ANNOTATED BIBLIOGRAPHY FOR WHITEBARK PINE ECOLOGY

Additions December 2013- March 2014

Prepared by Nancy Bockino, Grand Teton National Park

Notes:

a. Using the most recent science contributes to the successful conservation of whitebark pine. This bibliography has become my annual contribution to this objective. Enjoy!

b. As always, if I missed any key work or if you have additional interpretations from any given paper, please let me know.

1. **Williams, M.I., Dumroese, R.K. 2013. Preparing for climate change: forestry and assisted migration. J.For.111 (4):287-297.**

Background & Objectives

This paper reviewed the concepts of, and current research and ideas, on assisted migration of forest tree species. It provides several excellent resources for decision making and available research findings.

Main Findings

- Current climate models predict plants may need to migrate 3000 to 5000 meters. This is much greater than their observed rates of 500 meters.
- Growing season length, temperature and light are the variables that play a role in adaptation and genetic variation.
- Trees are susceptible to pests and weather events when their phonological events are not synchronized with the above mentioned seasonal cycles.
- Assisted migration is one proposed strategy to facilitate adaptation.
- Current seed transfer guidelines do not incorporate climate change.
- Seed transfer beyond current guidelines may be necessary to preserve forest productivity and conserve species. Some provinces in Canada have modified their policies.
- Three methods are proposed:
    - Assisted population migration: trees moved within their current range
    - Assisted range expansion: from their current range to suitable areas just outside
    - Assisted species migration: movement to location far outside current range

Implications

- Table 1. Provides a list of resources for plant transfer guidelines
- Paper contains a decision framework to determine adaptation strategies that incorporates economics, ecology and social value.
- Transfer functions and provenance data have been developed to guide seed movement under climate change.
- Online tools are available to assist with decision making (Table 1).
- Target migration distance must short enough to allow survival, yet far enough to ensure adaptation. Target migration distances are being estimated and continually assessed.
- Conservation and management plans must incorporate climate change research.
- Documentation and later incorporation of management results are critical to adaptive management and further understanding.

2. **Backsen, J.C. and Howell, B. 2013. Comparing aerial detection and photo interpretation for conducting forest health surveys. West. J. Appl. For. 28(1): 1-7.**

Background & Objectives

This paper compares the findings of forest damage from ADS (Aerial Detection Surveys) and PIS (Photo Interpret Surveys) for a study site in the Black Hills. Ground plots were performed to determine actual mortality.

Main Findings

- PIS were less efficient, but more accurate than ADS.
- ADS data are useful for broad scale detection and monitoring, but less suitable for fine scale analysis.
- Satellite imagery is available at 1 m resolution in natural color and sometimes infrared; it is accurate and can also be used to determine damage.
    - Polygons can be coded for damaging agent and severity.
    - 700,000 acres were assessed in about 70 hours.
- Timing of photos and imagery are critical to promote optimal viewing of forest damage.

Implications

- This work suggests that aerial imagery is a valuable tool for assessing forest damage, especially when looking for a single agent of disturbance.
- PIS could become more efficient in the future with well-defined coding systems, larger screen etc.
- PIS is safer than ADS, as flight is eliminated.
- ADS accuracy may be increased by using a percent mortality rating rather than number of trees per acre.

3. **Liu, J.J. Zamany, A. Sniezko, R.A. 2013. Anti-microbial peptide (AMP): nucleotide variation, gene expression, and host resistance in the white pine blister rust (WPBR) pathosystem. Planta 237:43-54.**

Background & Objectives

This study seeks to understand white pine genetic resistance against white pine blister rust. 18 seed families from British Columbia to Washington and Oregon were used to analyze *PmAMP1.* This antimicrobial peptide protein is synthesized by white pine to inhibit microbial invasion through induced and constitutive resistances. This objective of this study was to investigate the natural variation in *PmAMP1* in white pines used in breeding programs and to determine if the protein level was related to disease resistance against blister rust.

Main Findings

- *PmAMP1* was most abundant in stems and shoots, in low levels in roots and rarely detectable in needles.
- *PmAMP1* levels varied with season.
- *PmAMP1* was significantly higher in infected seedlings and significantly higher in tree groups with complete stem resistance than tree groups with near complete susceptibility.

Implications

- A successful breeding program requires that molecular variations of gene sequences and proteins are correlated to resistance levels.

