark Pine in Peril: A Rangewide Assessment and Strategies for Restoration. USDA Forest Service, Forest Health Protection, Coeur d'Alene Field Office, Coeur d'Alene, Idaho R6-NR-FHP-2007-01. <http://www.fs.fed.us/outernet/r6/nr/fid/wbpine/papers/2007-wbp-status-schwandt.pdf>

Schwandt, J. W. (2011) Highlights of the Forest Health Protection Whitebark Pine Restoration Program. [Extended abstract] In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 355-356.

In 2005, Forest Health Protection (FHP) initiated a rangewide health assessment for whitebark pine (*Pinus albicaulis*). This assessment summarized the forest health condition of whitebark pine throughout its range and also documented information needs, potential

restoration strategies, and challenges to restoration that need to be addressed (Schwandt 2006). This led to the creation of a national whitebark pine restoration program coordinated by FHP. <http://www.treesearch.fs.fed.us/pubs/38248>

Schwartz, C. C., M. A. Haroldson, et al. (2010). "Hazards Affecting Grizzly Bear Survival in the Greater Yellowstone Ecosystem." Journal of Wildlife Management 74(4): 654-667.

During the past 2 decades, the grizzly bear (*Ursus arctos*) population in the Greater Yellowstone Ecosystem (GYE) has increased in numbers and expanded its range. Early efforts to model grizzly bear mortality were principally focused within the United States Fish and Wildlife Service Grizzly Bear Recovery Zone, which currently represents only about 61% of known bear distribution in the GYE. A more recent analysis that explored one spatial covariate that encompassed the entire GYE suggested that grizzly bear survival was highest in Yellowstone National Park, followed by areas in the grizzly bear Recovery Zone outside the park, and lowest outside the Recovery Zone. Although management differences within these areas partially explained differences in grizzly bear survival, these simple spatial covariates did not capture site-specific reasons why bears die at higher rates outside the Recovery Zone. Here, we model annual survival of grizzly bears in the GYE to 1) identify landscape features (i.e., foods, land management policies, or human disturbances factors) that best describe spatial heterogeneity among bear mortalities, 2) spatially depict the differences in grizzly bear survival across the GYE, and 3) demonstrate how our spatially explicit model of survival can be linked with demographic parameters to identify source and sink habitats. We used recent data from radiomarked bears to estimate survival (1983-2003) using the known-fate data type in Program MARK. Our top models suggested that survival of independent (age  $\geq$  2 yr) grizzly bears was best explained by the level of human development of the landscape within the home ranges of bears. Survival improved as secure habitat and elevation increased but declined as road density, number of homes, and site developments increased. Bears living in areas open to fall ungulate hunting suffered higher rates of mortality than bears living in areas closed to hunting. Our top model strongly supported previous research that identified roads and developed sites as hazards to grizzly bear survival. We also demonstrated that rural homes and ungulate hunting negatively affected survival, both new findings. We illustrate how our survival model, when linked with estimates of reproduction and survival of dependent young, can be used to identify demographically the source and sink habitats in the GYE. Finally, we discuss how this demographic model constitutes one component of a habitat-based framework for grizzly bear conservation. Such a framework can spatially depict the areas of risk in otherwise good habitat, providing a focus for resource management in the GYE. <http://onlinelibrary.wiley.com/doi/10.2193/2009-206/abstract>

Schwartz, C. C., M. A. Haroldson, et al. (2006). "Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem." Wildlife Monographs(161): 1-68.

<http://www.cfc.umt.edu/grizzlybearrecovery/pdfs/Schwartz%20et%20al.%202006e.pdf>

Scott, G. L. M., Ward W. (2006). Whitebark Pine Guidelines for Planting Prescriptions. In: Riley, L.E.; Dumroese, R.K.; Landis, T.D., tech. coords. 2006. National Proceedings: Forest and Conservation Nursery Associations - 2005. Proc. RMRS-P-43. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 84-90.

This paper reviews general literature, research studies, field observations, and standard Forest Service survival surveys of high-elevation whitebark pine plantations and presents a set of guidelines for outplanting prescriptions. When planting whitebark pine, the recommendations are: 1) reduce overstory competition; 2) reduce understory vegetation,

especially grasses and sedges; 3) avoid outplanting in swales or frost pocket areas; 4) provide shade protection; 5) plant where there is protection from heavy snow loading; and 6) provide adequate growing space. <http://www.treesearch.fs.fed.us/pubs/26661>

Scott, G. L. M., Ward W.; Izlar, Kay (2011) Guidelines for whitebark pine planting prescriptions. [Extended abstract] In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 362-364.

Whitebark pine (*Pinus albicaulis*) is a keystone species in high-elevation ecosystems of the western United States. Unfortunately many fragile subalpine ecosystems are losing whitebark pine as a functional community component due to the combined effects of an introduced disease, insects and succession. Planting whitebark pine is one part of a multifaceted restoration strategy (Keane and Arno 2001). Once seedlings are established, they have the potential to be a long term seed source where existing trees have been lost. The practice of growing and planting whitebark pine is relatively new compared to traditional conifers, and with the high cost of cone collection and seedling production, survival is particularly important. This paper describes the planting guides created by Scott and McCaughey (2006) and further refined by McCaughey and others (2009). The planting guidelines should help increase survival making wise use of limited funds, and further the restoration of whitebark pine. <http://www.treesearch.fs.fed.us/pubs/38254>

Scott, J. D. T., Diana F.; Wunder, Michael B. (2011). "Determining Clark's nutcracker use of whitebark pine communities in regard to stand health in Waterton-Glacier International Peace Park. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 61-62."

Whitebark pine (*Pinus albicaulis*), one of five stone pines worldwide, is found at treeline and subalpine elevations in the mountains of western North America (McCaughey and Schmidt 2001). Considered a keystone species, it helps maintain subalpine biodiversity, protects watersheds and promotes post-fire regeneration (Tomback and others 2001). The Clark's nutcracker (*Nucifraga columbiana*) and whitebark pine are co-evolved mutualists (Tomback 1982). Nutcrackers remove seeds from whitebark pine cones and cache them in high- and low-elevation forests and terrain, returning to feed on the seeds for up to a year. Nutcrackers are the principal mode of seed dispersal for whitebark pine, and unretrieved seeds are the primary source for regeneration (Hutchins and Lanner 1982; Tomback 1982, 2001). <http://www.treesearch.fs.fed.us/pubs/38196>

Scott, J. M., P. Morgan, et al. (2001). "Representation of natural vegetation in protected areas: capturing the geographic range." *Biodiversity and conservation* 10(8): 1297-1201. <http://www.springerlink.com/content/tt7477016016p747/fulltext.pdf>

Shoal, R., Aubry C., and Ohlson T. (2008) Land Managers guide to whitebark pine restoration in the Pacific Northwest 2009-2013. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 37p, 27MB. <http://www.fs.fed.us/r6/genetics/documents/publications/pub803.pdf>

Shoal R., a. A. C. (2006) Core data attributes for whitebark pine surveys. Pacific Northwest Region, USDA Forest Service.

