Annotated Bibliography for Whitebark Pine Ecology
December 2008
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1. **Comments:**
   a. I hope that you enjoy these annotations; I attempted to keep them brief. Most are 'cut and paste' from the abstract and discussion portions of each document.
   b. The precarious state of whitebark pine is distressing and it critical that we make decisions based on the most scientifically informed and accurate understanding of the life history of whitebark pine, historic disturbance regimes, and the current situation. Our current concepts of whitebark pine ecology originated from valuable whitebark pine research that emerged when we first discovered the amazing ecosystem associated with this pine. Presently, we are faced with a growing body of research findings that build upon this earlier foundation. It is imperative that we continually incorporate these findings into our management strategies; many of the information gaps we acknowledged in earlier work are being addressed.
   c. *One emerging concept is that the retention of the maximum available source of seed on the landscape is critical – for genetic diversity, natural selection that promotes rust resistance, and natural regeneration.* Lack of adjacent seed is the fundamental limiting factor cited in nearly all work regarding whitebark regeneration, even in papers published in the 1990s. These ideas have evolved into the current proactive approach to whitebark conservation.
   d. I plan to continually update this document. If I missed any key work or if you have additional interpretations from any given paper, please let me know.

2. **2007 Proceedings on the Conference of Whitebark Pine: A Pacific Coast Perspective. USDA Forest Service, Forest Health Protection, R6-NR-FHP-2007-01.**
   a. **Aubry, C.A. & Rochefort, R. 2007. Whitebark pine in the Pacific Northwest: what's next?**
      Key Conclusions
      - Whitebark pine stands are diverse - restoration strategies must encompass these differences.
      - Maintain whitebark on landscape, as a seed source and to encourage natural selection for blister rust resistance.

   b. **Bentz, B.J., & Schen-Langenhiem. 2007. The mountain pine beetle and whitebark pine waltz: has the music changed?**
      Key Conclusions
      - Mountain pine beetle are highly responsive to changes in temperature.
      - Currently, in high elevation whitebark a variety of mpb cohorts are emerging at any given time resulting in high rates of mortality.
      - This variety of voltinism patterns results in mpb population success.

   c. **Bower, A.D., & Aitken, S.N. 2007. Genetic diversity and geographic differentiation in quantitative traits, and seed transfer guidelines for whitebark pine.**
      Key Conclusions
      - Provenances from higher latitudes and lower winter temperatures flush earlier in spring, suffer less cold injury, and allocate greater biomass to roots and shoots.
      - These seedlings can withstand greater abiotic stresses associated with site-specific climate.
      - Seedlings should not be moved greater that 3° latitude north and 1° latitude south.
      - No elevational range limitations are necessary.

   d. **Kegley, S.J., & Gibson, K.E. 2007. Using verbenone to protect whitebark pine from mountain pine beetle attack.**
      Key Conclusions
      - Verbenone successfully protects even in areas of high mpb populations: >90% treated whitebark survived beetle attack.
      - Two 5 or 7.5 gram pouches per tree were used; mid-season replacement not necessary at this point.

   e. **Kegley, A., Sniezko, R.A., & Danchok, R. 2007. Influence of inoculum source and density on white pine blister rust infection and morality of whitebark pine: 2007 update on 2001 inoculations of Shoshone NF seedlings.**
      Key Conclusions
      - Seedlings used to test inoculum source were from a bulked cone collection from the Shoshone NF and showed low (11%) levels of rust resistance.
      - Geographic source and density of inoculum has little effect on seedling rust mortality.

f. **Lockman, I. B., & DeNitto, G.A. WLIS: the whitebark-limber pine information system and what it can do for you.**

Key Conclusions

- The WLIS database is a compilation database of numerous studies/surveys completed in the US and Canada.
- This promotes range-wide assessments of whitebark and limber pine.
- Location: **http://www.fs.fed.us/r1-r4/spf/fhp/prog/programs2.html**

g. **Lorenz, T.J. 2007. Radio-tagging Clark's Nutcrackers: preliminary data from a study of habitat use in Washington state.**

Key Conclusions

- Managers cannot duplicate the unique genetic structure, successional advantages and growth form characteristics enable by nutcrackers: nutcracker populations must be sustained.
- Most frequent nutcracker caching sites include: closed canopy forests, and steep, bare slopes.
- Least frequently selected caching sites include: forest openings.

h. **McDowell, S.A. 2007. Burn severity and whitebark pine (*Pinus albicaulis*) regeneration in the North Cascades.**

Key Conclusions

- Negative relationship between burn severity and whitebark seedling density.

i. **Murray, M.P. 2007. Fire and pacific coast whitebark pine.**

Key Conclusions

- Whitebark and subalpine fir both establish post fire.
- Allowing lightening ignited fire to burn whitebark is preferred to prescribed fire: lightening caused fires are spatially and temporally typical – they are smaller and occur at time of year when communities are adapted to burn.
- Prescribed fire could be used carefully, only in areas where evidence of frequent fire and appropriate fuels conditions exist.
- Areas with sparse fuels and no evidence of frequent burns likely didn't burn and prescribed fire should not be applied.
- Fire-induced mortality of potentially rust resistant trees should be strictly avoided. They are the life-link to the species future.
- Protection of remaining live, healthy trees is imperative

j. **Vogler, D.R. 2007. The role of disease resistance in the recovery of whitebark pine.**

Key Conclusions

- The rust resistance program is not necessarily guaranteed, fail-safe, certain or all inclusive.
- Key unknowns include: an absolute understanding of the mechanisms of resistance, technological success of resistance breeding and outplanting, limited spatial scale of our ability to deploy whitebark seedlings, and the amount of time required to test, propagate, and establish seed producing whitebark on landscape.

k. **Warwell, M.V., Rehfeldt, G.E., & Crookston, N.L. 2007. Modeling contemporary climate profiles of whitebark pine and predicted responses to global warming.**

Key Conclusions

- A bioclimate model derived from Canadian Global Climate Models and local temperature and precipitation suggest a rapid and large-scale decline in total area occupied by whitebark pine: 70% decline and 333 meter upward movement in altitude by 2030.
- This model predicts locations of sites where climate will be suitable of establishment and growth of whitebark.
- These areas should be targeted for conservation.

l. **Zeglen, S. 2007. Whitebark pine in British Columbia: current conditions and the state of our efforts.**

Key Conclusions

- One in five whitebark in British Columbia are dead. Of those remaining one-third have blister rust.
- A survey of 483 whitebark stands in British Columbia from 1998-2002 (Zeglen 2002) illustrate low levels of natural regeneration - half plots contain no whitebark regeneration and one-third have only 1-5 whitebark >1.3m.

3. Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrniodis, I., Watt, A.D., & Whittaker, J.B. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology. 8: 1-16.

Background & Objectives

Climate acts directly on insects by regulating growth and development rates or through direct mortality. This review paper explores the direct impacts of increased temperature on insect phenology, life cycles, and distribution in natural, rather than agricultural, systems in relation to the spatial variation of insect response.

Main Findings

- Life cycles events, such as voltinism, population density, rate of development, and extent of host plant exploitation, are impacted by temperature change.
- Temperature also regulates plant growth and seasonal availability. Insect herbivore synchrony with host phenology becomes increasingly important when climatic envelopes become smaller. This interaction regulates insect distribution.
- Warming will allow the majority of insects to increase their elevational and latitudinal distributions.
- Fossil evidence indicates that insects have responded to climate change in the past.
- Insect species that have a significant diapause event in their life cycle may experience range contraction as winter temperatures increase.
- Insect predation interactions will be altered.

Implications

- Insect respond to climate change and this impacts insect distribution and impacts on vegetation.
- Relative growth rates and diapause data for a specific insect can be applied to their framework to predict range expansion or contraction.

4. Barret, S.W. 1994. Fire regimes on andesitic mountain terrain in northeastern Yellowstone National Park, Wyoming. Int. J. Wld. Fire. 4(2): 65-76.

Background & Objectives

Fire history was studied for three forest community types in the Absaroka Mountains of Yellowstone National Park (YNP), Wyoming. Master fire chronologies were based on fire-initiated age classes and tree fire scars.

Main Findings

- High altitude whitebark pine forests had primarily stand replacing fires with >350-year mean intervals of mixed severity- or non-lethal underburns.

Implications

- While short interval fire regimes may have been altered by long-term fire suppression, fire exclusion apparently had only limited influence on the infrequently burned ecosystems

5. Bentz, B.J., Logan, J.A., & Vandygriff, J.C. 2001. Latitudinal variation in Dendroctonus ponderosae (Coleoptera: Scolytidae) development time and adult size. Canadian Entomologist. 133: 375-387.