4. **Progar, R.A, D. C. Blackford , D. R. Cluck , S. Costello , L. B. Dunning , T. Eager , C. L. Jorgensen , A. S. Munson , B. Steed , and M. J. Rinella. 2013. Population densities and tree diameter effects associated with verbenone treatments to reduce mountain pine beetle-caused mortality of lodgepole pine. Journal of Economic Entomology, 106(1):221-228.**

Background & Objectives

This study sought to determine the ability of verbenone treatments to protect lodgepole pine over long-term mountain pine beetle outbreaks. Study sites were distributed across Idaho, Wyoming, Utah and Colorado.

Main Findings

- Verbenone success varies with duration of infestation, beetle population size, tree size.
- Verbenone reduced mountain pine beetle infestation when beetle populations grew gradually and when outbreaks in surrounding untreated forests were moderately severe.
- Verbenone did not protect trees when MPB populations increased rapidly or at peak outbreak levels.
- MPB dynamics differ between high and low population levels.
- MPB preferred larger diameter trees.

Implications

- This work suggests that verbenone is a cost effective tool for protecting lodgepole pine, in some areas.
- Verbenone efficacy may be increased by combining it with other semiochemicals.

5. **Smith, C.M., Langor,D.W., Myrholm, C., Weber, J., Gillies, C. and Jon Stuart-Smith. 2013. Changes in white pine blister rust infection and mortality in limber pine over time. Can. J. For. Res. 43: 919 –928.**

Background & Objectives

This study assessed mortality and blister rust incidence on limber pine from 2003-04 to 2009 at 85 plots that extended across the range of limber pine in Canada, from Waterton Lakes National Park in southwestern Alberta to Golden, British Columbia. 12 of the stands visited were those from Kendall's 1996 work.

Main Findings

- Rust infection increased from 74% of the plots in 2003-04 to 88% of plots in 2009.
- Mortality increased slightly over the same time period, from 32% to 35%. 97% of mortality was attributed to blister rust; 3% to MPB.
- From 2003-04 to 2009, on live trees, rust infection increased from 33% in to 43%.
- In those stands originally visited in 1996, mortality increased and the percent of trees infected decreased slightly (in part attributed to tree mortality).
- Rust severity increased; in 2003-04, 27% of infected trees had stem cankers and this increased to 43% in 2009.
- Analyses indicated that live tree infection increased over time, but was not related to elevation or latitude.
- The proportion of dead trees decreased with increased latitude.
- Mature krummholz growth forms had higher infection and mortality rates.

Implications

- Rust development and spread may be slower at greater elevation and latitude, due to shorter growing season.
- Many limber pines in the study have active stem cankers, which will result in top kill and/or death within a decade.
- This will result in decreased seed production.
- Loss of krummholz limber pine on harsh sites could have a cascading effect near/at tree line.
- Limber pines patchy distribution and isolated populations make it vulnerable.
- Patterns of mortality and infection could help guide management priorities.
- Limber pine is listed as Endangered under The Wildlife Act in Alberta and a recovery strategy began in 2013.

6. Rapp, J.M., Eliot J. B. McIntire and Elizabeth E. Crone. 2013. Sex allocation, pollen limitation and masting in whitebark pine. Journal of Ecology. (101): 1345–1352.

Background & Objectives

This study used pollen and seed data for 29 trees across 7 sites in Montana to describe sex allocation patterns in whitebark pine. Masting, or synchronous seed and pollen production, is thought to increase reproductive success due to increased density of seed dispersal and pollination. Sex allocation theory predicts there is a trade-off between male and female propagules and depends on total resources invested in reproduction. This study investigated whether reproductive synchrony increases seed production, due to increased pollination efficiency.

Main Findings

- Whitebark seed cone maturation was higher with increased pollen cone production.
- Pollination efficiency is paired with greater seed dispersal and survival during mast years.
- Sex allocation differs among individual whitebark.
- Seed cone initiation was negatively correlated to pollen cone abundance.
- Seed cone initiation was synchronous within a population.
- Trees invest more resources toward female reproduction in mast years.
- Pollen was limited due to stand isolation and reduced whitebark density due to MPB.

Implications

- The benefits of density-dependent fitness may influence patterns of sex allocation.
- This study suggests that pollen limitations may lead to reduce cone maturation and altered masting patterns.
- Results suggests that reproductive benefits of coupling pollen with seed cone initiation may outweigh altered male/female propagule allocation when resources are changing, such as stand density and cone density. This may result in altered masting patterns.

