Annotated Bibliography for Whitebark Pine Ecology
Additions December 2009
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1. **Comments:**
   - **a.** The precarious state of whitebark pine remains 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.
   - **b.** *Once again 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.
   - **c.** If I missed any key work or if you have additional interpretations from any given paper, please let me know.
   - **d.** These literature updates are a habit now…….so expect one every December.

2. **Gillette, N.E., Erbilgin, N., Webster, J.N., Pederson, L., Mori, S.R., Stein, J.D., Owen, D.R., Bischel, K.M., and Wood, D.L. 2009. Aerially applied verbenone releasing laminated flakes protect *Pinus contorta* stands from attack by *Dendroctonus ponderosae* in California and Idaho. Forest Ecology & Management 257: 1405-1412.**

Background & Objectives

Current outbreaks of mountain pine beetle are the largest ever documented and are expected to continue. This paper reported on a test of area-wide protection of lodgepole pine with aerially applied verbenone releasing laminated flakes. Flakes were applied June 2005 at rate of 2.47 kg of formulated pheromone/ha.

Main Findings

- Mountain pine beetle host tree attack rates were significantly lower on sites treated with verbenone flakes.
- Mountain pine beetle attack rates were 2.7 to 3.7 times greater on untreated sites.
- Trees are more vulnerable when beetle populations are higher.
- Current beetle population level and subsequent damage drive the need for this area-wide treatment option.

Implications

- The authors suggest that efficacy of verbenone may be enhanced on sites with very high beetle populations by simultaneous use of verbenone and attractant-baited trapping.
- Current EPA application rates are 3 times greater than those tested in this study and should be tested
- Authors suggest helicopter application of verbenone flakes in whitebark pine sites.

3. **Lundquist, J.E., & Bentz, B.J. 2009. Beetles in a changing climate. In The Western Bark Beetle Research Group: A Unique Collaboration With Forest Health Protection Proceedings of a Symposium at the 2007 Society of American Foresters Conference, Portland, Oregon.**

Background & Objectives

Current outbreaks of mountain pine beetle are the largest and most severe in recorded history. Several factors, including climate change are driving the outbreaks.

Main Findings

- Global average temperature has increased dramatically in the past two decades and this pattern will continue.
- Insect population life history timing and density respond dramatically to small changes in climate.
- Altered precipitation patterns result in affects to host tree defenses; prolonged drought makes them more susceptible to beetle attacks.
- Bark beetle outbreaks result from a combination of conditions at different scales.
- Elevated temperatures increase reproduction and growth cycles and reduce cold-induced mortality.
- Climate change will also affect the predators of bark beetles and the symbiotic fungi the beetles carry with them.
- Bark beetle distributions will move upward in elevation and latitude with changing climate.

Implications

- Forest management must be highly adaptable, because the current conditions are novel. The best management tools are currently unknown and will change as discoveries are made.
- Because climate and forests are changing so dramatically, management based on recreations of the past will likely be unsuccessful.
- Management must be based on the most current science.

4. **Lorenz, T.J., & Sullavin, K.A. 2009. Seasonal differences in space use by Clark's nutcrackers in the Cascade Range. The Condor. 111(2): 326-340.**

Background & Objectives

This paper explains year-round patterns of habitat use by the Clark's Nutcracker. Specifically, the tested whether nutcrackers migrate altitudinally.

Main Findings

- Nutcrackers can transport seeds great distances, but most seeds are caches within a few kilometers of the harvest trees.
- Some nutcrackers remained on a single home range year round (residents); others left study area (emigrants).
- Nutcrackers did not migrate altitudinallly.
- All nutcrackers home ranges contained steep south-facing slopes or cliffs.
- In late autumn, nutcrackers shift their seed harvesting efforts to lower elevations, but within a single home range.
- Resident nutcrackers do not need to migrate because seeds of at least one tree species are available.

Implications

- Nutcracker populations are affected by position of their home range to autumn seed sources.
- Understanding nutcracker caching decisions is critical to optimize the number of whitebark seeds effectively dispersed to suitable sites.

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

Background & Objectives

This paper reports on surveys to assess the status of whitebark pine in relation to white pine blister rust.

Main Findings

- 53% of 2173 sampled overstory trees had blister rust; 38% of saplings had blister rust.
- Rust infection rates increased with elevation and from west to east.
- 78% of infected trees were severely infected.
- Whitebark regeneration was present on most sites; dominant only on open stands.
- Fire evidence was highly variable

Implications

- Whitebark pine's precarious state is range-wide
- Fire exclusion and mountain pine beetle were not contributing to whitebark mortality; blister rust was agent to population decline.