Background & Objectives

This paper investigates the difference between adult mountain pine beetle size and development time from a northern (central Idaho) and southern population (southern Utah). Because insects often respond phenotypically to the local environment, the authors wanted to determine if these life history parameters were controlled by genetics or environmental factors. Prior to this paper, the genetic diversity of the species was unclear and this differentiation is key to understanding bark beetle population dynamics at specific geographic regions.

Main Findings

- Median emergence time was shorter from northern populations.
- Brood from southern populations was larger than from northern.
- Brood food source, or host tree species, was not a statistically significant explanation of differences in developmental rates or adult beetle size between populations from different latitudes. Host tree species, however, was influential on a local spatial scale.

Implications

- By removing the influence of temperature on mountain pine beetle development, this work shows that there are genetically based traits which are dissimilar for beetles from varying latitudes.
- In colder environments, selection for faster development time would be stronger and in warmer environments, where time available for development would be greater would result in larger adult size.

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

Background & Objectives

This study 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; whitebark pine density; and diffusion by non-alternate host species influence probability of selection by the mountain pine beetle for individual whitebark pine.

Main Findings

- 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.
- Beetle activity increased significantly in whitebark pine with heavy blister rust.
- Mountain pine beetle preferentially select whitebark pine over lodgepole pine.
- Whitebark pine diameter, rust severity, and overstory tree species composition all influence beetle selection of host trees.

Implications

- Interactions between the beetle and blister rust may enhance whitebark pine mortality and widespread population decline.
- Beetle preference for whitebark with severe blister rust alter the proportion of rust resistant whitebark in the remaining population.

7. Burns, K.S., Schoettle, A.W., Jacobi, W.R. & Mahalovich, M.T. 2008. Options for the management of whitepine blister rust in the Rocky Mountain region. USDA Forest Service, Rocky Mountain Research Station, RMRS-GTR-206.

Background & Objectives

This document summarizes current information on blister rust in the Rocky Mountain region including the disease cycle, detection and evaluation and provides concise management options.

Main Findings

- Management options include:
  - Fungicide to prevent rust spread in urban, nursery and high value sites.
  - Pruning infected branches of mature cone-bearing trees to prolong life.
  - Mechanical thinning to reduce stand density to prevent mature tree loss to fire, remove other conifer species, and decrease suitability of microclimate for rust spread.
  - Identify and protect putatively rust resistance trees.
  - Artificial regeneration on sites without seed source or natural resistance- seedlings need bright sunlight.
  - Encourage natural regeneration – protect seed trees, create canopy openings, retain remaining trees.
  - Eliminate fuels around white bark to reduce threat of fire damage.

Implications

- We need to protect remaining cone-bearing trees from fire, beetles, lethal stem cankers – many of them may be rust resistant.
- Maintenance of large gene pool of whitebark pine upon which selection for rust resistance acts is critical.
- Create landscape of diverse age and size classes – protect old trees, promote survival of present seedlings and saplings, and encourage new recruitment (natural & artificial).
- Seed availability controls natural regeneration.

8. Campbell, E.M. & Jackson, S. 2008. Assessing the threat of mountain pine beetle outbreaks to whitebark pine in British Columbia. FIA-FSP Project M08-6048. Research Branch, British Columbia Ministry of Forests and Range.

Background & Objectives

This project sought to quantify fundamental factors contributing to the decline of whitebark pine, including the role of a shift in climatically suitable beetle habitat, a description of stand dynamics and disturbance history, and the ability of whitebark pine to resist beetle attack.

Main Findings

- The current number of beetle infestations in previously unsuitable whitebark habitat is three times greater than in the late 1970s and early 1980s due to:
  - An increase in the number of days that are warm enough for univoltine life cycles.
  - Decrease in frequency of -40° C underbark temperatures
- Stand conditions and dynamics are variable:
  - Whitebark regeneration is occurring on open, dry sites with current rust infection
  - Some mixed conifer stands have little ABLA/PIEN regeneration and multiple age cohorts of whitebark.
  - Stands with heavy beetle mortality and abundant ABLA will experience accelerated succession.

- Whitebark not killed by beetles may experience growth release.
  - Stands exhibit evidence of continual recruitment – soil seed banking and successional regeneration, not just disturbance related.
  - Evidence of stand-replacing events suggest 250 to 300 year return intervals.
- Some whitebark exhibit a hypersensitivity secondary response indicating a level of resistance to attack by the mpb.
- Whitebark pine monoterpenes (tree chemical compounds that are used in defense mechanisms) are variable among sites and differ significantly from lodgepole.

Implications
- Management must address a wide-variety of stand dynamics and historic disturbance regimes.
- Resistance to the mpb is possible.

9. Campbell, E.M. & Antos, J.A. 2003. Post-fire succession in *Pinus albicaulis-Abies lasiocarpa* forests of southern British Columbia. Can. J. Bot. 81: 383-397.

Background & Objectives

This project examined post fire succession in whitebark pine forests in two areas of contrasting climate.

Main Findings
- Whitebark continues to establish in late seral stands.
- Whitebark pine growing beneath a closed canopy for 150 to 200 years respond to overstory removal
- Lodgepole density influences population dynamics of whitebark: abundant lodgepole limits whitebark abundance; sites with no or little lodgepole are dominated by whitebark throughout succession.
- In mixed conifer, mid-elevation sites vegetative succession results in increased density of subalpine fir and Engelmann spruce.
- Whitebark pine are not as shade-intolerant as once believed and never completely out competed by more shade-tolerant species
- Fire plays multiple roles in whitebark pine ecosystems depending on stand structure, microclimate, season of burn, and synoptic climate patterns.
- Successional replacement by fir and spruce takes more than 500 years, but may be accelerated by blister rust.
- Whitebark pine is both a pioneer and long-lived species; more appropriately considered highly tolerant of stress.

Implications
- Site specificity and associated inherent successional processes drive whitebark stand dynamics– restoration must identify sites that can support whitebark and strategies must be site specific.
- Multiple successional pathways exist due to whitebark life history characteristics, pre-disturbance/initial stand vegetation composition, disease, and interactions of all factors.

10. Carroll, A.L., Taylor, S.W., Regniere, J. & Safranyik, L. 2003. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. *In* Mountain Pine Beetle Symposium: Challenges and Solutions. October 30-31, 2003, Kelowna, British Columbia. T.L. Shore, J.E. Brooks, & J.E. Stone (eds.) Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria, BC. 298 p.

Background & Objectives

This paper addresses the current increase in the number of mountain pine beetle infestations since 1970 into formerly thermally unsuitable habitats. The authors wished to quantify the effect of global warming on mountain pine beetle populations in North America.

There were two questions addressed in the paper. First, has there been a shift in climatically suitable habitats during the recent past? Second, have mountain pine beetle populations expanded into these novel habitats?

In order to perform this study, a model developed in the late 1970s was adapted to evaluate the impact of climatic conditions on the establishment and persistence of mountain pine beetles. Climatic variables included in the model are: number of degree days above 5.5°C, minimum winter temperatures, average maximum August temperatures, total precipitation April to June, variability of growing season precipitation and an aridity index. This information was used to create a map of the spatial distribution of climatically suitable habitats as a function of climate norms derived from historic daily weather from 1921. Mountain pine beetle infestation grids, in the form of GIS shape files, were overlaid on climatic layers. In addition, the infestations were regressed against the historic distribution of climatically suitable habitats.

Main Findings
- Areas suitable for mountain pine beetle have expanded dramatically.
- Present mountain pine beetle epidemics correlate very closely to the areas predicted to be suitable by the model.
- Areas previously considered optimal have experienced declines in outbreaks due to reduced host trees and adverse effects on beetle synchrony due to warmer temperatures.
- Eastern expansions into areas where mountain pine beetle have not previously been recorded threaten jack pine forests.

Implications

- This study provides evidence that changes in climate explain the current increase in occurrence of mountain pine beetle into previously unsuitable habitats, regardless of forest stand age.
- In the absence of an extreme cold winter event that, in the past has resulted in the collapse of an outbreak, current outbreak duration and extent may increase.

11. Coop, J.D. & Schoettle, A.W. *In press*. Regeneration of Rocky Mountain bristlecone pine (*Pinus arista*) and limber pine (*Pinus flexilus*) three decades after stand-replacing fire. For Eco Mgmt.

Background & Objectives

This paper examined patterns of limber and bristlecone pine regeneration on three, 29-year old, high severity fires. Specifically, how did the abundance of each species change post-fire and what microsite conditions promote or hinder seedling establishment. Although interesting, results from the bristlecone pine portion of this study are not applicable, as bristlecone pine are a wind-dispersed species.