7. Donato, D.C. 2013. Limits to upward movement of subalpine forests in a warming climate. PNAS. 110 (20):7971–7972

Background & Objectives

This commentary discusses current research and the variables that will influence shifts in the geographic ranges of subalpine forests. The author brings to light that warming temperature is only one factor that will drive tree line migration and geologic, landscape, and interspecific relationships will also influence species movement.

Main Findings

- Some theories predict that for alpine ecosystems, upper elevations will be most climatically suitable and this shift will reduce the extent of this ecosystem to isolated "sky islands".
- The actual nature of shift is unknown.
- Prior models of tree line shifts focused on temperature and moisture envelopes relative to tree physiology.
- Recent work shows that geomorphic features, like topography and soils must also be incorporated.
- The availability of growing substrates a high elevation will slow tree colonization.
- Connectivity of the landscape, altered disturbance regimes, pathogens and pests, and competition among species will influence species movement.

Implications

- The incorporation of landscape-level ecological and geomorphology into our understanding of changing mountain tree line with result in more accurate theories and thus management strategies.

8. Youngblut, K. and Luckman. B.H. 2013. Evaluating the temperature sensitivity of radial growth patterns from whitebark pine in the western Canadian Cordillera. Dendrochronologia 31: 16– 28.

Background & Objectives

This study assessed the dendroclimatology of whitebark pine in the western Canadian Cordillera across a broad range at 13 study sites.

Main Findings

- Ring-width records exceeded 1000 years.
- Dendrochronological characteristics seen were typical of high elevation conifers – low sensitivity and high autocorrelation among individuals.
- Synchrony was seen in radial growth patterns throughout much of the 20th century; lower sustained growth from 1950s onwards.
- Temperature signals were strongly influenced by minimum summer temperatures.
- Tree growth response to summer temperature decreased over time.
- Reduced radial growth coincides with the arrival of blister rust.

Implications

- The authors suggest that reduced sensitivity is due to an interaction between diurnal temperatures, cloud cover, snowpack and moisture stress.
- The observed decline in radial growth beginning in the early 1950s may be related to MPB and blister rust.
- Increased temperature reduces radial growth due to moisture-stress, specifically initiated by earlier snowmelt.
- Long-lived whitebark provide an excellent opportunity to investigate past climate variability.
- More work is needed to quantify the influence of blister rust and MPB.

9. **Creeden, E.P., Jeffrey A. Hicke, J.A., and Buotte, P.C. In Press. Climate, weather, and recent mountain pine beetle outbreaks in the western United States. Forest Ecology and Management.**

Background & Objectives

This study assessed climate and weather variables associated with mountain pine beetle outbreaks, through modeling and field observations, at five locations across western North America. Variables assessed were: year round temperatures that affect adaptive seasonality, low temperature that result in mortality, and drought stress of host. Beetle outbreak data was acquired from the USDA Aerial Detection Survey database. Climate data was acquired from PRISM and the NWS Coop.

Main Findings

- Analyses indicated that during outbreaks, year-round temperatures were higher, winter temperatures were higher and drought was present.
- Warming and drought was associated with increased beetle-caused tree mortality.
- Drought was not required to maintain large outbreaks.
- Conditions that supported adaptive seasonality, warm summer and winter temperatures, were more favorable during outbreak years than non-outbreak years.
- Decreases in tree mortality were not related to maladaptive seasonality, cold-induced mortality or drought stress.
- The relationship between climate and weather variables and outbreaks was highly variable among sites.

Implications

- Variation in the proximity to oceans and latitude result in different limiting factors related to climate and weather.
- Drought and warming facilitated transitions to larger beetle outbreaks.
- Authors did not find strong evidence outbreak declines related to weather factors.
- The authors suggest that host depletion results in decreased tree mortality.
- Understanding variability in beetle outbreaks over space, time and weather and climate factors will result in better understanding of future outbreak patterns.

10. **Kearns, H.S., W. R. Jacobi, R. M. Reich, R. L. Flynn, K. S. Burns and B. W. Geils. 2013. Risk of white pine blister rust to limber pine in Colorado and Wyoming, USA. Forest Pathology.**

Background & Objectives

This study assessed the environmental conditions associated with the distribution of blister rust in limber pine in Colorado and Wyoming.

Main Findings

- 77% of the plots sampled were infested; the range of infection was 30% to 90% of limber pine.
- Significant model variables included: May relative humidity, May maximum temperature, September relative humidity and August daily temperature range.
- Percent slope, topographic position, mean live crown ratio, *Ribes* density and diameter class distributions were all significantly related to rust distribution and incidence.
- Logistic regression model forecast 41% of limber pine in Colorado at risk of infestation and 61% of limber pine in Wyoming.