6. **Bonan, G.B. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science. 320: 1444-1449.**

Background & Objectives

This review paper provides a brief, but complete outline of the role forests play in climate change and the influence of climate change on forests. Included in this paper are several great diagrams and explanation of climate models.

Main Findings

- Forests store 45% of terrestrial carbon; and contribute 50% of terrestrial net primary productivity.
- Evapotranspiration by forests helps to cool the planet.

Implications

- Losses of forests to wildfire and insect outbreaks weakens terrestrial carbon sequestration

7. **Murray, M. 2008. Fires in the high cascades: new findings for managing whitebark pine. Fire Management Today. 68(1): 26-29**

Background & Objectives

This paper addresses a critical question about the role of fire in whitebark pine in the Casade Ecosystem.

Main Findings

- Very wide range of fire frequency was detected.
- Both lethal stand-replacing and low severity events were detected.

Implications

- Whitebark pine stand type and site conditions likely drive fire disturbances.
- Pure whitebark stands with sparse fuels should receive low priority for burning.
- Protection of disease resistant trees should be a priority.

8. Larson, E.R. 2009. Status and dynamics of whitebark pine (*Pinus albicaulis*) forests in southwest Montana, central Idaho, and Oregon, USA. PhD. University of Minnesota. 190 pages.

Background & Objectives

This research sought to assess blister rust infection levels, patterns in the distribution and abundance of regeneration, and the patterns of disturbance in whitebark pine.

Main Findings

- Inventoried 2,666 whitebark pine: on average 37% infected with blister rust, 33% dead (as high as 69% in Idaho).
- Rust infection higher in open stands, cooler/moist aspects, stands with greater proportion of whitebark.
- Mountain pine beetle primary cause of mortality – 83% mortality was MPB.
- MPB mortality greatest: stands with lower density and larger trees, drier springs, lower June and higher August temperatures.
- Blister rust infects trees of all sizes and ages across the landscape.
- MPB distribution is dictated by spatial arrangement of host trees and topographic barriers.
- Regeneration ubiquitous: 97% of study sites had whitebark regeneration.
  - ✓ Regeneration positively and strongly correlated with density of whitebark, MPB killed whitebark, stand and lodgepole density, cooler/drier sites, relative elevation.
  - ✓ Negative correlation with subalpine fir density.
  - ✓ Establishment of new cohorts of whitebark has been successful at all sites over recent past.
  - ✓ No difference in regeneration between burned and unburned.
  - ✓ Fire in areas with heavy MPB results in a severe lack of seed trees and therefore, little to no regeneration.
  - ✓ Strong relationship between regeneration density and MPB killed whitebark.
- Wide variety of disturbance frequency, effects and stand composition and age.
  - ✓ Most stands developed following severe stand-replacing events.
  - ✓ Only a few stands have multiple cohorts, indicating mixed-severity regimes.
  - ✓ Pioneering species, but also establishing beneath canopy.
- Single, large, infrequent disturbances have different effects than multiple disturbances (like current MPB and rust).
- Evidence of post-MPB growth release & cohort establishment evident.
- Frequent fire scars indicate important role of fire.
- Little evidence of advanced succession due to fire suppression.
- 33% of sites had evidence of fire (fire scars or post-disturbance cohorts present).
- Forest composition was strongly influenced by site-specific climate conditions.

Implications

- Author stresses the importance of recognizing and understanding that whitebark communities are diverse and complex in structure and dynamics.
- Author suggests planting seedlings beneath canopies of mature whitebark with heavy MPB activity.
- Target cold, drier stands for planting.
- Natural regeneration is key to landscape level species preservation and it promotes mechanisms for whitebark to adapt to changing environment and blister rust.
- Sufficient genetic diversity (seed-sources) is critical to species ability to adapt.

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

Background & Objectives

This paper addresses the degree of local adaptive traits of whitebark pine measured by assessing phenotypic traits including: height increment, biomass, root to shoot ratio, date of needle flush, fall and spring cold injury and survival. These tests were performed in a common garden experiment. This information is critical to establishing geographic guidelines on seed transfer.