Main Findings

- Regeneration is very prolonged – 29 years post-fire limber pine densities are lower than nearby unburned stands – beneficial responses may take decades to be achieved.
- Regeneration dynamics were highly variable – depending on burn severity and distance to seed source.
  - Partially burned sites show limber pine population increase.
  - Limber pine populations were reduced in high-severity burns.
- Post-fire relative abundance of limber pine was low.
- Fire increased alternate blister rust hosts – *Ribes* and *Castilleja* species.
- Fire regimes are highly variable
  - On open, rocky sites with no fuels – fire is rare.
  - Mixed stands – fire reduces abundance of other conifers and creates openings.

Implications

- Microsite factors measured: ground cover, canopy cover, sky cover, direct and indirect radiation.
  - Too much canopy shade inhibits seedling establishment, while not enough leads to mortality due to excessive solar radiation & night-time heat-loss.
  - Dense understory plant cover prevents establishment; some cover ameliorates extreme edaphic conditions.
  - Post-fire soil erosion may prohibit establishment.
  - Seedlings exhibited affinity for sites with multiple protective objects - tree trunks, woody debris, cobbles, and boulders.
  - Seedling establishment in interior of severe burns depends on seed source.
- Management options will be limited by availability of seed sources.
- Prescribed fire may encourage regeneration when burns are small, mixed-severity, seed sources are available, and subsequent steps are taken to reduce abundance of other conifer seedlings.
- Seedlings need microsites to survive.
- Burning may promote spread of blister rust through increased *Ribes* abundance.

12. Ellison, A.M. 2005. Loss of a foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment. 3: 479-486.

Background & Objectives

In many forested ecosystems, the architecture and functional ecology of certain tree species define forest structure and their species-specific traits control ecosystem dynamics.

Main Findings

- The loss of foundation tree species changes the local environment on which a variety of other species depend; this disrupts fundamental ecosystem processes, including rates of decomposition, nutrient fluxes, carbon sequestration, and energy flow; and dynamics of associated aquatic ecosystems.

Implications

- Research tools, models, and metrics are needed to identify foundation species.
- We need to 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.

13. Gibson, K., Skov, K., Kegley, S., Jorgensen, C., Smith, S., & Witcosky, J. 2008. Mountain pine beetle impacts in high-elevation five-needle pines: current trends and challenges. USDA Forest Service, Forest Health Protection, R1-08-020.

Background & Objectives

- This paper is a summary of some of the current conditions in whitebark pine, provides some management alternatives, and addresses challenges and unanswered questions.

Main Findings

- Mountain pine beetle have been in whitebark in the late 1920s and early 1930s.
- The current mortality is due to warmer temperatures, longer summer drought periods, decreased host vigor, and favorable beetle survival and development conditions.
- FHP ADS data shows that among the nine western states, 470,000 acres of whitebark pine have been killed by mountain pine beetle since 1998.
- An additional 124,000 acres of limber pine, 50,000 acres of Rocky Mountain bristle cone pine, 450 acres of Great Basin bristlecone pine, and no foxtail pine have been killed.
- Rough estimates conclude that nearly 6 million five-needle pines have killed by the mountain pine beetle in the past 8 to 10 years.

Implications

- This paper illustrates the magnitude of five-needle pine mortality in the Intermountain West.
- Unanswered questions posed by this paper:
  - Elevational variation in MPB life cycles.
  - Assessment of impacts of MPB eruption.
  - Role of fire in high-elevation ecosystems and post-beetle.
  - Influence of widespread whitebark loss on nutcrackers.
  - Use of silvicultural treatments to hasten recovery.
- Potential management alternatives include:
  - Silvicultural techniques that promote age and size class diversity and tree vigor.
  - Prescribed fire may enhance some types of whitebark stands.
  - Blister rust resistance programs
  - Short-term, individual-tree insecticide or pheromone beetle prevention.

14. Hoff, R.J., Hagle, S.K. & Krebill, R.G. 1994. Genetic consequences and research challenges of blister rust in whitebark pine forests. *In* Proc. International Workshop on Subalpine Stone Pines and Their Environment: the Status of My Knowledge, September 5-11, 1992, St. Moritz, Switzerland, USDA Forest Service, Intermountain Research Station, INT-GTR-309. Ogden, UT. 118-126.

Background & Objectives

This report summarizes the progress on studies that assess the level of susceptibility and resistance to blister rust of whitebark pine over its entire range.

Main Findings

- All reports indicate that whitebark pine is the most susceptible to rust of all five-needle pines due to higher susceptibility of first year needles and longer needle retention.
- One mechanism of resistance exhibited by whitebark pine is premature needle shed – needs with rust are shed to avoid further spread.
- For western white pine, 3000 parent trees is considered the minimum number to assure maintenance of resistance against variable races of rust.
- Severe inbreeding in remaining whitebark populations will result in loss of genetic variability, rust resistance, survivability and growth.
- Unknowns include: out planted seed transfer and survivorship and extent of inbreeding occurring in areas with high mortality.

Implications

- We need to know the natural level of rust resistance in remaining whitebark on the landscape.
- We must protect all remaining seed sources – pruning and beetle deterrent.
- Maintenance of natural regeneration function is critical.

15. Harvey, A.E., Byler, J.W., McDonald, G.I, Neuenschwander, L.F., & Tonn, J.R. 2008. Death of an ecosystem: perspectives on western white pine ecosystems of North America at the end of the 20th century. USDA Forest Service, RMRS-GTR-208.

Background & Objectives

This paper summarizes the history of western white pine ecosystems – their function, characteristics, and loss. Most importantly this paper provides invaluable perspectives and insights from the loss of this species that apply directly to the current situation with other five-needle pines.

Main Findings

- Increase rust resistance and artificial regeneration efforts.
- Promote natural regeneration by maintaining as much as possible of the surviving whitebark in current forests.
- Develop broader understanding of rust ecology and adaptation to varying environments and potential resistance.
- Expand the genetic base for rust resistant stock
- Emphasize coordinated efforts.
- Aggressive planting helps maintain/extend genetic base for future.

Implications

- Identify and protect more plus trees and those that have some level of rust resistance.
- Support research that improves scientific understanding of rust.
- Support rust resistance screening.
- Initiate breeding program?
- Protect all remaining seed sources.

16. Izlar, D.K. 2007. Assessment of whitebark pine seedling survival for Rocky Mountain plantings. M.S. Thesis. University of Montana.

Background & Objectives

This research investigated the survival rates and factors for planted whitebark pine seedlings on thirty-six planting sites throughout the GYE. This thesis work also provides a summary of whitebark pine planting activities in Idaho, Montana & Wyoming.

Main Findings

- History of plantings: 120 whitebark planting sites in Idaho, Montana & Wyoming & 211,000 whitebark planted from 1995-2005.
- Among sites, and 114, 677 seedlings, overall mean seedling survival was 42%; first-year survival was 78%; for years 3-15 the range of survival was 10% to 81%, with a mean of 38%.
- Direct solar radiation decreased survival rates; survival is greater on north-facing slopes.
- Seedling survival with a microsite was significantly greater (89% vs. 11%); logs and rocks within 40 cm upslope or to the side of a seedling support highest survival and growth rates.
- Well-drained soils, intact whitebark habitat, and sites with steeper slopes had higher seedling survival.
- No differences observed among burn severity, but the sample size may have been too small.
- Mycorrhizal colonization did not appear to impact survival, but may have affected growth of survivors.

Implications

- Seedlings need microsites.
- Do not plant in saturated soils.
- Do not plant on flat ground.

17. Jorgensen, S.M. & Hamrick, J.L. 1997. Biogeography and population genetics of whitebark pine, Pinus albicaulis. Can. J. For. Res. 27(10): 1574-1585.

Background & Objectives

Levels of genetic variation were estimated within and between 30 populations of Pinus albicaulis sampled from across the species range in the mountains of western North America.

Main Findings

- The genetic diversity maintained in the species (He=0.102) and within populations (He=0.092) was low relative to other pine species.
- Few differences in allele frequencies were seen among hierarchical groupings of the populations by mountain ranges and regions

Implications

- Management strategies must seek to maintain genetic diversity.

18. Klutsch, J.G., Goodrich, B.A., Jacobi, W.R. 2008. Assessment of whitebark pine regeneration in burned areas of the Shoshone and Bridger-Teton National Forests and Wind River Reservation, Wyoming. Final report, USDA, Forest Health Protection.

Background & Objectives

The purpose of this study was to quantify the amount of regeneration in burned and unburned stands, and to determine the site factors that influence regeneration. This study was performed in the GYE with E. Davy, E. Jungck & E. Rhodenbaugh as cooperators.

Main Findings

- Loss of mature, cone-bearing whitebark will impact future regeneration.
- Greater than 25% of the sampled (burned & unburned) stands did not have whitebark regeneration.
- Whitebark pine regeneration abundance was significantly lower in burned stands than unburned.
- On burned sites regeneration was positively correlated to nearness and basal area of seed source, shrub cover, years since fire and lodgepole density.
- Although regeneration density was lower, whitebark seedlings grew more rapidly on burned sites.