- Paper includes excellent maps of the distribution of limber pine at risk of infection by blister rust.

Implications

- The authors suggest that this work provides land managers with tools to reduce uncertainty in the expected distribution of blister rust.
- For rust to increase rapidly across a landscape, susceptible hosts must be present with the pathogen in a favorable environment.
- The most important factors from this study are: Ribes abundance, stands with large trees and elevated crowns, flat valley or ridge sites, wet June and July climates and warmer September temperatures.

11. Schotzko, K., Cook, S., Jorgensen, C., Kegley, S., Schwandt, J., Lazarus, L., and Hoffman, J. 2013. Whitebark pine stand conditions after mountain pine beetle outbreaks in Idaho, Wyoming and Montana. 2013. University of Idaho, Moscow, Idaho and Forest Health Protection, Boise, Idaho.

Background & Objectives

This study assessed 20 different sites for mountain pine beetle impacts to mature whitebark pine and abundance and condition of regeneration in Central Idaho, Wyoming and Montana.

Main Findings

- Substantial whitebark mortality due to mountain pine beetle.
- Decreased regeneration of whitebark relative to subalpine fir.

Implications

- Summary reports for each site will be available.
- Results can be used to make restoration recommendations and decisions.
- Data will be used to develop predictive model for whitebark pine loss.

12. Tomback, D.F. 2013. Final report: conservation of Clark's Nutcrackers in the Crown of the Continent – Clark's Nutcracker summer use of whitebark pine communities. CESU Agreement. Crown of the Continent Learning Center, Montana, USA.

Background & Objectives

This study was conducted from 2009 to 2010 in Glacier National Park and Waterton Lakes National Park. The objectives of the study were to determine: if nutcrackers occur in the whitebark communities and at what densities, if and how nutcracker densities vary with cone production, and how cone production varies with whitebark abundance and health. These findings were compared to those in McKinney et. al. 2009 and Barringer et. al. 2012.

Main Findings

- Blister rust infection rates ranged from 33% to 80%.
- 65 nutcrackers were detected in 2009 and 2010, observed transporting seeds. No direct caching behavior was observed.
- Both years were NOT bumper cone crop years. Across years and study sites the mean cone density was 67 per hectare.

- Nutcrackers occur in whitebark communities when cone production is low.
- The density of nutcrackers and activity levels are low.

Implications

- High cone production years are unlikely, due to mortality and blister rust infection caused canopy kill.
- Cone production, seed dispersal and subsequent regeneration are not dependable at the study sites.
- Nutcrackers remain in whitebark stands when cone production is low and this is hopeful for the future.

13. Hessburg, P.F., Reynolds, K.M., R. Brion Salter, R.B., Dickinson, J.D., Gaines, W.L., and Harrod, R. 2013. Landscape Evaluation for Restoration Planning on the Okanogan-Wenatchee National Forest, USA. Sustainability (5) : 805-840.

Background & Objectives

This study reviews several published landscape evaluation software packages designed at eastern Washington State to aid land managers in multi-scale restoration planning. These packages are designed to develop decision support tools, evaluate key landscape patterns and departures from historic, integrate climate change reference conditions, and provide evaluation of restoration tools as alternative scenarios. The case study used in the paper included whitebark pine habitat.

Main Findings

- Programs are only frameworks to build customized applications.
- Ecosystem Management Decision Support System (EMDS) integrates landscape evaluation and planning.
- NetWeaver Logic Engine evaluates landscape data using formally specified logic supplied by the user.
- The two work together, as EMDS evaluates NetWeavers outcomes.
- Program output is restoration priority rankings.

Implications

- Managers can use output to prioritize and determine the degree to which progress can be made to restoration goals.
- Benefits include – equal integration of landscape conditions into decision making, interactions of changes in different landscape conditions can be seen, derivations of the evaluations are transparent.
- Managers and stakeholders can understand what was evaluated, what the outcomes were and where the restoration could occur.

14. Welch, C.M. 2013. The impacts of mountain pine beetle on forest snowpack: accumulation and ablation. M.S. Thesis. Montana State University. Bozeman, MT.