Main Findings

- Significant variation was observed among populations for growth and cold related traits.
- Height, survival and needle growth were greater in cold treatment.
- Populations from colder, higher latitude climates had greater survival, allocated more biomass to shoots, had earlier needle flush, thus more spring cold damage. These trees also had less overall growth and less fall cold injury.
- Rocky Mountain populations differed from other populations most in height growth and date of needle flush.
- The majority of genetic variation in whitebark pine is among individuals within populations, suggesting natural selection drives local adaptation.
- Individuals from northern latitudes had faster response to warming spring temperatures.
- Date of needle flush is was used to assess seed transfer guidelines; for the Rocky Mountain Region, they suggest a climate transfer maximum of 1.0° C or 320 meters in elevation.

Implications

- Seed transfer should be guided by natural levels of genetic variation and local adaptation to promote successful restoration efforts and the facilitation of migration.
- Understanding genetic variation is critical to addressing the effects of climate change.
- Authors suggest that the strategy for successful seed transfer under changing climate would be unidirectional transfer seed to the maximum extent allowable from mild to cold climates.
- Future climate conditions are unknown, making seed transfer guidelines very difficult.
- Mitigation may be to mix seeds from different populations within the acceptable transfer guidelines to increase the probability of survival.
- In the future these thresholds may be too conservative and it may become optimal to transfer seeds greater distances and accept the risks.
- Whitebark experience a migration lag due to their dependence on the Clark's nutcracker. Facilitated migration through restoration plantings may help maintain viability.

10. Hood, S.M., Cluck, D.R., Smith, S.L., Ryan, K.C. 2008. Using bark char codes to predict post-fire cambium mortality. Fire Ecology. 4(1): 57-73.

Background & Objectives

This paper assessed conifer post-fire survival using the degree of cambium injury. The authors were also testing the use of previously established bark char codes as a proxy for cambium damage.

Main Findings

- Cambium injury can be assessed using bark char codes.
- Whitebark pine fit into the "thin barked" category and light to moderate char was strongly correlated to mortality.
- A trees susceptibility to cambium injury is primarily influenced by heat duration and bark thickness.

Implications

- Bark char can be used to assess post-fire injury
- Whitebark pine have thin bark, in relation to fire injury.

11. Kipfmueller, K.F. 2008. Reconstructed summer temperature in the northern Rocky Mountains wilderness, USA. Quaternary Research. 70: 173-187.

Background & Objectives

This research used ring widths from whitebark pine to reconstruct high elevation summer temperature anomalies. The importance of these reconstructions is to assess long-term climate variability and how climate is linked to disturbances, such as beetle outbreaks and fire events.

Main Findings

- Whitebark pine are valuable in reconstructing climate due to their great age.
- There was a significant decrease in ring-widths in the late 20th century.
- Synchronous reduction in growth suggests climate mechanism.
- Whitebark pine growth exhibits dramatic reduction after the 1960s.
- Site-specific characteristics such as slope, soil, aspect may modify local climate and mute regional patterns seen in rings.

Implications

- Author suggests that whitebark growth rates may have been influenced by blister rust
- Understanding past climate variation is key to understanding forests response to future climate-disturbance relationships.
- Local-scale variation is important when investigating fire or insect outbreaks.

12. Larson, E.R., Van De Gevel, S.L., & Grissino-Mayer, H.D. 2009. Variability in fire regimes of high-elevation whitebark pine communities, western Montana, USA. Ecoscience. 16(3): 282-298.

Background & Objectives

This paper investigated whitebark stand history to characterize fire regimes, historic disturbance agents and to explore the potential influence of fire suppression. They sought to understand climate-fire relationships, and the biophysical variation among whitebark pine stands. The understanding of fire regimes in whitebark pine represents a gap in our understanding of mixed severity fire regimes. Fire studies in whitebark to date have relied on age-structure data and not cross dated fire scars.

Main Findings

- Recent research (Veblen & Sibold, 2001; Buechling & Baker, 2004) show that high elevation forests are within their historic range of variability and have not been affected by fire suppression.
- The whitebark pine on all three study sites established around 1500 AD.
- The earliest date of mortality to mountain pine beetle (blue stain fungus indicator) was late 1600s.
- Fire scar records may be missing tree data from trees that were consumed by fire.
- Frequent fire scars were detected but little to no evidence of ecological change was seen in age structure of stand = fires were low severity and small.
- Site with the most fire scars had the earliest establishment of and most abundant subalpine fir.
- Whitebark fire regimes are too diverse to classify as one type.
- Fuels drive the extent to the fires – open dry whitebark stands do not experience extensive fire, but those with abundant fuels do.
- Local conditions drive fire-climate rather than large-scale climate patterns.
- Fire suppression may have limited the spread of some fires, but subalpine fir establishment occurred well before fire suppression.
- Differences detected were result of distinct biophysical settings of each forest.