Implications

- Among burned sites cool, wet, north-facing slopes exhibit the greatest density of whitebark regeneration.
- Microsite conditions directly affect regeneration.
- The current loss of seed source/mature trees to mpb will hinder natural establishment of whitebark in recently burned areas.
- Planting, coupled with reduction of competing grasses, is recommended.

19. Krakowski, J., Aitken, S.N., & El-Kassaby, Y.A. 2003. Inbreeding and conservation genetics in whitebark pine. Cons. Gen. 4: 581-593.

Background & Objectives

The objective of this paper was to quantify genetic variation and the mating system of whitebark pine in its northern range to provide a basis for effective conservation measures.

Main Findings

- Avian seed distribution by the nutcracker appears to be the overriding factor influencing genetic patterns

Implications

- Encourage regeneration success and nutcracker caching.
- Since whitebark pine can only expand their range through seed dispersal and have a very long generation time - *in situ* adaptation to climate change is a critical component of any conservation strategy. Targeting genetically diverse and unique populations is the most efficient use of resources.
- Rust-resistant individuals, as opposed to populations, must be targeted for seed collection and subsequent propagation and planting in high-risk areas – high mortality and little or no natural regeneration.
- A key goal of whitebark pine conservation should be to capture a sufficient percentage of disease resistance genes or genotypes.

20. 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.

Background & Objectives

This research investigates the role of fire in whitebark forests – the fire frequency, severity, and seasonality and the relationship between fire, climate, and tree establishment and growth. Study includes a comprehensive literature review and results from data collected on the Lolo National Forest in ABLA habitat types.

Main Findings

- Fire regime research has evolved over time – losses of trees to fire and decay used in dendrochronological reconstruction may have underestimated return intervals.
- Fire-scar data alone is insufficient in characterizing fire regimes – in corporation of age-structure data, cross-dating and synoptic weather patterns is needed.
- Fire suppression has not influenced high-elevation whitebark ecosystems – mean fire return intervals >350 years.
- Widespread fire activity recorded *ca* AD 1800-1850.
- Fire suppression has decreased frequency of fire at some lower elevation sites.
- Some whitebark stand experiences frequent, low-intensity fires but were established following infrequent, stand replacing events.
- Forest structure indicates pulses of establishment corresponding to widespread disturbance.
- Subalpine fir was established on mixed conifer sites at stand establishment, not as result of fire suppression.
- Succession is driven by climate and related to the time since last large fire.

Implications

- Northern Rockies experience highly variable, mixed-severity fire regimes – sources of change/variation not easy to ascertain.
- Fire suppression has had a limited effect on some whitebark forests; however a blanket approach toward restoration of fire to the ecosystem is inappropriate.
- Overall – site-specific approach to use of fire management is recommended – local climate, topography, cover, and moisture availability drive site regime.
- Restore ecosystem processes and promote resilience, do not focus on historic range of variability of forest structure.

21. Logan, J.A., & Powell, J.A. 2005. Ecological consequences of climate change altered forest insect disturbance regimes. *In* F.H. Wagner (ed.) Climate change in western North America: evidence and environment effects. Allen Press.

Background & Objectives

The objectives of this paper were to describe the application of a mathematical model used to predict mountain pine beetle response to temperature and climate to three ongoing beetle outbreaks.

The mathematical framework for evaluation of adaptive seasonality was able to capture the temperature dependence of the mountain pine beetle, in particular their lack of a physiological timing mechanism for development. This insect phenology model includes a sequence of developmental stages, in which the duration of each is controlled by temperature.

Main Findings

- Mountain pine beetle outbreaks have intensified within their historic distribution, shifted their populations northward, and invaded easterly into jackpine forests.
- Mountain pine beetle population dynamics change immediately in response to changes in climate, making them valuable indicator species for climate change.
- Warming climate has shifted some thermally marginal habitats into those that are thermally suitable to the mountain pine beetle, specifically high elevation whitebark pine habitats.

Implications

- Currently mountain pine beetle outbreaks are occurring with greater intensity, in locations where they have not previously been recorded, and for greater durations than those previously experienced.
- Whitebark pine ecosystems are highly susceptible to mountain pine beetle outbreaks.
- Outbreaks occurring in novel habitats have potentially devastating ecological consequences.

22. Logan, J.A., Regniere, J. & Powell, J.A. 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and Environment, 1(3): 130-137.

Background & Objectives

This review paper summarized the state of knowledge, data, and modeled predictions of forest pest dynamics in relation to climate change to illustrate the current and future impacts of climate change on forest resources. In addition, this paper promotes cooperation among researchers and managers to pool their current software tools, databases and models to monitor, evaluate and manage events.

Main Findings

- Overall, the majority of assessments of pest species response to climate change indicate increased outbreak severity.
- Insects will shift their distributions and increase outbreak intensity.
- Models provide a way to evaluate future events.
- Current high-resolution databases used to build models are improving and becoming more accessible.

Implications

- This study provides evidence that forest pests are valuable indicators for assessing climate change.
- Models currently available provide the building blocks for systematic assessments.

23. Logan, J.A. & Powell, J.A. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist. 47(3):160-172.

Background & Objectives

Although the five-needle pines found at higher elevations are suitable hosts for the mountain pine beetle, high-elevation habitats are most often too harsh for mountain pine beetle populations to flourish. Such habitats lack sufficient thermal input for the mountain pine beetle to complete its life cycle in one season. Univoltinism appears to be basic to maintaining an appropriate seasonality for this beetle and, therefore, population success.

This paper addresses the question through consideration of beetle thermal ecology: will climate change improve the success of the mountain pine beetle in high-elevation systems?

Main Findings

- A warming of average annual temperature of a little over 2ºC resulted in shifting a semivoltine population to a synchronous univoltine population.
- The thermal environment in whitebark pine is shifted from hostile to benign for the mountain pine beetle and the net result is that the in-place plant community is subjected to influences, such as mountain pine beetle, that are foreign to the co-evolved dynamics of the system.
- The model presented in this paper (accurately, as we now know) predicted increasing temperatures resulting in a dramatic invasion of mountain pine beetle population in whitebark pine.

Implications

- Restoration efforts must incorporate beetle susceptibility information so that rust resistant/restored sites are not impacted by future beetle activity.

24. Lorenz, T.J., Aubry, C., & Shoal, R. 2008. A review of the literature on seed fate in whitebark pine and the life history traits of Clark's nutcracker and pine squirrels. PNW-GTR-742. USDA Forest Service, Pacific Northwest Research Station.

Background & Objectives

This paper provides a review of the current literature relating to seed fate in whitebark pine, including the seed harvest, caching, and retrieval behaviors of the vertebrates that are known to directly influence the fate of whitebark pine seeds and the life history traits of the species that harvest most whitebark pine seeds –nutcracker and pine squirrels.

Main Findings

- Seed fate has a profound effect on population dynamics
- The number of seeds effectively dispersed depends on: the number of seeds produced within a population of whitebark pine, the size and mobility of populations of dispersers, and the availability of alternate foods for such dispersers.
- Most seeds are cached within 100 meters of the tree from which they are collected.
- Nutcrackers are attracted to closed canopy forests, steep slopes, needle litter, rocks/boulders, and tree trunks.
- The predation of whitebark pine cones by pine squirrels affects the dispersal probabilities of whitebark pine seed. In regions facing strong selective pressure from pine squirrels, nutcrackers disperse fewer seeds compared to regions where pine squirrels are absent.
- Pine squirrels are able to exert selection pressures on whitebark pine that are arguably as strong as the selective pressures exerted by the nutcracker. The influence of squirrels should not be underestimated.
- Pine squirrels are more common and abundant in mid-elevation, mixed-conifer stands.
- In years of moderate or high cone production, most nutcrackers appear to be high-elevation residents or short-distance altitudinal migrants. Widespread and simultaneous failures in cone crops can cause population migration to areas outside their usual range.
- Results from the Breeding Bird Survey show a slight overall increase in nutcracker across its range since 1966. In the past 20 years, counts in the Rocky Mountains and Great Basin have recorded fairly stable or slight increases in numbers. Conversely, counts have recorded consistent declines in the Cascades and Sierra Nevada.

Implications

- Because nutcrackers cache within close proximity to seed source, retention of cone-bearing trees is critical.
- As seed abundance decreases, the proportion of seed lost to squirrel predation become more significant.
- High elevation sites, with less squirrel seed predation, may provide greater natural regeneration success
- Not all whitebark pine trees are equally likely to have their seeds dispersed in a manner that will enable germination. Trees in pure stands and isolated trees in open areas will have the greatest proportion of their seeds harvested by nutcrackers and fewer of their seeds will be lost to pine squirrel predation.
- Conversely, whitebark pine in mixed stands would have a greater proportion of their cones harvested by pine squirrels, and the likelihood of regeneration for such individuals is lower.
- Whitebark pine regeneration is also influenced by temporal changes in nutcracker and rodent populations.