This document contains recommendations for core data attributes to be collected in whitebark pine survey and health assessment field activities in the U.S. Department of Agriculture (USDA), Forest Service, Pacific Northwest Region (Region 6), Oregon and Washington. This list of core data attributes applies to whatever type of survey method people choose to use: transect, circular, or other plot type; relevé or random sampling; inventory, long-term monitoring, etc. These core data attributes were developed in an effort to standardize whitebark pine data collection and reporting across the region. They represent the minimum information that should be collected in field surveys intended to assess or monitor the condition of whitebark pine. Other types of data can, of course, also be collected to address additional objectives or to provide more detail. The survey objectives and core data attributes below were identified and in some cases adapted from published methods (see bibliography and references section), from conversations with whitebark pine researchers and field technicians working in Oregon and Washington, and from the author's own field experience.

<http://www.fs.fed.us/r6/genetics/documents/publications/pub602.pdf>

Siderius, J. a. M. M. (2004). An initial assessment of the fire histories of two whitebark pine sites in the Washington Cascades. In: Taylor, L. (ed.), *Symposium Proceedings: Mixed Severity Fire Regimes: Ecology and Management*. Washington State University, Pullman, Washington, pp. 137-147. <https://fireecology.net/docs/proceedings/2005/75002.pdf>

Siepielski, A. M. and C. W. Benkman (2007). "Convergent patterns in the selection mosaic for two north American bird-dispersed pines." *Ecological Monographs* 77(2): 203-220.

The strength and outcome of interspecific interactions often vary across the landscape because of differences in community context. We investigated how the presence or absence of pine squirrels (*Tamiasciurus* spp.) influences the ecology and (co)evolution of seed-dispersal mutualisms between Clark's Nutcrackers (*Nucifraga columbiana*) and limber (*Pinus flexilis*) and whitebark (*P. albicaulis*) pines. Nutcrackers are the primary seed dispersers of these pines. Therefore both nutcrackers and pines potentially benefit from the evolution of a cone structure that enhances seed harvest by nutcrackers. Pine squirrels are the dominant predispersal seed predator of these pines throughout the Sierra Nevada-Cascades and Rocky Mountains and do not disperse seeds, so that pines benefit from deterring seed harvest by pine squirrels. To determine whether pines have evolved in response to selection by nutcrackers and pine squirrels, we conducted studies in ranges with pine squirrels and in ranges in the Great Basin and northern Montana where populations of the pines have apparently evolved without pine squirrels for 10000 years or more. Cone evolution was convergent between both pines and among phylogeographically independent populations with and without pine squirrels, consistent with variation in selection by nutcrackers and pine squirrels. Where pine squirrels were present, they out-competed nutcrackers for seeds, nutcrackers were less abundant, and selection by pine squirrels constrained the evolution of cone and seed traits that facilitate seed dispersal by nutcrackers. In the absence of pine squirrels, nutcrackers were more than twice as abundant, selection by pine squirrels on cone structure was relaxed, and selection on cone structure by nutcrackers resulted in cones that increased the foraging efficiency of nutcrackers and improved their potential for seed dispersal.

Siepielski, A. M. and C. W. Benkman (2007). "Extreme environmental variation sharpens selection that drives the evolution of a mutualism." *Proceedings of the Royal Society B-Biological Sciences* 274(1620): 1799-1805.

The importance of infrequent events for both adaptive evolution and the evolution of species interactions is largely unknown. We investigated how the infrequent production of

large seed crops (masting) of a bird-dispersed tree (whitebark pine, *Pinus albicaulis*) influenced phenotypic selection exerted by its primary avian seed predator-disperser, the Clark's nutcracker (*Nucifraga columbiana*). Selection was not evident during common years of low seed abundance, whereas it was replicated among areas and favoured traits facilitating seed dispersal during infrequent years of high seed abundance. Since nutcrackers act mostly as seed predators during small seed crops but as seed dispersers during the largest seed crops, trees experienced strong selection from nutcrackers only during infrequent years when the interaction was most strongly mutualistic. Infrequent events can thus be essential to both adaptive evolution and the evolutionary dynamics of species interactions. <http://rspb.royalsocietypublishing.org/content/274/1620/1799.full.pdf>

Siepielski, A. M. and C. W. Benkman (2007). "Selection by a predispersal seed predator constrains the evolution of avian seed dispersal in pines." *Functional Ecology* 21(3): 611-618.

1. Previous studies have demonstrated that wind dispersal is an effective mode of seed dispersal for pines (*Pinus*, Pinaceae) with seeds weighing < 90 mg, but not for larger-seeded ( $\geq 90$  mg) pines. Consequently, most large-seeded pines rely on birds in the family Corvidae for seed dispersal, but some do not, and most of their seeds fall near the parent tree. Why seeds of these pines are not dispersed by corvids, and have not evolved traits that facilitate seed dispersal by corvids, is enigmatic. 2. One factor that may constrain the evolution of seed dispersal by corvids in pines, or in other plants that rely on birds for seed dispersal, is predispersal seed predation. The most important predispersal seed predators of pines are often tree squirrels in the genera *Tamiasciurus* and *Sciurus*, which have repeatedly been shown to drive the evolution of seed defences in conifers. 3. We first use published data showing how selection on cone traits of two bird-dispersed pines by tree squirrels (*Tamiasciurus*) favouring increased seed defences, conflicts with selection by a corvid (*Nucifraga columbiana* Wilson) for cone traits that facilitate seed dispersal, to make predictions about changes in cone and seed structure of large-seeded pines that should evolve in response to selection by either tree squirrels or corvids. 4. The cone and seed structures from several other large-seeded pines in regions with and without pine squirrels were consistent with these predicted changes. Consequently, large-seeded pines that co-occur with *Tamiasciurus* or other tree squirrels are well defended against both squirrels and corvids, and instead probably rely on other animals, such as ground-foraging rodents, that disperse fallen seeds (secondary seed dispersal). Only where tree squirrels are uncommon or absent are conifers likely to evolve traits that enhance seed harvest by corvids in large-seeded pines.