Implications

- Site-specific, temporally precise data is critical in when assessing the use of fire as a restoration tool.

13. Curtis-McLane, S., & Aitken. S. 2009. Can whitebark pine grow north of its current species range under climate change? A genetic analysis using common gardens. Centre for Forest Conservation Genetics. University of British Columbia.

Background & Objectives

This paper addresses facilitated migration of whitebark pine.

Main Findings

- Study still in progress…
- Initial observations that germination varied with seed weight, snow pack persistence, population origin and seed treatment, but not geographic location.

Implications

- Whitebark facilitated migration may be successful.

14. Sniezko, R.A., Kegley, A., Danchok, R., Schoettle, A.W., Burns, K.S., & Conklin, D. 2007. *Cronartium ribicola* resistance in whitebark pine, south western white pine, limber pine, and Rocky Mountain bristlecone pine. Preliminary screening results from first tests at Dorena GRC. *In*: McWilliams, M.G. editor: Proceedings of 55th Western International Forest Disease Work Conference. Sedona, AZ. Oregon Department of Forestry.

Background & Objectives

This paper reports on rust resistance trials for four five-needle pine species, including whitebark pine from the central Rockies screened at Dorena.

Main Findings

- Preliminary data shows that whitebark show genetic variation in resistance.
- At least a small number of whitebark families show resistance.
- Initial data suggests a geographic trend in the resistance trait of hypersensitive response.

Implications

- Rust resistant seedlings in future may be a reality.

15. Gross, D. 2008. Mountain pine beetle fecundity and offspring size differ among lodgepole pine and whitebark pine hosts. PhD. Utah State University.

Background & Objectives

This study used laboratory experiments to quantify the relative productivity of mountain pine beetle in different pine hosts. Specifically assesses was beetle fecundity, offspring size, and brood sex-ratio between two hosts, lodgepole pine and whitebark pine.

Main Findings

- Host species affects the life history and fitness of mountain pine beetle.
- Phloem is significantly thicker in lodgepole pine than whitebark pine.
- Beetles do not have greater fecundity if they attack the same host species from which they originated – they can attack either.
- Beetles reared in lodgepole had greater fecundity that those in whitebark.
- Brood from whitebark pine were significantly larger.
- Author thinks that some of his results may be do to affects of fungal symbionts.

Implications

- More research needed on interactions of whitebark and mountain pine beetle.
- Mountain pine beetle are not limited, physiologically, by the species of host in which they originated.

16. Lahr, E.C., & Sala, A. 2009. Mountain pine beetle outbreaks in whitebark pine: do sapwood carbohydrates influence beetle success?

Background & Objectives

This work seeks to explain some surprising observations of dramatic depletions of non-structural sapwood carbohydrates in whitebark pine following attack by mountain pine beetle.

Main Findings

- Preliminary results indicate that host tree nutritional quality plays an important role in mountain pine beetle preference of whitebark pine over lodgepole pine.

Implications

- Mountain pine beetle and fungal symbiont appear to benefit from sapwood carbohydrates.
- Further research to understand the use of host tree carbon and other nutrients by mountain pine beetles.

17. Millar, C.I., Stephenson, N.L., Stephens, S.L. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications. 17(8): 2145-2151.

Background & Objectives

Future environments under which forest ecosystems must be managed are uncertain. This paper offers a conceptual framework for managing forested ecosystems that includes flexible approaches, incremental steps, ongoing learning and modification.

Main Findings

- Novel stressors such as pollution, fragmentation, invasive plants, interactions among stressors suggests that it may not be possible or optimal to attempt to maintain or restore conditions defined by historic conditions.
- Management should focus on maintaining ecosystem resistance and resilience.
- Suggestions include: assist transitions (ie: facilitate migration); increase redundancy; maintain existing and expand genetic diversity; promote connected landscapes; anticipate threshold effects; experiment with refugia.

Implications

- Strategies for management must include both short and long-term approaches.
- No single approach will fit.
- Planning that assumes that future is not known and allows for adaptation and multiple approaches will be required.
- This paper is a great resource as it suggests hands-on and substantive management tools.