25. Mahalovich, M.F., Burr, K.E., & Foushee, D.L. 2006. Whitebark pine germination, rust resistance, and cold hardiness among seed sources in the Inland Northwest: planting strategies for restoration. USDA Forest Service Proceedings, RMRS-P-43.

Background & Objectives

- Whitebark has the highest susceptibility to blister rust of any five-needle pine.
- The tree improvement program is two-pronged: first, families exhibiting rust resistance are selected after inoculation and then individuals within superior families are selected for additional rust resistance, cold hardiness and height performance.
- This paper presents the results of mid-winter cold hardiness testing at the Coeur d'Alene nursery.
- Rust resistant and cold hardy seed sources have been identified for six seeds zones, including GYGT.

Main Findings

- Whitebark is hardy and drought tolerant, but seedlings/germinants are highly susceptible to frost pockets & cold swales.
- Addressing cold hardiness is equally crucial as rust resistance in restoration efforts.
- Overall rust resistance after the fourth screening was 48%.
- Resistance is moderately heritable (0.56); survival (0.64); and height (0.85).
- No physiological tradeoff between allocating resources for rust resistance at the expense of growth.
- Taller seedlings have slightly greater rust resistance and lower cold hardiness.

Implications

- This paper contains a table with the rust resistance, cold hardiness, and 6-yr height rank for all plus trees in the program for the GYGT seed zone!
- Although rust resistant, survival and height are heritable traits there is currently no breeding program for whitebark pine; there is only a rust resistance screening and seed orchard program.
- Further testing is occurring to determine if mid-winter, late summer/early fall, or of late winter/early spring cold hardiness is the most critical.
- Planting recommendations:
  - Choose rust resistant sources within proper seed zone.
  - Ensure cone collections have a minimum 20 trees separated by 67 meters to reduce inbreeding.
  - Within a seed zone there are no elevation restrictions on seed transfer.
  - Do not plant seeds collected from areas with low rust infection in areas with high rust infection.
  - Collect cones from top three resistant sources from each seed zone.
  - Within 10 years collect from three new areas to broaden genetic base for outplantings.
  - Avoid swales and cold pockets for planting.
  - Seedlings need shade and moisture during early establishment: plant near microsite – stump, log, rocks, roots.

26. Mahalovich, M.F & Dickerson, G.A. 2004. Whitebark Pine genetic restoration program for the Intermountain West (United States). *In* Sniezko, R.A., Salmon, S. Schlarbaum, S. & Kriebel, H.B. (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, CO. RMRS-P-32: 181-187.

Background & Objectives

This paper provides a summary of the strategy to restore whitebark communities through the tree improvement program.

Main Findings

- Rust resistance testing also includes early growth and survival testing.
- Western white pine restoration that incorporated only thinning or prescribed fire has led to increased blister rust infection levels by opening up stands and encouraging *Ribes* establishment.
- Successful natural regeneration is dependent upon sufficient blister rust resistant seed available on site.
- An effective restoration strategy depends on genetic variation.
- Assignments of approximately 100 plus-trees within seed zones facilitates broad sampling among National Forests and Parks, emphasizing broadly adaptable populations for blister rust resistance development and isolated populations supporting unique gene frequencies or adapted gene complexes for gene conservation.
- 650 total plus- trees is very small sample, compared to 3100 minimum for western white pine.

Implications

- When blister rust infection levels vary within a zone, seeds collected for immediate rehabilitation efforts should not be moved from areas with low (less than 49 %) to moderate (50 to 70 %) infection levels to planting sites with higher infection levels (>70%).
- Seeds collected from phenotypically resistant trees in areas with high infection levels are suitable for planting on sites with low, moderate or high infection levels
- Operational cone collections should be from no fewer than 20 individuals separated by 67 meters within a zone to ensure a broad genetic base in the seed lot.

27. McDonald, G.I., Zambino, P.J. & Sniezko, R. 2004. Breeding and rust-resistant five-needle pines in the western United States: lessons from the past and a look to the future. *In* Sniezko, R.A., Samman, S., Schlarbaum, S.E., & Kriebel, H.B. (eds) Breeding and genetic resources of five-needle pines: growth, adaptability, and pest resistance. Proc RMRS-P-32, USDA Forest Service, Rocky Mountain Research Station. Fort Collins, CO p 124-135.

Background & Objectives

This paper describes rust-resistance breeding programs, their effectiveness, and provides information about the challenges facing rust-resistant outplantings.

Main Findings

- There are distinct genetic differences between southern and northern whitebark populations resulting in variable susceptibility to blister rust.
- Variation in aeciospore source results in variable rates of rust incidence (needle lesions)
- Ontogenesis and maturity of seedlings strongly influences rust incidence; testing two-year old seedlings may over estimate rust resistance.
- Some trees exhibit induced defenses to rust.
- Successful breeding and deployment of rust-resistant requires significant understanding of epidemic function across time and space: what is the relative importance of local inoculum?
- We don't know the degree of phenotypic plasticity or the possible range of genetic expression of resistance across environmental gradients (elevation, light, nutrients, temperature).

Implications

- Rust resistant tree stock may not have equal survival due to variability in rust virulence, environmental influences acting on genetic expression of resistance in tree, and age of seedlings at outplanting.
- Site qualities and edaphic conditions play a significant role in outplanted seedling survival.

28. McKinney, S.T. 2007. Ecological processes and the blister rust epidemic: cone production, cone predation, and seed dispersal in whitebark pine (*Pinus albicaulis*). PhD Dissertation. University of Montana.

Background & Objectives

This extensive work addresses the impact of whitebark pine's decline on species interactions and ecological processes within subalpine forests including: the affect of whitebark decline on the relationship between whitebark pine and the Clark's Nutcracker; habitat use of whitebark pine forests by red squirrels; and tree-level ecological process - predispersal cone survival, as a function of coarse scale whitebark pine abundance. This research was conducted in three ecosystems in the Rocky Mountains – the Northern Divide in northwest Montana; the Bitterroot Mountains in central Idaho; and the Greater Yellowstone.

Main Findings

- Nutcracker occurrence and probability of seed dispersal were strongly related to whitebark pine cone
- production, which was positively correlated with live whitebark pine basal area, and negatively correlated with tree mortality and rust infection.
- A threshold level of ≈ 1,000 cones ha-1 is needed to ensure seed dispersal by nutcrackers, and that this level of cone production can be met by forests with average whitebark pine basal area > 5.0 m2/ha.
- When cone production declines from 700 to 300 cones/ha he estimated frequency of nutcracker occurrence declines from 0.4 to 0.12 and probability of seed dispersal from 0.7 to 0.3.
- The risk of mutualism disruption is greatest in the Northern Rocky Mountains, where three-year mean cone production and basal area are below these threshold levels, and nutcracker occurrence, seed dispersal, and whitebark pine regeneration were the lowest of the three ecosystems.
- The original frequency of rust-resistant alleles was estimated to be only 1-5%.
- Blister rust is acting as a selective force by causing differential survival among whitebark pine trees in rust-infected forests.
- Surviving whitebark pine trees from high-mortality stands possess higher levels of heritable resistance than trees from low-mortality stands and > 40 % of the progeny of high-mortality survivors display resistance to blister rust (Hoff et al. 2001).
- Squirrels can greatly diminish cone crops where there is severe whitebark damage and mortality, thus leaving few seeds available for nutcracker seed dispersal.
- Whitebark abundance was higher, mortality and rust infection lower in the Greater Yellowstone compared to the Northern Divide Ecosystem.

Implications

- Protect/conserve remaining mature, cone-bearing trees on landscape level.
- Priority conservation strategy is to increase frequency of genetic resistance to the blister rust pathogen within populations is the most promising management strategy for conserving whitebark pine by planting seedlings grown from stock with known genetic resistance.

- Because restoration planting is costly, spatially restricted, and uncertain in outcome, the natural regeneration approach should be implemented wherever feasible.
- In the Northern Rocky Mountains management must move beyond returning historical fire regimes and waiting for natural regeneration.
- The tools employed, however, would be dependent upon the forest type.
  - Some mixed species stand types may benefit from: allowing wildland fires to burn, applying silvicultural cutting and prescribed burning to remove fir and spruce. Planting rust-resistant seedlings following treatment may be critical.
  - Stands dominated by whitebark must be protected as seed sources for natural regeneration by nutcrackers.

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

Background & Objectives

This is the publication is a portion of the above doctoral work.

Main Findings

- Areas with higher rust infection have higher rates of seed predation relative to cone abundance, lower predispersal seed survival, and fewer observations of nutcracker seed dispersal.
- As blister rust damage increases, likelihood of nutcracker dispersal decreases.
- Increasing frequency of genetic rust resistance within remaining population is most promising management strategy.