Siepielski, A. M. and C. W. Benkman (2008). "Seed predation and selection exerted by a seed predator influence subalpine tree densities" *Ecology* 89(10): 2960-2966.

Strongly interacting species often have pronounced direct and indirect effects on other species. Here we focus on the effects of pine squirrels (*Tamiasciurus* spp.), which are a dominant pre-dispersal seed predator of many conifers including limber pines (*Pinus flexilis*) and whitebark pines (*P. albicaulis*). Pine squirrels depress seed abundance by harvesting most limber and whitebark pine cones on their territories. Pine squirrels further reduce seed availability for Clark's Nutcrackers (*Nucifraga columbiana*), the primary seed disperser of these pines, because selection exerted by pine squirrels has reduced the number of seeds per cone and causes seeds to be less accessible. We predicted that, if fewer seeds were available for dispersal by nutcrackers, pine recruitment should be suppressed in areas with pine squirrels. In support of this prediction, stand densities were about two times greater in areas where pine squirrels are absent than in areas where they are present. Alternative explanations that we considered do not account for these differences; however, precipitation may limit stand densities in the absence of seed

limitation by pine squirrels. In sum, pine squirrels apparently depress limber and whitebark pine stand densities, with the potential for ecosystem impacts because these pines are foundation species within Western subalpine ecosystems.

Six, D. L. and J. Adams (2007). "White pine blister rust severity and selection of individual whitebark pine by the mountain pine beetle (Coleoptera : Curculionidae, Scolytinae)." Journal of Entomological Science 42(3): 345-353.

We investigated whether white pine blister rust (*Cronartium ribicola*) (J.C. Fischer in Rabenh.) severity, tree diameter at breast height (DBH), bark and phloem thickness, and sapwood moisture content influence the preference of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) for individual trees of whitebark (*Pines albicaulis* Engelm.) and lodgepole pine (*P. contorta* Loud.). We measured these variables at 5 sites in Montana and Idaho and found a significant relationship between blister rust severity and attack of trees by *D. ponderosae*, with trees exhibiting greater blister rust severity being more likely to be attacked by the beetle. Sapwood moisture content was negatively correlated ( $P = 0.0004$ ) with blister rust severity indicating that as severity increases there is an increasingly negative effect on water relations within the tree. Sapwood moisture content was significantly lower in *P. albicaulis* than in *P. contorta* at sites with beetle activity suggesting that there may be an interaction between blister rust severity and drought stress that, in turn, may affect beetle preference. DBH and bark and phloem thickness did not appear to influence beetle preference for individual trees. As blister rust spreads in *P. albicaulis* stands across the western U.S., this may translate to increasing levels of beetle-caused mortality in these areas.

Six, D. L. and M. Newcomb (2005). "A rapid system for rating white pine blister rust incidence, severity, and within-tree distribution in whitebark pine." Northwest Science 79(2-3): 189-195.

Whitebark pine is an ecologically important high-elevation tree species distributed across much of the western United States and Canada. Unfortunately, this species is now undergoing rapid decline in many portions of its range due to an exotic disease, white pine blister rust. The objective of this research was to develop a practical, time efficient, yet accurate. method for rating white pine blister rust disease severity in whitebark pine. The system provides estimates of disease severity at the single tree or stand level, and of the within-tree distribution of infection. It can also be used to provide an overall estimate of disease incidence in a stand. Results of our rapid rating system were compared with a more time-consuming canker counting method. Overall estimates of disease severity using the rapid rating system and the canker-counting system were comparable. Both mean total canker counts and % incidence were highly correlated with mean total disease severity rating scores.

Skovlin, J. M., G. S. Strickler, et al. (2001). Interpreting landscape change in high mountains of northeastern Oregon from long-term repeat photography.. Gen. Tech. Rep. PNW-GTR-505. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 78 p.

We compared 45 photographs taken before 1925 to photographs taken as late as 1999 and documented landscape changes above 5,000 feet elevation in the Wallowa, Elkhorn, and Greenhorn Mountains of northeastern Oregon. We noted the following major changes from these comparisons: (1) the expansion of subalpine fir into mountain grasslands, (2) the invasion of moist and wet meadows by several tree species, (3) a loss of **whitebark pine** from subalpine habitats, (4) continued soil erosion stemming from livestock grazing long since discontinued, and (5) a high rate of natural gravitational mass wasting. The most important factor contributing to changes in woody vegetation has been a reduction in

fire frequency. Fires that occurred before 1925 were nine times more frequent than those that occurred at the end of the 20th century. Historical land uses and origins of place names are described. <http://www.treesearch.fs.fed.us/pubs/3079>

Smith, C. M., T. Carolin, et al. (2008). "Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana " Canadian Journal of Forest Research 38(5): 982-995.

In 2003-2004, we examined 8031 whitebark pine (*Pinus albicaulis* Engelm.) trees and 3812 seedling-establishment sites in 170 plots for mortality and incidence of white pine blister rust (*Cronartium ribicola* A. Dietr.). We found blister rust in all but four plots (98%), and 57% of all trees assessed for blister rust were either already dead or showed signs of blister rust infection. Mean percentage of trees infected was highest in the southern Canada -- United States border area (approximately 73%), decreasing to a low in the northern region of Banff National Park, Alberta (approximately 16%), and then rising (approximately 60%) in the northern end of the study area in Jasper National Park, Alberta. Stands with higher infection, mortality, and canopy kill of trees and higher presence of rust on seedlings tended to be located on the western side of the Continental Divide. In the eight stands in Waterton Lakes National Park, Alberta, that had been previously assessed in 1996, infection levels increased from 43% to 71%, and mortality increased from 26% to 61%, whereas no change was apparent in Glacier National Park, Montana, stands. The impacts of high mortality and infection levels, high crown kill, and reduced regeneration potential, suggest that the long-term persistence of whitebark pine in the southern part of the study area is in jeopardy.