18. Garcia, R. Siepielski, A.M., & Benkman, C.W. 2009. Cone and seed trait variation in whitebark pine (Pinus albicaulis: Pinaceae) and the potential for phenotypic selection. American Journal of Botany. 96(5): 1050-1054.

Background & Objectives

The goal of this study was to quantify the amount of variation in cone and seed size among and within whitebark pine in Yellowstone National Park. The purpose of this investigation was to understand if the variation affected the potential for phenotypic selection. Variation among individuals is necessary for natural selection to operate.

Main Findings

- High variation among individual whitebark pine.

Implications

- Variation in cone and seed traits allows seed consumers and disseminators to discriminate among trees.
- This variation promotes genetic variation and adaptive evolution.
- Supports ideas from paper #9 - greatest genetic variation is among individuals.

19. McDowell, S.A. 2009. Burn severity and whitebark regeneration. M.S. Western Washington University. Defending November 12….she will email me a pdf soon!

Background & Objectives

Implications

Main Findings

20. Progar, R.A. Five-year operational trial of verbenone to deter mountain pine beetle (*Dendroctonus ponderosae*: Coleoptera: Scolytidae) attack of lodgepole pine (*Pinus contorta*). Environmental Ecology. 34(6): 1402-1407.

Background & Objectives

This study tested verbenone over five years in campgrounds near Redfish Lake, Idaho. Twenty Pherotech, 5 gram pouches were placed 10 meters apart on a 30 by 67 meter plot (0.2 hectares).

Main Findings

- Verbenone protects at beginning of outbreak.
- Under very high beetle pressure with few remaining host trees, verbenone pouches were ineffective.
- Over the course of an outbreak, mountain pine beetle aggressiveness and behavior changes.

Implications

- It is important to consider complementary protection or management strategies to ensure long-term success.
- This study was done in lodgepole pine in 2000 – the results may not be applicable to whitebark pine in 2009.

21. Notes from the Whitebark Ecosystem Foundation Annual Meeting. 2009. Nelson, British Columbia.

a. King, J. 2009. Eurasian stone pine and blister rust.

Key Conclusions

- Siberian pines seem to have much higher canker free in same inoculation tests as North American pines (70-90%)
- Some actually “tolerate” the rust – it can be found in the cells.
- Might be able to do some hybridization
- Further work needed to determine physiological resistance mechanism.
- Northern populations tend to have more resistance than southern.

b. McOntire, E. 2009. Masting in whitebark pine.

Key Conclusions

- Large-scale synchrony observed.
- Masting seems to be positively related to density of cone producing trees – this could be a problem when there are less whitebark remaining, as seed will be consumed by predators.

c. Lorenz, T. 2009. Cache site selection by Clark’s nutcracker.

Key Conclusions

- 91% of cache sites were in home range; 43% of seeds were collected in home range.
- Avoided mixed-low elevation; preferred cliff/talus and parkland.
- 58% of seeds were cached in tree canopies
- Seemed to prefer edges
- Very little use of burns

d. Smith, Cyndi. 2009. Trend of health status of limber and whitebark pine.

Key Conclusions

- 98% of 114 plots had blister rust present.
- 28% trees dead from blister rust; 52% of live trees are infected
- Larger diameter regeneration had greater blister rust infection.

e. Esch, Evan. 2009. Mountain pine beetle phenology, condition, and survival in whitebark pine.

Key Conclusions

- 1930s and 1980s mortality linked to temperature.
- Beetles prefer whitebark over lodgepole
- Quantity of beetles is lower in whitebark, but size is greater.

22. Vogler, D.R. 2007. The role of disease resistance in the recovery of whitebark pine. USDA Forest Service R2-NR-FHP-2007-01. 80-81.

Background & Objectives

The author makes the important assertion that our efforts to research and develop genetic resistance to blister rust is a monumental task that has failed in three commercial white pine species in the past.

Implications

- We must address the following considerations:
  1. Is blister rust the primary cause of decline? Will deployment of rust resistant seedling reverse the decline?
  2. Are the mechanisms of resistance in whitebark pine observable, repeatable, robust?
  3. Does the mode of inheritance provide the proper mechanism to propagate resistance on the landscape?
  4. Are the long-tern resources, will and political support in place?
  5. Do we know how to successfully plant whitebark pine?