Implications

- Whitebark regeneration in heavily rust infected areas may not occur without planting.

30. Mohatt, K.R., Cripps, C.L., & Lavin, M. 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. 86:14-25.

Background & Objectives

This study addresses the need to discover the ectomycorrhizal (ECM) fungi critical to whitebark pine. This study was conducted across five mountain ranges in the northern GYE.

Main Findings

- 32 ECM species of fungi were identified in whitebark stands.
- The low number of ECM is consistent with other pines in harsh habitats.
- Whitebark associate with specialist and generalist fungi; currently the implications of this are unknown.
- A potential disadvantage to hosting specialist fungi is that they may not be available under some conditions; an advantage may be that these species may not be shared by competing conifer species.

Implications

- The influence of mycorrhizal associations varies by the successional role played by whitebark: pioneering versus seral in mixed conifer stands.
- The availability of ECM pine associates may influence competition dynamics among recruiting conifer species.

31. Moody, R.J. 2006. Post-fire regeneration and survival of whitebark pine (*Pinus albicaulis*). M.S. Thesis. University of British Columbia.

Background & Objectives

The recruitment trends of whitebark were investigated in 18 recently burned stands in the Canadian Rockies and the North Cascades. Recruitment in recently burned and control stands was compared with ecological and seed source variables. Along a chronosequence, whitebark pine recruitment was compared with precipitation and with Pacific Decadal Oscillation (PDO).

Main Findings

- Recruitment episodes are more limited by seed availability or growing season length than by moisture conditions or availability of suitable seedbeds.
- Distance to and size of seed source were important predictors of whitebark pine recruitment;
- During years of recruitment, whitebark pine regeneration densities were lower on warm steep rocky sites and high on cooler aspects.
- Recruitment correlated to periods of higher precipitation. However, periods of high precipitation occurred more frequently than did episodes of high recruitment, indicating that seed availability may be more limiting than suitable moisture conditions
- Most stands were composed of mixed conifers, but only lodgepole pine appeared to limit the growth of whitebark.
- Whitebark recruitment was slow and episodic on all stands, and recruitment years were correlated among many stands separated by large distances.

- Episodic recruitment may be due to more than cone masting as recruitment in several stands was also correlated with growing season precipitation and positive Pacific Decadal Oscillation values, which may increase the length of growing season.
- The percentage of whitebark pine trees infected by white pine blister rust on a site increased with time since fire and rust infection most common on older seedlings.
- Whitebark pine may take decades to reproduce and recruitment to pre-fire densities may take equally as long.
- Dispersal of seed to burned stands greater than 1 km from seed sources was found to be unlikely, resulting in formerly forested stands converting to meadows.
- Fire is not always required for recruitment, although burning may increase whitebark pine recruitment on some sites.
- Fires that remove competition from mesic-submesic stands may promote recruitment of whitebark

Implications

- It is unclear whether the increased recruitment in some burned stands outweighs the foregone reproductive output lost to seed trees killed by fire, as seeds may be dispersed out of mature closed canopy stands to nearby open areas.
- All prescribed fires and wildfires should address retention of whitebark pine seed trees on site; maintaining seed sources within the burn would greatly improve the likelihood of whitebark pine recruitment in the area.
- The potential loss of large seed sources destroyed by fire, increasing the distance to seed for most stands, may prevent these fires from promoting whitebark pine regeneration. The greatest utility of these fires may be the preparation of suitable seedbeds for restorative planting. Future fire suppression activities should attempt to leave a landscape which mimics mixed severity burns, resulting in a landscape characterized by competition free burned areas in close proximity to seed sources. Therefore, it is suggested that some suppression activity be applied to subalpine forests containing whitebark pine, despite the fact that many of these sites border on alpine environments.
- Stands containing a high percentage of whitebark pine may be more valuable as a seed source for other stands than as a site for the application of prescribed fire. Given that whitebark may expand its distribution into competition free stands, managers should consider burning directly below or adjacent to existing stands of whitebark.
- Whitebark pine in open canopied stands often displayed a self replacing potential and such stands should not be considered for prescribed burning.
- All recently burned stands in this study would benefit from increased stocking of whitebark by planting
- On stands with individuals phenotypically resistant to blister rust, fire should be limited or suppressed until cones can be collected.
- Seed collection and direct sowing program may be the most restore effective restoration strategy: Seeds may be accumulated over time and planted during years with early snow melt; selecting seeds can be selected from phenotypically rust resistant trees, possibly expediting the rate at which rust resistant trees are established across the landscape.
- The areas available for planting treatment are vast. Recent wildfires have created an array of suitable treatment sites.

32. Newcomb, M. 2003. White pine blister rust, whitebark pine, and Ribes species in the Greater Yellowstone Area. M.S. Thesis. University of Montana.

Background & Objectives

This study was aimed at detecting and describing spatial patterns, or associations, of white pine blister rust disease severity in whitebark pine hosts and landscape features related to the ecology of the *Ribes* host species. This paper also characterizes the ecology of *Ribes* hosts in the GYA and initiates the development of a more comprehensive approach to the white pine blister rust pathosystem.

Main Findings

- Distances to 5th order streams and nearest streams at or below 2621 meters are related to rust severity.
- Sites with extended forest cover greater than 65% were associated with low estimated disease severities.
- Supports a link between relative blister rust severities in whitebark and distances to expected habitat for susceptible *Ribes* species.
- Nine *Ribes* taxa are known to occur in the GYA: each *Ribes* species is a unique host group that exhibits a distinct spatial association with the pine hosts and a distinct genotypic and phenotypic susceptibility to infection by *Cronartium ribicola*.

Implications

- The significant relationships between disease severity and distances to landscape features found in this study show that a spatial pattern of disease severity exists; implying that predictive abilities related to disease progression in this system may be possible.

- A biologically meaningful interpretation of the autocorrelation between the two variables is that sites that are distant from 5th order streams (such as the major river valleys of the Yellowstone and Snake rivers) tend to be more within the interior of mountain ranges and also tend to be distant from streams at elevations below 2621 meters. These tend to be sites at high-elevations.
- It is critical to consider the role of *Ribes* in disease intensification at a species-level taxonomic resolution.
- The significant relationships found among topographic features, *Ribes* species, and rust severity suggest that predictive abilities related to disease progression in this system are possible.

33. Owens, J.N., Kittirat, T. & Mahalovich, M.F. 2008. Whitebark pine (*Pinus albicaulis* Engelm.) seed production in natural stands. Forest Ecology and Management 255: 803-809.

Background & Objectives

The purpose of this study was to do cone and seed analyses to determine the seed potential of whitebark pine cones collected from two natural stands.

Main Findings

- The seed efficiency per cone, or filled and likely viable, was 70%.
- This is high-seed efficiency and filled seeds per cone for a high-elevation conifer species and indicates that whitebark pine was a good seed producer in these two natural stands in 2004.
- Whitebark pine could be a good seed producer in lower elevation seed orchards if good cone production can be obtained, pollen production and pollination are satisfactory and insect and disease problems are controlled.

Implications

- At least 10 filled seeds per half cut-face should be sought before expending resources to collect cones from whitebark pine.

34. Parker, T.J., Clancy, K.M., & Mathiasen, R.L. 2006. Interactions among fire, insects, and pathogens in coniferous forests of the interior western United States and Canada. Agricultural and Forest Entomology, 8: 167-189.

Background & Objectives

This paper reviews literature on the relationships among fire, insects and disease. The propensity for bark beetles to attack fire-damaged trees has led to an emerging concern about how the amount and distribution of bark beetle-caused tree mortality will be affected by large-scale restoration of fire-adapted forest ecosystems in the Interior West via prescribed fire.

Main Findings

- Prescribed fire is a necessary tool, but it is also crucial to understand the effects it has on secondary mortality agents such as bark beetles.
- Tree weakened by pathogens may also suffer greater morality during fire than uninfected trees.

Implications

- Detailed knowledge of the potential effects of prescribed fire on insect and pathogen communities is critical.
- The effects of prescribed burns on insect and pathogen communities must also be monitored to ensure that land management objectives are met.

**35. Perkins, J.L. 2004. *Pinus albicaulis* seedling regeneration after fire. PhD Thesis. University of Montana. Missoula, Montana, USA. *****Currently working on getting this entire work through interlibrary loan – should be here soon. This information is from the abstract.*

- In some stands fire is not a necessity for seedling recruitment.
- Seedling density may not always increase following fire
- Greater seedling growth rates are observed in burned stands due to an increase in NO_3^- and a potential increase in available phosphorus following fire.

36. Powell J.A., Jenkins, J.L., Logan J.A. & Bentz B.J. 2000. Seasonal temperatures alone can synchronize life cycles. B Math Biol. 62: 977–98.