<http://www.nrcresearchpress.com/doi/abs/10.1139/X07-182>

Smith, C. M. S., Brenda; Gillies, Cameron; Stuart-Smith, Jon (2011). "Re-measurement of whitebark pine infection and mortality in the Canadian Rockies. [Extended abstract] In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 238-241."

Whitebark pine (*Pinus albicaulis*) populations are under threat across the species' range from white pine blister rust (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*), fire exclusion and climate change (Tomback and Achuff 2010). Loss of whitebark pine is predicted to have cascading effects on the following ecological services: provision of high-energy food for wildlife (Tomback and Kendall 2001), facilitation of succession (Callaway 1998) and retention of snowpack (Tomback and others 2001).

<http://www.treesearch.fs.fed.us/pubs/38230>

Smith, E. K., L. M. Resler, et al. (2011). "Blister Rust Incidence in Tree line Whitebark Pine, Glacier National Park, USA: Environmental and Topographic Influences." Arctic Antarctic and Alpine Research 43(1): 107-117.

Whitebark pine (*Pinus albicaulis*) is a foundation and keystone species of upper subalpine and treeline ecosystems throughout the western United States and Canada. During the past several decades, *Cronartium ribicola*, an introduced fungal pathogen that causes white pine blister rust in five-needled pines, has caused significant declines in whitebark pine throughout its range. Our research objectives were to examine geographic variation in blister rust infection (total canker density) in whitebark pine found at six alpine treelines east of the Continental Divide in Glacier National Park, Montana, and to determine which environmental factors have the greatest influence on blister rust infection at treeline.

Within a total of 30 sampling quadrats (five at each treeline study site), we measured the



number of cankers on each whitebark pine in order to assess how blister rust infection varied throughout our study area. We created high-resolution digital elevation models to characterize surface microtopography, and used a geographic information system (GIS) to derive environmental variables of interest. A mixed effects, Poisson regression model determined environmental correlates of blister rust from the resulting set of field and GIS-derived variables. We found that rates of infection varied considerably among treelines, and that treeline sites exhibiting high flow accumulation rates, greater distances to wetlands, slopes facing southwest, higher curvature, greater wind speeds, and close proximity to Ribes and perennial streams had the highest rates of blister rust infection.

Smith, J. K. and N. E. McMurray (2000). FireWorks curriculum: featuring ponderosa, lodgepole, and whitebark pine forests. Gen. Tech. Rep. RMRS-GTR-65. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 270 p.

FireWorks is an education programme for students in grades 1-10. The programme consists of the curriculum in this report and a trunk of laboratory materials, specimens, and reference materials. It provides interactive, hands-on activities for studying fire ecology, fire behaviour, and the influences of people on three fire-dependent forest types - Pinus ponderosa (ponderosa pine), Pinus contorta var. latifolia (interior lodgepole pine), and Pinus albicaulis (whitebark pine). Wildland fire provides a rich context for education because it promotes understanding and integration of numerous concepts: properties of matter, ecosystem fluctuations and cycles, plant and animal habitat and survival, and human interactions with ecosystems. The curriculum links each activity to national and local educational standards; research has shown it increases student understanding of wildland fire. FireWorks is most appropriate for students in locations where the three featured tree species occur, and it may serve as a prototype for wildland fire education in other geographic areas. <http://www.treesearch.fs.fed.us/pubs/4572>

Smith, J. P. and J. T. Hoffman (2001). "Site and stand characteristics related to white pine blister rust in high-elevation forests of southern Idaho and western Wyoming." Western North American Naturalist 61(4): 409-416.

Successful infection of white pine species by white pine blister rust (WPBR) is contingent upon environmental conditions that are favorable to the spread and development of Cronartium ribicola. Site and stand factors related to this process have been studied elsewhere within the distribution of the disease, but few studies have concentrated on the high-elevation white pine forests of southern Idaho and western Wyoming. We found that mean summer precipitation, average tree diameter, and elevation were the most important variables in 3 logistic regression models of WPBR presence and intensity. The models were tested on a randomly chosen portion of our data set. The model with 9 variables correctly predicted categories of low-, moderate-, and high-disease incidence in 79% of cases. The 2 models with fewer variables had lower predictive efficiencies but were more parsimonious and generally easy to measure. The ability to use easily measured or remotely sensed site and stand characteristics to predict WPBR spread or intensification could be an important asset to land managers who need to decide where to focus disease mitigation efforts and predict disease effects on water quality, wildlife habitat, recreation potential, and other land-management activities.

Smith, J. P., J. T. Hoffman, et al. (2000). "First report of white pine blister rust in Nevada." Plant Disease 84(5): 594-594.

<http://apsjournals.apsnet.org/doi/abs/10.1094/PDIS.2000.84.5.594A>

Smith, S. B., D. C. Odion, et al. (2011). "Monitoring direct and indirect climate effects on whitebark pine ecosystems at Crater Lake National park." Park Science 28(2).

Whitebark pine (*Pinus albicaulis*) is the distinctive, often stunted, and picturesque tree line species in the American West. As a result of climate change, mountain pine beetles (*Dendroctonus ponderosae*) have moved up in elevation, adding to nonnative blister rust (*Cronartium ribicola*) disease as a major cause of mortality in whitebark pine. At Crater Lake National Park, Oregon, whitebark pine is declining at the rate of 1% per year. The Klamath Network, National Park Service, has elected to monitor whitebark pine and associated high-elevation vegetation. This program is designed to sample whitebark pine throughout the park to look for geographic patterns in its exposure to and mortality from disease and beetles. First-year monitoring has uncovered interesting patterns in blister rust distribution. Incidence of rust disease was higher on the west side of the park, where conditions are wetter and more humid than on the east side. However, correlating climate alone with rust disease is not straightforward. On the east side of the park, the odds of blister rust infection were much greater in plots having *Ribes* spp., shrubs that act as the alternate host for a portion of the rust's life cycle. However, on the park's west side, there was not a statistically significant increase in blister rust in plots with *Ribes*. This suggests that different species of *Ribes* associated with whitebark pine can increase pine exposure to blister rust disease. There is also convincing evidence of an association between total tree density and the incidence of blister rust. Warmer temperatures and possibly increased precipitation will affect both whitebark pine and *Ribes* physiology as well as tree density and mountain pine beetle numbers, all of which may interact with blister rust to cause future changes in tree line communities at Crater Lake. The Klamath Network monitoring program plans to document and study these ongoing changes.