Background & Objectives

This thesis work addresses environmental changes that will impact snow dynamics, specifically the massive outbreaks of mountain pine beetle in lodgepole pine forests in the western USA and Canada. Snow melt rates were compared among homogeneous green stands, heterogeneous green stands, and MPB infected red stands. The study site was the Tenderfoot Creek Experimental Forest in Montana.

Main Findings

- Loss of needles due to MPB mortality impacts the wind transport of snow, temperature gradients and snow interception, and the shortwave/long wave flux.
- Needle fall decreases reflectance (albedo) of snow and shading of snow causing more rapid melting.
- Albedo of an intact stand is 16 to 34% greater than red stands.
- Canopy interception of snow is decreased, and may result in increased accumulation in some areas.
- Red stands have enough needles and branches that shortwave radiation contributions are similar to a forested site.

Implications

- There is a range of impacts on snow accumulation; radiation flux and snow melt among various canopy loss during a MPB outbreak.

15. Schoettle, A.W., Klutsch, J.G. and R.A. Sniezko. 2013. Integrating Regeneration, Genetic Resistance, and Timing of Intervention for the Long-Term Sustainability of Ecosystems Challenged by Non- Native Pests – a Novel Proactive Approach. General Technical Report PSW-GTR-240

Background & Objectives

This report presents a proactive approach to managing for long-term sustainability of ecosystems impacted by white pine blister rust. The paper is an excellent resource that provides a concrete, concise framework to sustain resilience, including recovery capacity after a disturbance, adaptive capacity over time and multi-generational persistence. This approach can be used in degraded ecosystems as active management or in threatened ecosystems not yet impacted.

Main Findings

- The foundation of the approach is baseline genetic and ecological characteristics of the species and ecosystem in order to design timely, appropriate interventions.
- Genetic resistance is essential tool for management.
- Two basic management tools are resistance deployment and landscape-level management of a mosaic of stand age class structure.
- Where heritable resistance is present, a mosaic of stand ages can facilitate selection and accelerate evolution of resistance.
- Maintaining a regeneration cycle is essential, as it results in recovery and the accumulation of selected traits in a population.
- The greater the regeneration capacity, the greater the capacity of the population to recover and tolerate disease pressure.
- Increasing heritable disease resistance is essential to reduce the effect of the disease on survival and fecundity.
- Young, smaller trees are killed more rapidly by blister rust so selection for resistance proceeds more rapidly in younger cohorts.

Implications

- Early deployment of genetic resistance through artificial regeneration and the stimulation of natural selection of genetic resistance prepare threatened ecosystems.
- Estimates of resistance mechanisms and frequencies identify populations that are least/most susceptible.

- Collections of seed, pollen, scion from intact ecosystems ensures gene conservation prior to diversity reduction by blister rust.
- Components of this management approach include: (1) increasing regeneration to increase genetic combinations and offset disease-caused mortality; (2) deploying resistance in a temporal and spatial array to promote population persistence and gene flow; (3) diversification of the age class structures on the landscape to increase the rate of for rust resistance, mitigate impacts of mortality, and promote further adaptive capacity; and (4) preservation of genetic diversity with in situ and ex situ conservation.

16. Six, D.L. 2013. The Bark Beetle Holobiont: Why Microbes Matter. J Chem Ecol (2013) 39:989–1002

Background & Objectives

This review article provides an overview of the importance of insect-microbe holobionts and how this understanding is critical to understanding insect hosts and its interaction with the environment. A holobiont is an animal or plant and all its associated microbes.

Main Findings

- The symbioses with microbes are one of the main reasons insects are so successful and diverse.
- Partnering with microbes, insects can exploit new adaptive zones and genomic variation.
- Bark beetles are associated with an array of fungi and yeast, which are mainly filamentous.
- Bacterial communities are also associated with bark beetles, and likely contribute to beetle nutrition.
- Some provide nutritional benefits, detoxification of tree defensive compounds and assist with pheromone production.

Implications

- Anthropogenic influences of climate change and the introduction of exotics effects insects and their associated microbes, as both are very sensitive to temperature.
- Decreases or increases in some fungi, yeast or bacteria will alter/impact beetle-microbe holobionts.
- Temperature driven shifts in fungi could affect the natural enemies of bark beetles, thus affecting their populations.
- Beetle fitness may be impacted by climate induced changes in the bacteria associated with bark beetle nutrition.
- Applying this information to broader ecological problems will be critical in the accurate prediction of range expansion/contraction and population dynamics of bark beetles in the future, under changing climate.