Background & Objectives

This paper utilizes existing models to illustrate the effects of yearly temperature variation on the development and seasonal occurrence of poikilotherms. These models are based on mathematical developmental rate equations based on insect life history traits and environmental temperature, the integration of multiple equations for each life stage to predict cycles and synchrony, and then the application of these equations to the mountain pine beetle.

Main Findings

- Synchrony of mountain pine beetle emergence occurs in part due to a lack of the diapause physiological mechanism.
- Insect seasonality is under direct temperature control when: 1) there is sufficient thermal energy for development of each life stage in a single season; and 2) at least one of the developmental thresholds is significantly greater than the mean threshold.
- Seasonal temperature variation, in combination with life stage developmental thresholds, can synchronize the seasonality of a poikilotherm, specifically the mountain pine beetle.

Implications

- We will likely continue to see shifts in beetle phenology that may result in multiple emergence events per season, increased productivity and continued movement upward in altitude and latitude.

37. Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G, & Romme, W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. BioScience. 58(6): 501-517.

Background & Objectives

This paper illustrates how landscape patterns are linked to processes, specifically the mechanisms that contribute to and constrain bark beetle eruptions. The authors seek to provide an understanding of conifer-bark beetle interactions to improve the success of management in these systems.

Main Findings

- The extent and severity of the current beetle outbreak will change biogeophysical processes such as nutrient cycling, water dynamics, vegetation patterns, etc.
- Mass attack success depends on beetle population density, weather, and physiological stress of host tree.
- Homogeneous forest age and structure facilitate beetle coalescence and spread.
- Bark beetle population eruptions are the result of complex and multivariate interactions on multiple scales.

Implications

- Because of inherent interactions, stand-level approaches may not be effective.
- Stand-level management may prevent stand-level eruptions, but once landscape-level thresholds have been breached no management strategy can stop an eruption.
- Broad-scale management that reduces the extent of susceptible hosts and social action to address climate change could reduce the likelihood of future biome-wide beetle outbreaks.

38. Rasmussen, L.A., Amman, G.D., Vandygriff, J.C., Oakes, R.D., Munson, S.A. &Gibson, K.E. 1996. Bark beetle and wood borer infestation in the Greater Yellowstone area during four post-fire years. USDA Forest Service. Intermountain Research Station, INT-RP-487.

Background & Objectives

This study aimed to determine the relationship between fire damage and insect infestation following the 1988 fires.

Main Findings

- Most insect-caused mortality of whitebark pine was due to *Dendroctonus ponderosae* and *Ips pini*.
- Delayed mortality attributed to fire injury accounted for more mortality than insects.
- Both types of mortality greatly altered the original fire-killed/green tree mosaics that were apparent immediately after the fires.
- Insect infestation was strongly and positively correlated with the percentage of basal circumference of the tree killed by fire for all species

Implications

- The high level of infestation suggests that insect populations built up in fire damaged trees and then spread to adjacent trees.

39. Resler, L.M. & Tomback, D.F. 2008. Blister rust prevalence in krummholz whitebark pine: implications for treeline dynamics, Northern Rocky Mountains, Montana, USA. Arctic, Antarctic, Alpine Res. 40(1): 161-170.

Background & Objectives

The prevalence of blister rust and its impact on treeline dynamics remain to be determined. This study examines the potential importance of whitebark in tree island dynamic, documents the presence of rust in whitebark in the alpine community, and characterizes the incidence and intensity of blister rust in krummholz. Study sites were located in Glacier National Park.

Main Findings

- Whitebark is the primary colonizer of tree islands – therefore impacts vegetation patterns at treeline.
- Thirty percent of all sampled krummholz whitebark were infected with rust.
- Cankers were found on both isolated trees and those associated with tree islands.

Implications

- Whitebark's role as a treeline facilitator will diminish as rust increases – patterns of tree islands will change and the associated impacts to microclimate for other plant species.
- Although climate change may promote the upward movement of treeline, the intensification of blister rust may inhibit this response.
- The loss of whitebark on high elevation sites will impact avalanche activity and local hydrology.
- Managers should consider planting rust resistant whitebark at treeline.

40. Schoettle, A.W. & Sniezko, R.A. 2007. Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. Can. J. For. Res. 12: 327-336.

Background & Objectives

Current restoration strategies often focus on severely impacted areas, however because blister rust elimination is impossible management objectives must seek to increase the frequency of rust resistance in the remaining five-needle pine populations. This paper reviews proactive management options that promote the maintenance of the greatest absolute number of individual trees available for selection.

Main Findings

- The facilitation of genetic rust resistance means concurrent efforts to manage impacted and threatened areas to position the ecosystem for greater resilience.
- The success of these strategies depends on the size of the original population, the frequency of genetic resistance, the type of resistance mechanisms, and the amount of natural regeneration.
- The proportion of rust resistant individuals is much greater in younger cohorts because the cone-bearing trees have sustained selective pressure. Selection for rust resistance on these cohorts occurs more rapidly than on older cohorts.
- Capitalization on indigenous rust resistance is critical in the maintenance of functional genetic reservoirs.

Implications

- Although restoration efforts in areas with high levels of rust infection, canopy mortality, and low regeneration rates are important, it is also critical to proactively protect stands and individual trees that provide a source of seed, genetic variability, and a diversity of age cohorts.
- Early intervention to accelerate the selection for rust resistant individuals.
  - Programs in place currently:
  - Estimations of the frequency of rust resistance in limber and bristlecone populations
  - Studies investigating geographic distribution of adaptive traits.
  - Silvicultural treatments to stimulate regeneration are being implemented and tested for success.
  - Seed collections are occurring to archive genetic diversity and prepare for artificial regeneration projects.
  - Planting resistant stock prior to the loss of overstory.
  - Location of resistant individual trees.
- The authors suggest that the following management options are likely to be most successful:
  - improving tree vigor and promoting regeneration by removal of competing vegetation
  - removal of ladder fuels to prevent loss of mature trees to fire
  - protection of trees from mountain pine beetle
  - out planting resistant tree stock
  - identification and protection of seed trees with resistance traits (both those identified through rust screening and those remaining in areas of heavy rust infection)
  - proper seed zone transfer to eliminate seedling loss to fall cold injury.

41. Schwandt, J.W. 2006. Whitebark pine in peril: a case for restoration. USDA Forest Service, Forest Health Protection. R1-06-28.

Background & Objectives

- This paper provides a range-wide overview of the perilous situation of whitebark pine, describes some the of possible restoration strategies and describes information needs and challenges to restoration.

Main Findings

- Whitebark pine are in peril.
- Challenges to restoration include the loss of whitebark pine as seed sources, slow growing nature of the species, remote location of most of the remaining trees, and the limitations of blister rust resistant outplantings.
- Information needs:
  - What is the frequency and genetic basis for rust resistance?
  - How can we accelerate growing (grafting, improve germination rates)?
  - Understanding of the variation in rust infection levels to help predict potential infection rates.
  - What is the best use of fire? How can we use it safely?
  - What is the role of nutcrackers in declining stands?
  - How rapidly will whitebark continue to decline?

Implications

- The following conservation strategies can be employed:
  - Range-wide assessment of current conditions – surveys and permanent plots.
  - Conservation of genetic diversity – archive seed and pollen.
  - Harness natural resistance to rust – proactive strategy to identify and protect the trees remaining on the landscape that exhibit rust resistance, in addition to outplanting resistant stock.
  - Reduce competing vegetation – cut existing vegetation where mature whitebark remain.
  - Burning areas where whitebark pine is absent, but there is a seed source very nearby.
  - Promote natural regeneration
  - Prevent bark beetle loss – verbenone.

42. Six, D. & Adams, J. 2007. White pine blister rust severity and selection of individual whitebark pine by the mountain pine beetle (Coleoptera: Curculionidae, Scloytinae). J. Entomol.Sci. 43(3): 345-353.

Background & Objectives

This study investigated the relationship among rust severity, tree diameter, bark and phloem thickness, sapwood moisture in relation to mountain pine beetle preference for whitebark pine. This study was conducted at 5 sites in Montana and Idaho.

Main Findings

- Tree exhibiting greater blister rust severity were more likely to be attacked.
- Selection of individual whitebark by mountain pine beetle may be influenced by blister rust severity
- Sapwood moisture was lower in trees with greater blister rust severity and on sites with greater beetle activity.

Implications

- Drought stress may interact with blister rust to affect beetle preference.
- As blister rust spreads across the western US, beetle-caused mortality may increase.

43. Smith, C.M., Wilson, B., Rasheed, S., Walker. R.C., Carolin, T. & Shepard, B. 2008. Whitebark pine and white pine blister rust in the Rocky Mountains of Canada and northern Montana. Can. J. For. Res. 38: 982-995.