Sniezko, R. A., A. Kegley, et al. (2009). "Resistance to *Cronartium ribicola* in whitebark pine - family variation and effect of inoculum density." Phytopathology 99(6): S122-S122.

Sniezko, R. A., A. J. Kegley, et al. (2008). "White pine blister rust resistance in North American, Asian and European species - results from artificial inoculation trials in Oregon." Annals of Forest Research 51: 53-66.

Dorena Genetic Resource Center (DGRC) has used artificial inoculation trials to evaluate progenies of thousands of *Pinus monticola* and *P. lambertiana* selections from Oregon and Washington for resistance to white pine blister rust caused by *Cronartium ribicola*. In addition, early results are now available for *P. albicaulis* and *P. strobiformis*. DGRC has also recently evaluated seed orchard progenies of *P. strobus*, as well as bulked seedlots from *P. armandii* and *P. peuce*. The majority of *P. monticola*, *P. lambertiana*, *P. albicaulis*, and *P. strobus* progenies are very susceptible to blister rust. However, resistance exists in all these species. *P. strobiformis* showed relatively high levels of resistance for the eight progenies tested. Resistance in *P. armandii* was mainly reflected in the very low percentage of cankered seedlings; for *P. peuce*, the high percentage of cankered seedlings alive three years after inoculation was notable, R-genes are present in some of the North American five-needle pine species, but partial resistance traits (e.g. bark reaction) will play a major role in breeding activities for *P. monticola* and *P. lambertiana* and will likely be the key to developing durable resistance.

Sniezko, R. A., A. J. Kegley, et al. (2006). Variation in resistance to white pine blister rust among 43 whitebark pine families from Oregon and Washington—Early results and implications for conservation. In: Proceedings, Whitebark Pine: A Pacific Coast Perspective, Ashland, OR. USDA Forest Service R6-NR-FHP-2007-01. pp. 27-31.

. <http://www.fs.fed.us/outernet/r6/nr/fid/wbpine/papers/2007-wbp-wpbr-resist-sniezko.pdf>

Snieszko, R. A. S., Anna; Dunlap, Joan; Vogler, Detlev; Conklin, David; Bower, Andrew; Jensen, Chris; Mangold, Rob; Daoust, Doug; Man, Gary (2011). "Ex Situ gene conservation in high elevation white pine species in the United States-a beginning. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 147-149."

The eight white pine species native to the western United States face an array of biotic and abiotic challenges that impact the viability of populations or the species themselves. Well-established programs are already in place to conserve and restore *Pinus monticola* Dougl. ex D. Don and *P. lambertiana* Dougl. throughout significant portions of their geographic ranges. More recently, programs have been initiated for the other six species: *P. albicaulis* Engelm., *P. aristata* Engelm., *P. balfouriana* Grev. & Balf., *P. flexilis* James, *P. longaeva* D.K. Bailey, and, *P. strobiformis* Engelm. In December 2008, concerns about the future of one of these species, *P. albicaulis* (whitebark pine), led one group to propose 'Listing' of this species under the Endangered Species Act (Natural Resource Defense Council 2008); a status review of the species is now underway, and a 12-month petition finding is expected in July 2011 (U.S. Fish and Wildlife Service 2010).

<http://www.treesearch.fs.fed.us/pubs/38212>

Stone, J. S., Anna; Snieszko, Richard; Kegley, Angelia (2011). "Histological observations on needle colonization by *Cronartium ribicola* in susceptible and resistant seedlings of whitebark pine and limber pine. [Abstract] In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 243."

Resistance to white pine blister rust based on a hypersensitive response (HR) that is conferred by a dominant gene has been identified as functioning in needles of blister rust-resistant families of sugar pine, western white pine and southwestern white pine. The typical HR response displays a characteristic local necrosis at the site of infection in the needles during the early stages of needle colonization by *Cronartium ribicola*. The localized host cell death early in the infection process is thought to prevent the pathogen from reaching the shoot tissue, thereby preventing further disease development. However, variation in macroscopic symptoms of needle reactions has been observed within and between different pine species and families. <http://www.treesearch.fs.fed.us/pubs/38233>

Tillman-Sutela, E., A. Kauppi, et al. (2008). "Variant maturity in seed structures of *Pinus albicaulis* (Engelm.) and *Pinus sibirica* (Du Tour): key to a soil seed bank, unusual among conifers?" *Trees* 22(2): 225-236.

The seeds of Cembrae pines are dispersed by nutcrackers (Genus *Nucifraga*), which cache seeds in soil during autumn. The dispersal and establishment of seedlings via this mutualistic relationship is highly successful. On the other hand, irregular quality of seed crops and lack of detailed knowledge on germination process of Cembrae pine seeds hamper effective seedling production in the nursery. Therefore we studied basic structures and maturity of whitebark pine (*Pinus albicaulis* Engelm.) and Siberian stone pine (*Pinus sibirica* Du Tour) seeds, as well as structural changes during a multi-step treatment of whitebark pine seeds, using field emission scanning electron microscopy, transmission electron microscopy and light microscopy. The most striking differences compared to many other conifer seeds were the solid surface structures, early structural differentiation

of the embryo, clustering of the thin-walled megagametophyte cells, and great accumulation of starch in both the untreated and treated seeds. Protein bodies of the embryo were in early developmental stages, whereas in the megagametophyte their stages varied. The number, form and size of lipid bodies also varied within different parts of the seed, and lipids dissolved easily. Our results indicated that despite maturity of the seed coat and advanced differentiation of the embryo, the embryo and the megagametophyte were still immature. These morphological features and a notable proportion of storage reserves remaining in unstable form may, however, be advantageous for maintaining viability and reaching maturity within a soil seed bank. Well-controlled pre-treatment simulating natural conditions should result in improved germination. <http://www.springerlink.com/content/x1237w8737440462/>

Tomback, D. F. (2001). Clark's Nutcracker: Agent of Regeneration. In: Whitebark Pine Communities: Ecology and Restoration. Tomback, D.F., S.F. Arno, and R.E. Keane (Eds.), Island Press, Washington D.C., USA, pp. 89-104.

Tomback, D. F. and P. Achuff (2010). "Blister rust and western forest biodiversity: ecology, values and outlook for white pines." *Forest Pathology* 40(3-4): 186-225.