17. Robert JA, Pitt C, Bonnett TR, Yuen MMS, Keeling CI, et al. 2013. Disentangling Detoxification: Gene Expression Analysis of Feeding Mountain Pine Beetle Illuminates Molecular-Level Host Chemical Defense Detoxification Mechanisms. PLoS ONE 8(11): e77777. doi:10.1371/journal.pone.007

Background & Objectives

Host conifers contain toxic specialized metabolites that bark beetles must tolerate or detoxify in order to successfully reproduce. This research used RNA-seq analysis to monitor gene expression patterns of resistance or tolerance of mountain pine beetles during colonization.

Main Findings

- Beetle-vectored fungi inoculated during attack assist in overcoming host defenses.

- Metabolic changes occur in the beetles shortly after host colonization, suggesting a detoxification and preparation for reproduction.
- Several transcripts were identified in enzyme groups likely important in the detoxification of host defenses mechanisms of mountain pine beetle.
- These transcripts play a role in the metabolism of terpenoid alcohols found in tree resin, oxidative stress, damage control, immune response, antiviral and antimicrobial defense, luciferun-regeneration, reproduction, and pheromone flux.

Implications

- Provides new information on the ability of the mountain pine beetle to cope with toxic host defenses.
- This may assist in the prediction of beetle population expansion rate and extent.

18. Schoettle, A. W., R. A. Sniezko, A. Kegley and K. S. Burns. 2013. White pine blister rust resistance in limber pine: evidence for a major gene. Phytopathology. In Press.

Background & Objectives

This work provides findings from extensive inoculation trials of individual tree seed collections from over 100 limber pines. Data confirms the R-gene (Cr4) is inherited a results in the stem-symptom free trait.

Main Findings

- The frequency of the Cr4 allele ranges from 0 to 13% and averages 5.0%.
- Cr4 is in equilibrium which suggests it is not a recent mutation.
- Spot and needle necrosis traits are also associated with resistance.
- The R allele in limber pine responds differently than the R allele in western white pine.

Implications

- Confirms limber pine as the fourth North American white pine species with a major gene for resistance to white pine blister rust.
- As the pressure from rust increases and selection intensifies, the authors suspect that the genetic frequency of the Cr4 allele will increase. This may already be the case in younger cohorts, but cannot be tested until the cohort bear seed.
- The presence of the Cr4 gene in North American white pines that evolved in the absence of blister rust remains a puzzle. One theory is that abiotic stress tolerance may relate to disease resistance.
- This sample of limber pine will serve as monitors for the evolution of the vCr4 virulent gene in blister rust.
- The authors do not recommend relying on Cr4 alone to sustain limber pine populations and suggest the continuation of current investigations into other types of resistance.
- This information is useful for predicting short-term impacts and for guiding long-term management strategies.

19. Hicke, J.A., Arjan J.H., Meddens, A.J.H., Allen, C.D., and Kolden, C.A. 2013. Carbon stocks of trees killed by bark beetles and wildfire in the western United States. Environ. Res. Lett. 1-8.

Background & Objectives

The objective of this meta-analysis work was to quantify the amount of carbon in trees killed by fire and beetles in recent decades. Existing spatial data sets were combined to estimate above and below ground carbon in killed trees.

Main Findings

- From 1984-2010, fire and beetles killed trees contained >100 Tg C $year^{-1}$
- This represents 9% of total tree carbon in western forests.
- Fire killed more trees in lower elevation forests and beetles killed more trees in higher elevation forests.
- Notable high fire years include: 1987-88, 2000, 2002-03, and 2006-08.
- Bark beetle mortality increased from 1997 to 2010, in two major sets:
    - First ips, fir engravers, Douglas-fir beetle and spruce beetle.
    - This subsided as mountain pine beetle increased and remained high through 2010.
- Over 15% of the carbon in lodgepole pine and spruce/fir forests was in trees killed by beetles.
- Post disturbance carbon dynamics will differ between these two disturbance types.

Implications

- Fires and beetles play a major role in the carbon budget in North America.
- Provides documentation of fire and beetle disturbances in western forests.
- Provides a key, first step toward understanding the influence of natural disturbances on the carbon budget, the spatial pattern of fire and beetles (available at: stacks.iop.org/ERL/8/035032).
- Further work is needed to assess the carbon flux due to the shift of the killed tree carbon to dead carbon pools, slowly decaying over decades, the carbon flux of regrowth, the influence on carbon flux resulting from the decrease in carbon uptake by the trees that were killed.