Background & Objectives

Data on the decline of whitebark is critical to designing and implementing restoration. This project sought to determine if tree mortality and rust infection depend on geographic location. In addition they determine change in mortality and infection rates over time.

Main Findings

- Higher mortality and blister rust infection rates in southern distribution of whitebark and on the west side of the continental divide. The authors attribute this to climate suitability for rust spread.
- Taller seedlings had greater rust infection rates, due to increased exposure time and needle surface area.
- They calculated a 5%/year increase in mortality and 3%/year in rust infection.

Implications

- The authors suggest that managers focus their restoration efforts on areas with high levels of rust infection, canopy mortality and low regeneration rates.
- Trees remaining on the landscape with phenotypic rust resistance must be identified, protected and their cones collected.

44. Stahl, K., Moore, R.D., & McKendry, I.G. 2006. Climatology of winter cold spells in relation to mountain pine beetle mortality in British Columbia, Canada. Climate Research. 32: 13-23.

Background & Objectives

This paper was written to relate the role of synoptic and large-scale climate trends to recent epidemics of mountain pine beetle, specifically in relation to the frequency and distribution of extreme wintertime cold events that result in beetle mortality.

There were two overall objectives of this paper. First, was to examine connections between winter beetle mortality cold events and large-scale climate modes. Second was to understand the influence of synoptic-scale circulation patterns on these same cold events.

Main Findings

- The highest frequency of potential cold mortality days were found in northeastern British Columbia (BC), where arctic air masses dominant during winter. Overall, cold mortality days have decreased since 1957.
- Cold mortality events were associated with a synoptic circulation pattern when cold Arctic air flows coastward from the interior mountains of BC.
- The frequency of synoptic circulation patterns depends on large-scale climatic modes, including the El Nino Southern Oscillation, Pacific Decadal Oscillation, and Pacific North American pattern.
- The frequency of cold-mortality events coincides with strong negative Pacific Decadal Oscillations and all teleconnection patterns. Recently the PDO has been in a positive or neutral phase resulting in less frequent or severe cold events.

Implications

- Lethal temperature thresholds vary among phases of beetle life history.
- Mountain pine beetle are the least susceptible to cold events and exhibit the greatest physiological "cold-hardening" traits during winter.
- Beetles are more susceptible to temperature variability during the shoulder seasons.

45. Tomback, D.F., Anderies, A.J., Carsey, K.S., Powell, M.L., & Mellman-Brown, S. 2001. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. Ecology. 82(9): 2587-2600.

Background & Objectives

Natural whitebark pine regeneration following the 1988 Yellowstone fires was investigated 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.

Main Findings

- Synchronous delayed seed germination occurred throughout both study areas.
- Cached seeds may delay germination for one or more years in part because of underdeveloped embryos at the time of seed dispersal.
- Whitebark pine exhibit a soil seed bank strategy that is unique among pines.
- Most germination followed two winters of seed dormancy.
- Regeneration densities were consistently highest on moist sites.
- High correlation between weighted means for new regeneration and March-plus-April precipitation.

Implications

- Regeneration can occur continuous and on years without seed production or for several years following loss of cone-bearing trees.

46. Tomback, D.F., Clary, J.K., Koehler, J., Hoff, R.J., & Arno, S.F. 1995. The effects of blister rust on post-fire regeneration of whitebark pine: the Sundance Burn of northern Idaho (U.S.A.). Con. Bio. 9(3): 654-664.

Background & Objectives

Densities of whitebark pine regeneration and the incidence and severity of blister-rust infection of seedlings and saplings were examined in the 25-year-old Sundance Burn in the Selkirk Range of northern Idaho, an area heavily infected by blister rust.

Main Findings

- Low densities of whitebark pine regeneration were attributed to the severe damage to the seed source on the burn perimeter resulting from previous infestation of mountain pine beetle and blister rust.
- Lack of seed production in the adjacent forest and blister rust mortality results in slow regeneration of whitebark pine.

Implications

- Available seed is critical to regeneration – protect remaining seed sources.
- Prescribed fires for managing whitebark pine ecosystems should be restricted to small areas or should require plantings of rust-resistant seedlings.

47. Tomback, D.F., Sund, S.K., & Hoffman, L.A. 1993. Post-fire regeneration of Pinus albicaulis: height-age relationships, age structure, and microsite characteristics. Can.J.For.Res. 23(2):113-119.

Background & Objectives

A study was made of the establishment of post-fire *Pinus albicaulis* seedlings in the Sleeping Child burn (26 years after a wildfire) and the Saddle Mountain burn (28 years after a wildfire) in W. Montana.

Main Findings

- A disproportionately high percentage of regeneration was established between 1977 and 1985, about 17-25 years after fire.
- Whitebark regeneration was more frequently associated with occurrence of *Vaccinium scoparium*.
- Age differences of 1-8 years occurred among seedlings in 65-86% of the seedling and tree clusters sampled.

Implications

- This study indicates delayed germination of some cached seeds.
- Major regeneration events following stand-replacing events may be episodic.

48. Tomback, D.L. & Linhart, Y.B. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology. 4: 185-219.

Background & Objectives

This paper describes the biogeographical and ecological consequences of seed dispersal by corvids and the mutualisms between birds and pines and reviews previous studies and ideas on the evolution of these mutualisms.

Main Findings

- Seed-caching occurs: on steep and south-facing, exposed rocky sites; under logs, trees, plants, and stones; in moss and lichen; in loose forest litter; at the base of trees or among tree roots; under forest canopy; in trees; on barren ledges and fissures on rock walls; in forest floor of burned and live krummholz pine; and at edges of meadows.
- Large seed size is an adaptation to xeric and competitive conditions. Semi-desert and timberline environments are all characterized by short growing seasons and long, dry and/or cold periods. Under these circumstances, large seeds are advantageous, as they provide more nutrients and allow for more rapid early growth and establishment.

Implications

- Seed-caching sites are highly variable and diverse – sites to cache seeds are likely not a limiting factor, rather seed availability.
- Whitebark pine have evolved to live in very harsh, unpredictable environments - .

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

Background & Objectives

This study was conducted to evaluate the effects of whitebark pine restoration treatments on the distribution of bark beetle attacks. Restoration treatments included a variety of: felling of overstory and understory, slashing and burning.

Main Findings

- There was an increase in bark beetle attacks after prescribed burning.
- Mountain pine beetle appeared to prefer whitebark pine to lodgepole.
- *P. fossifrons* (typically a minor, secondary beetle) exhibited aggressive behavior not previously recorded in small-diameter whitebark.
- Populations of both the pine engraver and red turpentine beetle were higher in treated areas.

Implications

- If bark beetle populations are high at the time of implementation, our results indicate that increases in beetle activity would be expected in some treatments.
- Removal of the overstory canopy altered the microclimate - resulting in higher temperatures, increased wind flow, and changes in soil moisture. This may have promoted *P.fossifrons*.
- Managers should consider and monitor the bark beetles when implementing restoration treatments.

50. Walsh, J.R. 2005. Fire regimes and stand dynamics of whitebark pine (*Pinus albicaulis*) communities in the Greater Yellowstone Ecosystem. M.S. Thesis. Colorado State University, Fort Collins, CO.

Background & Objectives

The research investigated the stand structure, fire history and successional dynamics of seven whitebark sites in the GYE. All study sites were above 2600 meters

Main Findings

- Whitebark are "stress tolerators" – their competitive advantage is to live a long time, inhabit harsh sites and pioneer.
- Fire regimes in whitebark-dominant upper subalpine forest of GYE may not have been substantially altered by suppression.
- Average age of canopy whitebark exceeded 300 years
- Site structure and dynamics were highly variable – pulse and continuous recruitment were observed.
- Three of seven sites contain evidence of low-severity fire. The remaining four contain no evidence of fire.
- Three regeneration modes exist: 1) catastrophic – mass-regeneration following stand-replacing event; 2) gap-phase – episodic on a small scale; and 3) continuous – understory continually recruits.

Implications

- Whitebark system disturbance regimes are highly variable – some stands are initiated by stand-replacing events, some experience low-severity fire and others do not.
- Variation in forest disturbance regimes produces multiple successional pathways.
- Some stands are self-replacing in the absence of fire.
- Management efforts must account for the variability in fire frequency, type, and extent in whitebark.

51. Yanchuck, A.D. & Lester, D.T. 1996. Setting priorities for conservation of the conifer genetic resources of British Columbia. Forestry-Chronicle. 72(4): 406-415.

Background & Objectives

Gene conservation of native conifer species is considered necessary primarily to safeguard the future evolutionary potential of the species to climate change and new biotic challenges. Whitebark pine is of greater concern due to a generally poor natural regeneration potential.

Main Findings

- Options include: (i) maintaining existing protected areas; (ii) creating new reserves for in situ management; and (iii) ex situ collections of various types.

Implications

- Gene conservation via in situ protection and collections is critical.