Eight white pine species are widely distributed among the forests of western Canada and the United States. The different forest communities with these species contribute biodiversity to the western landscape. The trees themselves provide various ecosystem services, including wildlife habitat and watershed protection. White pine communities range in elevation from lower to upper treeline, in successional stage from seral to climax, and in stand type from krummholz to closed-canopy forest. Many white pine species are moderately to strongly fire-dependent for regeneration; several species are extreme stress tolerators and persistent on harsh sites. Among the white pines are the oldest-living trees, the world's largest pines, species dependent on birds for seed dispersal, species important for grizzly bear habitat and species of high commercial timber value. The principal threats to white pine populations are blister rust (*Cronartium ribicola*, pathogen), fire suppression, succession, mountain pine beetle and climate change. Severe population declines in several white pine species are attributed to losses caused by these factors acting either alone or together, and sometimes in concert with logging and other land-use changes. The importance and particular interactions of these threats vary by region and species. For example, many northern and western populations of whitebark pine are seriously declining from a combination of mountain pine beetle outbreaks and severe blister rust infestations. As whitebark pines provide many keystone services on high-elevation sites, their loss would impact forest composition and structure, succession, biodiversity, and ecosystem services. Although there are serious challenges to science-based management and conservation (especially in remote American wilderness areas), prompt and effective intervention promoting regeneration of blister rust-resistant white pines could mitigate these severe impacts.

Tomback, D. F., P. Achuff, et al. (2011). The magnificent high-elevation five-needle white pines: Ecological roles and future outlook. [Plenary paper]. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; and Smith, Cyndi M., eds. 2011. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. [http://www.fs.fed.us/rm/pubs/rmrs\\_p063/rmrs\\_p063\\_002\\_028.pdf](http://www.fs.fed.us/rm/pubs/rmrs_p063/rmrs_p063_002_028.pdf)

Tomback, D. F., S. F. Arno, et al. (2001). Whitebark pine communities: ecology and restoration. Washington; USA, Island Press.

Whitebark pine (*Pinus albicaulis*) occurs in the northwestern USA and southwestern Canada and is disappearing. This book contains 20 chapters which are organized into 4 parts: (1) a statement of the problem; (2) biology of whitebark pine; (3) threats and consequences to whitebark pine communities; and (4) restoration of whitebark pine communities. Topics covered include: the coevolutionary relationships within whitebark pine communities; reproductive biology of whitebark pine; integral relationship of various species in this ecosystem; epidemiology of white pine blister rust (caused by *Cronartium ribicola*) and the mortality of whitebark pine due to *Dendroctonus ponderosae*; successional changes brought about by fire suppression; and genetic diversity among whitebark pine communities.

Tomback, D. F. and K. C. Kendall (2001). Biodiversity losses: the downward spiral. In: *Whitebark pine communities: ecology and restoration*. Edited by DF Tomback, SF Arno, and RE Keane. Island Press, Washington, DC. pp. 243-262.

Tomback, D. F., M. L. Powell, et al. (2001). "Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires." Ecology 82(9): 2587-2600.

Whitebark pine (*Pinus albicaulis*) seeds are dispersed by Clark's Nutcracker (*Nucifraga columbiana*), a bird that makes caches under 2-3 cm of soil. Cached seeds may delay germination for one or more years in part because of underdeveloped embryos at the time of seed dispersal. Consequently, whitebark pine may show a soil seed bank strategy that is unique among pines (*Pinaceae*, *Pinus*). From 1990 to 1995 we studied natural whitebark pine regeneration following the 1988 Yellowstone fires to determine: (1) whether whitebark pine typically exhibits delayed seed germination and, if so, (2) how this affects patterns of regeneration over time, and (3) whether germination is the result of seed maturation or is stimulated by high levels of moisture availability. We established 275 permanent plots, each 20 m<sup>2</sup> in area, divided between Henderson Mountain, Gallatin National Forest, Montana, and Mt. Washburn, Yellowstone National Park. In the Henderson Mountain study area, the ecological conditions or "treatments" included: dry, burned; moist, burned; dry, unburned; and moist, unburned. In the Mt. Washburn study area, the ecological treatments were dry, burned; moist, burned; and moist, moderately burned. Synchronous delayed seed germination occurred throughout both study areas. The greatest densities of new seedlings appeared in the summers of 1991 and 1993, but the greatest cone crops were produced in 1989 and 1991. Most germination followed two winters of seed dormancy. Regeneration densities were consistently highest on the Mt. Washburn moist treatments. High correlation between weighted means for new regeneration and March-plus-April precipitation, as well as the results of residual and multiple regression analyses, suggests that cone production two years prior and March-plus-April precipitation together account for the regeneration patterns in the Mt. Washburn study area. The role of precipitation requires further study. Delayed seed germination, producing a soil seed bank, may be an ecological strategy in whitebark pine that is the product of selection. Although underdeveloped embryos may be a consequence of both a short growing season and premature seed dispersal by nutcrackers, seed caching may further select for slow embryo maturation, as well as moisture-resistant seed coats to reduce nonadaptive germination.

Tomback, D. F. and L. M. Resler (2007). "Invasive pathogens at alpine treeline: Consequences for treeline dynamics." Physical Geography 28(5): 397-418.

The potential impact of invasive forest pathogens on alpine treeline dynamics has not previously been considered. Whitebark pine (*Pinus albicaulis*), a foundation and keystone species of subalpine forests and major component of alpine treeline in the northern Rocky Mountains of the United States and southern Canada, is infected nearly range-wide by the exotic pathogen *Cronartium ribicola*, which causes white pine blister rust. A major component of treeline in the northern Rocky Mountains, whitebark pine initiates tree islands on the eastern slope in northwestern Montana more than any other conifer species. Blister rust infects whitebark pine throughout the region, and both infection and mortality are already evident at treeline. We discuss the cascading ecological effects of the loss of treeline whitebark pine and expected changes in landscape vegetation patterns. Potential implications of the loss of whitebark pine for northwestern Montana treelines are examined in the context of climate change within a conceptual model. We speculate that exotic pathogens could potentially confound predictions of treeline responses to global warming in many geographic regions.

Tomback, D. F. S., Anna W.; Perez, Mario J.; Grompone, Kristen M.; Mellmann-Brown, Sabine (2011) Regeneration and survival of whitebark pine after the 1988 Yellowstone fires. In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 66-68.