20. Dematus, C.R. 2013. Effective methods of regenerating whitebark pine (Pinus albicaulis) through direct seeding. M.S. Thesis. Montana State University. Bozeman, MT.

Background & Objectives

This thesis work looked at the effectiveness of direct seeding at six sites in the northern Rocky Mountains. Tests included warm stratification, scarification, caging, and planting caches next to nursery seedlings.

Main Findings

- Seeds that received warm stratification treatment had highest combined germination and survival rates.
- Caging increased germination and survival under certain circumstances, possibly due to the shade provided by the cage.
- Initial results indicate that survival rates of directly sown seeds were higher than nursery seedlings.

Implications

- Direct seeding with warm stratification could be a successful and cost effective restoration method.
- Long-term monitoring of survival rates is needed.

21. Fettig, C.J., Gibson, K.E., Munson, S.A., and Negron, J.F. 2013. Cultural practices for prevention and mitigation of mountain pine beetle infestations. For. Sci.

Background & Objectives

This paper reviews tree, stand and landscape factors associated with MPB infestations and analyzes the effectiveness of treatments including fire, insecticides, semiochemicals, sanitation harvest, thinning, and alteration of age and size classes and species composition.

Main Findings

- Reductions in stand density effect microclimates that affect beetle fecundity, fitness, phenology and voltinism, pheromone plumes and colonization dynamics.
- Stand density also affects host vigor.
- Stand susceptibility is based on four factors: percentage susceptible basal area, average stand age, stand density, and geographic location.
- Direct control methods, such as sanitation harvest, attempt to slow the rate of MPB spread and protect individual trees or stands.
- Indirect control methods attempt to alter the age-class and species structure of the forest to influence MPB outbreak intensity and severity.

Implications

- Designing MPB control strategies is an opportunity for interdisciplinary collaboration and can achieve a range of ecosystem services
- The situation created by MPB tree mortality requires that land managers strive for applications that enhance resiliency as they plan for future forests.

22. Jenkins, M.J., Runyon, J.B., Fettig, C.J., Page, W.G., and Barbara J. Bent. 2013. Interactions Among the Mountain Pine Beetle, Fires, and Fuels. For Sci. In press.

Background & Objectives

This paper reviews current knowledge about how fire and mountain pine beetles interact. This review looks at how fuels reduction treatment and wildfire affect beetles and how beetles affect wildfires by changing the structure, moisture content and chemistry of fuels.

Main Findings

- The quantity and continuity of trees, as fuel or hosts, influences the dynamics of fire and beetle disturbance.
- Changes to fuel loads and location of fuel by MPB activity influences fire behavior.
- Surface fuels influence the majority of fire ignition and spread in lodgepole pole forests.
- Transition to crown fire is influenced by canopy height, presence of ladder fuels and foliar moisture content.
- Fuel reduction treatments result in the release of tree volatiles that influence physiology and behavior of bark beetles.
- Reduction in tree density alters the microclimate that influences beetle fecundity, fitness, and phenology.
- MPB caused tree mortality changes the “fuel profile” of affected stands and landscapes.
- The spatial arrangement and quantity of canopy fuel, vertical fuel and surface fuel changes over time on a “rotation” with bark beetle epidemics.
- Litter chemical composition is altered after MPB outbreaks, with higher concentration of terpenoids, which are associated with greater flammability.
- Post MPB epidemic crown fire intensity predictions are variable and difficult.
- During the early stages of MPB outbreak moisture contents, chemistry and resulting flammability are spatially heterogeneous, as the outbreak progresses heterogeneity decreases.
- Fire behavior varies with the relative abundance of green, yellow, red and needle-less trees.
- Recent wildfires suggest that recently attacked forests are capable of increased probability of crowning, torching and spotting.
- During the later stages of an epidemic, an accumulation of dead and down woody fuels occurs.

Implications

- The implications of MPB-caused tree mortality must be considered when assessing fire fighter safety, fire behavior, suppression strategies.
- Prescribed fire and post-fire management must incorporate options that address critical wildlife habitat needs and changes in bark beetle activity, such as susceptibility of fire injured trees to beetle attack.
- Greater understanding of the implications of MPB-caused tree mortality on fire behavior is urgent.

23. Raffa, K.F., Powell, E.N., and Townsend, P.A. 2013. Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. PNAS. 110(6): 2193-2198.

Background & Objectives

This work shows that whitebark pine has inferior defenses against mountain pine beetle compared to lodgepole pine.