Successional whitebark pine (*Pinus albicaulis*) communities are dependent on fire and other disturbances for renewal (Arno 2001). Where whitebark pine regenerates results from cache site selection by Clark's nutcrackers (*Nucifraga columbiana*) in relation to the environmental tolerances of seeds and seedlings (Tomback 2001). After the 1988 Yellowstone fires, we studied the development of upper subalpine forest communities with particular focus on the regeneration of whitebark pine in two study areas - Mt. Washburn in Yellowstone National Park, and Henderson Mtn. in Gallatin National Forest. Fire history and patterns of community regeneration of the predominantly seral lodgepole pine forests in the southcentral and southwestern regions of Yellowstone National Park have been well studied (e.g., Romme 1982; Turner and others 1997), whereas whitebark pine communities have been less studied. <http://www.treesearch.fs.fed.us/pubs/38198>

Trusty, P. E. C., Cathy L. (2011). "Influence of fire on mycorrhizal colonization of planted and natural whitebark pine seedlings: Ecology and management implications. [Extended abstract] In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 198-202."

Whitebark pine (*Pinus albicaulis*) is a threatened keystone species in subalpine zones of Western North America that plays a role in watershed dynamics and maintenance of high elevation biodiversity (Schwandt, 2006). Whitebark pine has experienced significant mortality due to white pine blister rust, mountain pine beetle outbreaks and successional replacement possibly due to fire suppression (Schwandt 2006; Smith and others 2008). Current management strategies include letting lightning fires burn or applying prescribed fire to provide habitat for natural seedling establishment or the planting of rust resistant seedlings (Keane and Parsons 2010a, 2010b). However survival rates after fire are variable and can be low (Izlar 2007; Keane and Parsons 2010a; Perkins 2004; Tomback and others 2001). <http://www.treesearch.fs.fed.us/pubs/38220>

Vogler, D. R. and D. A. Charlet (2004). "First report of the white pine blister rust fungus (*Cronartium ribicola*) infecting whitebark pine (*Pinus albicaulis*) and *Ribes* spp. in the Jarbidge Mountains of northeastern Nevada." Plant Disease 88(7): 772-772.

Vujanovic, V., M. St-Arnaud, et al. (2000). "Susceptibility of cones and seeds to fungal infection in a pine (*Pinus* spp.) collection." Forest Pathology 30(6): 305-320.

Thirty-one fungi, members of Ascomycota and Deuteromycota were isolated from cones/seeds of 28 hosts (*Pinus* spp.) originating from East Asia, Europe and North America, and growing at the Montreal Botanical Garden, Canada. A total of 21 taxa of these isolated fungi are considered pathogens. The damage severity was most prevalent on Diploxylon pines of European provenance (*Pinus nigra*, *Pinus mugo* and *Pinus sylvestris*), and one indigenous North American species (***Pinus albicaulis***). Twelve fungi occurred on different hosts, i.e. *Sphaeropsis sapinea* (12), *Herpotrichia juniperi* (8), *Truncatella hartigii* (7), *Ceuthospora* sp.(5), *Fusarium*, spp. (5), *Pestalotiopsis funerea* (3), *Phomopsis* sp.(3) *Valsa* spp. (anamorph. *Cytospora*) (3), *Diaporthe* sp. (3), *Fusicoccum* sp. (2) and *Sirococcus strobilinus* (2). *Sphaeropsis sapinea*, *Herpotrichia juniperi*, *Phomopsis conorum*, *Truncatella hartigii*, *Tubercularia* and *Valsa* spp. were related to high cone and seed damage. For the most frequently observed *Sphaeropsis sapinea* damage, the subgenus *Haploxylon* was less susceptible than *Diploxylon*, and *P. sylvestris* less than *P. nigra* and *P. mugo*. *Pinus resinosa* showed more tolerance to *S. sapinea*. *Truncatella hartigii* was more frequently associated with necrotic lesions on cones/seeds in comparison with *Pestalotiopsis funerea*. The results are discussed in the context of arboretum, seed orchard, nursery and quarantine management.

Ward, K., Shoal R., and Aubry C. (2006) Whitebark pine cone collection manual. Pacific Northwest Region, USDA Forest Service. Pacific Northwest Albicaulis Project. March 2006. <http://www.fs.fed.us/r6/genetics/documents/publications/pub603.pdf>

Ward, K., R. Shoal, et al. (2006) Whitebark pine in Washington and Oregon: a synthesis of current studies and historical data. USDA Forest Service, Pacific Northwest Region, Pacific Northwest Albicaulis Project, February 2006. 22 p. <http://www.fs.fed.us/r6/genetics/documents/publications/pub601.pdf>

Waring, K. M. and D. L. Six (2005). "Distribution of bark beetle attacks after whitebark pine restoration treatments: A case study." Western Journal of Applied Forestry 20(2): 110-116.

Whitebark pine (*Pinus albicaulis* Engelm.), an important component of high elevation ecosystems in the western United States and Canada, is declining due to fire exclusion, white pine blister rust (*Cronartium ribicola* J.C. Fisch.), and mountain pine beetle (*Dendroctonus ponderosae* Hopkins). This study was conducted to evaluate the effects of whitebark pine restoration treatments on the distribution of bark beetle attacks. At a site in Idaho, silvicultural treatments were implemented in summer 1998 and 1999, with prescribed burning implemented in Oct. 1999. Permanent plots (400m<sup>2</sup>) were established during summer 1999 within each treatment and monitored for 4 years. Within plots, tree characteristics were measured and a bark- beetle survey was conducted. Bark beetle attacks remained low throughout the study; however, there was an increase in bark beetle attacks in 2000 after the prescribed burning. By years 3 and 4, there were virtually no successful attacks. Although bark beetles were not a serious concern at the site assessed in this study, out- results indicate that managers should consider and monitor the bark beetle component of these ecosystems when implementing restoration treatments. If baseline bark beetle Populations are high at the time of implementation, our

results indicate that increases in beetle activity would be expected in some treatments, perhaps requiring mitigation.

Warwell, M. V., G. E. Rehfeldt, et al. (2006). Modeling contemporary climate profiles of whitebark pine (*Pinus albicaulis*) and predicting responses to global warming. pp. 139-142. In: Proceedings, of the Conference Whitebark Pine: A Pacific Coast Perspective. USDA Forest Service R6-NR-FHP-2007-01.

<http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.180.5937&rep=rep1&type=pdf>

Wenny, D. G., T. L. Devault, et al. (2011). "The Need to Quantify Ecosystem Services Provided By Birds." *The Auk* 128(1): 1-14.

<http://www.bioone.org/doi/full/10.1525/auk.2011.10248>

Wilson, B. (2011). "Establishment patterns of whitebark pine following fire in the Canadian Rockies. [Abstract] In: Keane, Robert E.; Tomback, Diana F.; Murray, Michael P.; Smith, Cyndi M., eds. The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium. 28-30 June 2010; Missoula, MT. Proceedings RMRS-P-63. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 207."

I examined the regeneration of whitebark pine (*Pinus albicaulis*) and four other high elevation conifers in young subalpine forest following two stand replacing fires in the Canadian Rockies. These were the Vermilion Pass fire of 1968, located in Kootenay and Banff national parks, and the Rock Canyon Creek fire of 1960, located approximately 125 km further southeast in the Invermere Forest District of British Columbia. I surveyed 103 100-m<sup>2</sup> plots in total, with roughly equal sampling intensity across the environmental gradients of altitude, aspect, and distance to the mature forest edge. I measured stand structural variables within each plot, including vegetation species cover and tree species seedling and sapling density. Both landscape and microsite scales of environmental variables were measured at each plot. <http://www.treesearch.fs.fed.us/pubs/38224>

Wilson, B., S. Rasheed, et al. (2008). "Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana." *Canadian Journal of Forest Research* 38(5): 982-995.

In 2003–2004, we examined 8031 whitebark pine (*Pinus albicaulis* Engelm.) trees and 3812 seedling-establishment sites in 170 plots for mortality and incidence of white pine blister rust (*Cronartium ribicola* A. Dietr.). We found blister rust in all but four plots (98%), and 57% of all trees assessed for blister rust were either already dead or showed signs of blister rust infection. Mean percentage of trees infected was highest in the southern Canada – United States border area (~73%), decreasing to a low in the northern region of Banff National Park, Alberta (~16%), and then rising (~60%) in the northern end of the study area in Jasper National Park, Alberta. Stands with higher infection, mortality, and canopy kill of trees and higher presence of rust on seedlings tended to be located on the western side of the Continental Divide. In the eight stands in Waterton Lakes National Park, Alberta, that had been previously assessed in 1996, infection levels increased from 43% to 71%, and mortality increased from 26% to 61%, whereas no change was apparent in Glacier National Park, Montana, stands. The impacts of high mortality and infection levels, high crown kill, and reduced regeneration potential, suggest that the long-term persistence of whitebark pine in the southern part of the study area is in jeopardy.

Wilson, B. C. and G. J. Stuart-Smith (2002) Whitebark pine conservation for the Canadian Rocky Mountain national parks. KNP-01. Cordilleran Ecological Research, Prepared for Parks Canada,



BC. 30pp.

<http://www.whitebarkfound.org/publications/ParksCaWBP%20Conservation%20Plan%2002-11.pdf>

Wood, C. and D. Smith (2004). "Dendroglaciological evidence for a Neoglacial advance of the Saskatchewan Glacier, Banff National Park, Canadian Rocky Mountains." Tree-Ring Research 60(1): 59-65.

Seventeen glacially sheared stumps in growth position and abundant detrital wood fragments were exposed by stream avulsion at the terminus of the Saskatchewan Glacier in 1999. The stumps lay buried beneath the glacier and over 5 m of glacial sediment until historical recession and stream incision exposed the 225- to 262-year-old stand of subalpine fir, Englemann spruce and whitebark pine trees. Crossdating and construction of two radiocarbon-control led floating tree-ring chronologies showed that all the subfossil stumps and holes exposed at this location were killed during a Neoglacial advance of the Saskatchewan Glacier 2,910 +/- 60 to 2,730 +/- 60 C-14 years B.P These findings support the Peyto Advance as a regional glaciological response to changing mass balance conditions. <http://www.bioone.org/doi/abs/10.3959/1536-1098-60.1.59>

Zeglen, S. (2002). "Whitebark pine and white pine blister rust in British Columbia, Canada." Canadian Journal of Forest Research 32(7): 1265-1274.

A survey of the health of whitebark pine (*Pinus albicaulis* Engelm.) was conducted throughout its range in British Columbia, Canada. Over 3 years, 24 070 trees were examined for mortality, incidence of white pine blister rust (*Cronartium ribicola* J.C. Fisch.), or other damage. About 19% of whitebark pine (>1.3 m in height) were dead, and another 31% had active blister rust infections. Tests of relationships between the proportion of healthy, infected, or dead trees and elevation, latitude, and longitude produced mixed results. The ratio of healthy to infected whitebark pine varies considerably across the province, with a trend of increasing incidence from west to east. Losses to mountain pine beetle (*Dendroctonus ponderosae* Hopkins) proved minor, but bark stripping by mammals was common. Whitebark pine seedlings (<1.3 m in height) revealed lower rates of mortality (11%) and rust infection (4%) than larger trees. However, the pioneer species whitebark pine was found in less than half the regeneration plots and was usually outnumbered by subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). The combination of mature tree mortality, lack of suitable substrate for regeneration, and the incursion of climax species indicates a continued decline in whitebark pine populations in British Columbia.

Zeglen, S. (2007). Whitebark Pine in British Columbia: Current Conditions and the State of Our Efforts. pp. 36-38. In: Proceedings of the Conference Whitebark Pine: A Pacific Coast Perspective. USDA Forest Service R6-NR-FHP-2007-01.

<http://www.fs.fed.us/r6/nr/fid/wbpine/papers/2007-wbp-status-zeglen.pdf>

Zeglen, S., R. Hunt, et al. (2009). "White pine blister rust forest health Stand Establishment Decision Aid." BC Journal of Ecosystems and Management 10(1): 97-100.

Greater Yellowstone Whitebark Pine Monitoring Working Group. 2010. Monitoring Whitebark Pine in the Greater Yellowstone Ecosystem: 2009 Annual Report. Pages 63-71 in C.C. Schwartz, M.A. Haroldson, and K. West, editors. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2009. U.S. Geological Survey, Bozeman, Montana, USA. [http://fedgycc.org/documents/GYE\\_WBP\\_2009\\_Annual\\_GRYNReport.pdf](http://fedgycc.org/documents/GYE_WBP_2009_Annual_GRYNReport.pdf) ;

See also: <http://fedgycc.org/WhitebarkPinePublicationsandArticles.htm>