Main Findings

- Whitebark pines exude lower quantities of resin than lodgepole pine.
- Whitebark pine resin has lower concentrations of toxic monoterpenes than lodgepole pine.
- Whitebark's chemical composition does not inhibit the pheromonal communication of mountain pine beetle; in fact whitebark have higher concentrations of alpha-pinene, which is a precursor used by beetle to produce aggregation pheromones.
- When attacked, lodgepole increased their total monoterpene concentrations; whitebark pine did so at a much lower rate.
- In stands containing less lodgepole, beetle attacks increased on whitebark pine.

Implications

- This suggests that sustained contact between bark beetles and whitebark pine has been insufficient to alter beetles behavioral mechanisms or evolved defenses in whitebark pine.
- In the past, cold temperatures provided a sufficient barrier against herbivores in high elevation pines and the trees allocated resources to other physiological processes, rather than in defense mechanisms.
- Climate change is reducing the viability of that evolved strategy.
- This work provides one mechanism for climate driven range expansions, which can be applied to other species.

24. Keville, M.P., Reed, S.C., & Cleveland, C.C. 2013. Nitrogen cycling responses to mountain pine beetle disturbance in a high elevation whitebark pine ecosystem. PLOS One 8(6): 1-8.

Background & Objectives

This work investigated how beetle-induced whitebark mortality affects nitrogen cycling with whitebark pine stands by measuring above and belowground nitrogen pools and fluxes for trees for three different "time since attack" and unattacked trees. This design was effectively a chronosequence. The study was performed in southwest Montana, on the Beaverhead-Deerlodge National Forest.

Main Findings

- In the organic horizon of the soil nitrogen concentrations increased following beetle attack, in red stage trees, which equates to double the ammonium (NH_4+).
- No significant differences in nitrogen were seen between attacked or unattacked in the mineral soil horizons.

- Net soil nitrogen mineralization rates were highest (but not statistically significant) under gray trees and lowest under green trees, in both the organic and mineral soil horizons.
- Soil pH did not vary among infestation stage.
- Soil moisture was higher under red and gray stage trees.
- Litterfall inputs were an order of magnitude greater under red stage trees, than green or gray.
- Soil microbial biomass C:N ratios were significantly lower in red stage trees compared to gray.
- Understory vegetation responses exhibited increased growth from green to red to gray.

Implications

- Nitrogen availability can limit forest regrowth, thus understanding this process is critical to understanding the trajectory of ecosystem recovery.
- Mountain pine beetle attacks result in a pulse of nitrogen to the organic horizon.
- Soil moisture was greatest in red stage trees; soil moisture affects microbial processes such as mineralization, respiration and decomposition.
- The findings of this study, that in the short-term beetle attacks do not have significant effects on soil biogeochemical cycles, were unexpected.
- From a nitrogen cycling perspective, the outlook for whitebark regeneration is promising.

25. Eisen, H.G. 2013. Changes in litter inputs and decomposition in headwater streams during a mountain pine beetle infestation of whitebark pine. M.S. Thesis. Middlebury College. Middlebury, VT.

Background & Objectives

This thesis work investigated how the widespread whitebark pine die-off in the Greater Yellowstone Ecosystem affects organic matter processing and invertebrate communities in headwater streams. Specifically, this work predicted an increase in litter inputs and nitrogen content of the litter inputs. Ten streams in two different basins, Sheep Basin and Branham Lakes Basin, in southwest Montana were sampled. One basin had high whitebark mortality (>80%) and the other <50%.

Main Findings

- Litter input from whitebark pine increased due to mountain pine beetle mortality, during the red stage.
- Vertical litter input increases are constrained to the first few years after beetle attack.
- Lateral input, or litter input from the forest floor, did not differ among attack versus unattacked.
- Lateral litter input continues to enter streams via lateral transport.
- The results of this study do not apply at a landscape scale, due to lack of replication, however within the study basins greater overall litter inputs occur with higher levels of whitebark pine mortality.
- Litter inputs did not change if the trees were not near the streams.
- A greater proportion of needles remained in the streams in the basin with low mortality than the basin with high mortality.
- Invertebrate quantity declined as whitebark mortality increased.
- Naturally shed needles decompose faster than needles from beetle-killed trees.

Implications

- Organic matter budgets for streams in catchments dominated by whitebark will change after a mountain pine beetle outbreak.
- All these findings are confounded by the autocorrelation between whitebark pine mortality and percent cover.