



Forests for Tomorrow Adaptive Management Initiative

Synthesis of Information on Selected Topics & Clarification of Key Uncertainties

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Introduction

The Forests for Tomorrow (FFT) program was established by the British Columbia Government in 2005 in response to the devastating impact of major fires and the mountain pine beetle (MPB) epidemic on the forest land base of the Province. The program is aimed at improving the future timber supply and protecting other forest values through the re-establishment of young forests on lands that would otherwise remain underproductive.

The mountain pine beetle epidemic had affected over 10 million hectares of forest land by 2008 and is expected to expand further. This loss in forest cover is unprecedented in both scale and complexity. Many forest types have been affected across a range of ecological conditions from the dry Chilcotin to moist sub-boreal and high elevation zones. These twin factors of scale and complexity have, in turn, created numerous uncertainties for forest managers. Adaptive management strategies have been proposed as one approach for dealing with these uncertainties.

An adaptive management workshop held on June 26, 2008 under the Forests for Tomorrow program for key staff engaged in restoring forest cover to the mountain pine beetle area raised a range of uncertainties or questions from participants. Our team was asked to review and synthesize information in the existing literature on the most pertinent of these questions for the FFT program.

This report contains our findings on the following topics:

Impact of falling (dead) trees on seedling survival: When stands are attacked by mountain pine beetle, and dead stands are under planted with seedlings, some of those seedlings may die as dead stems fall on them.

Overstory release in response to light: When stands are attacked by mountain pine beetle, some overstory trees survive. It is likely that these surviving trees will 'release' to expand in crown size, diameter and height. This release may shade seedlings, but may also increase stand volumes and provide crop trees earlier than expected.

Managing snowshoe hare damage: High levels of snowshoe hare damage have been detected in plantations in, or adjacent to, standing dead lodgepole pine killed by mountain pine beetle.

Viability of seed from dead lodgepole pine: Dead lodgepole pine stands have cones that contain seed that could contribute to regeneration. How long does seed from dead pine remain viable and have acceptable germination success? Seed viability affects both natural regeneration under stands attacked by mountain pine beetle and determines opportunity to collect seed from those stands.

Response of BC conifers to light conditions created by overstory mortality or removal: Understanding conifer responses to light is key to making silvicultural decisions in stands in BC that have been attacked by mountain pine beetle.

Management of pine grass competition: Pine grass (*Calamagrostis rubescens*) is a major competitor with conifer seedlings in the southern and central Interior, especially in the IDF and is one of several factors that make the dry, grassy Douglas-fir (*Pseudotsuga menziesii* (var. *glauca*) forests in interior British Columbia difficult to regenerate. There is

concern that pinegrass will flourish in the increased light under stands killed by mountain pine beetle and make it difficult to successfully underplant these stands.

Effect of the dwarf mistletoe on regeneration in beetle-killed lodgepole pine stands:

Lodgepole pine dwarf mistletoe (*Arceuthobium americanum*) poses a potential risk to lodgepole pine regeneration in beetle-killed pine stands. Dwarf mistletoe infecting live pine stems in the overstory of beetle-killed stands can proliferate and infect seedlings leading to growth losses.

Effects of stems rusts and a stem canker on regeneration in beetle-killed lodgepole pine stands: Several species of rust and one species of canker pose a risk to lodgepole pine regeneration in beetle-killed pine stands.

Risk of fire after mountain pine beetle: Concern has been expressed that uncontrollable wildfires similar to those experienced in Yellowstone National Park in 1988 will follow pine beetle attacks. Seedlings planted beneath dead stands may be at higher risk of mortality due to wildfire when compared to stock planted in clearcuts.

Impact of Falling Dead Trees on Seedling Survival

The Forests for Tomorrow (FFT) program was established by the BC Government in 2005 in response to the devastating impact of major fires and the mountain pine beetle (MPB) epidemic on the forest land base of the Province. The program is aimed at improving the future timber supply and protecting other forest values through the re-establishment of young forests on lands that would otherwise remain underproductive.

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The Issue

When stands are attacked by mountain pine beetle, and dead stands are under planted with seedlings, some of those seedlings may die as dead stems fall on them. The extent of mortality of seedlings is unknown.

Background

Many studies document rates of snag fall after beetle kill (see table 2 in the synthesis section on “Risk of fire after mountain pine beetle”), but no empirical studies or modelling efforts outlining effects of falling dead trees on seedling survival were found. Two studies, Forests Practice Board (2007) and Coates (2008) studied regeneration in stands that were killed by mountain pine beetle nearly 20 years ago and did not note damage to the understory by falling trees. The lack of observations may mean that tree fall does not have a significant impact on stand density. Similarly, damage by falling pine is not mentioned in broader literature on lodgepole pine succession, which also means it likely is not a large issue.

Basic Biology

A large number of factors interact to influence what mortality of seedlings could be expected under mountain pine beetle-killed stands. Although at first glance it seems it should be possible to model falling stems and estimate mortality, in fact the modelling is so complicated and will lead to such poor predictions that empirical studies would provide better guidance.

Several Issues Complicate Modelling Attempts¹

- Dead stems stay standing for various lengths of time depending on species and site. If the stems fall with branches intact, they will have greater impact on seedlings than if they fall after the main branches have dropped off. The impact (fly swatter effect) of falling branches is unknown.
- Stems will not all fall to the ground but instead will often be suspended on other stems for a time. Suspended stems likely won't kill seedlings immediately and may not kill them

¹ The information in the following sections results from discussions with Dr. D Huggard 604-986-1073.

when they eventually fall to ground. The likelihood and duration of suspension depends in part on how many branches remain.

- Stems will not generally fall randomly but be influenced by wind direction at the time when they are susceptible to blow down. The difference in expected mortality between random and directional falling of dead stems is unknown. The proportion of stands that experience random or directional falling of snags is also unknown.
- Breakage rates will also affect seedling mortality. Snags often break before the main stem falls over. These rates vary by species (which we know), but the impact of these smaller pieces that fall is difficult to estimate.
- Sometimes trees fall and roll, thus impacting more seedling than if they didn't roll. The impacts are dependent on topography and stand density, and also depend upon how many other trees have fallen.
- Natural ingress pattern, distribution, and density will also play an important role in determining impacts.

All in all, the complications to modelling will result in very poor predictions of mortality. We suggest embarking on some empirical studies.

Suggested Approaches

Empirical studies could be undertaken to see if mortality of seedling and saplings by falling trees is a large issue. Measures of cause of seedling mortality would be simple to add to the experimental work proposed by Forest for Tomorrow that will look at seedling responses under various canopy conditions. There may be opportunities to analyse data on falling trees impacting seedlings from the Opax and Ponderosa pine study sites (Vyse pers. comm.).

Key Uncertainties

Little information is available on the degree to which seedling damage and mortality is caused by falling overstory. Proposed experiments for FFT will measure overstory plots including rates of snag fall and down wood decay. As well, measures of seedling survival under different canopy densities will record causes of mortality and damage. Thus, the experiments will gain information on effects of tree fall.

Short-Term Learning

The information gained through the experiments will add information over the long term (5 to 10 years and longer). These experiments will not help decisions over the next few years. We suggest that seedling mortality due to falling trees will not be a large issue and should not affect the decision to under plant.

Literature Cited

Coates, D. 2008. Evaluation of stand dynamics after a 25-30 year old MPB attack in the Flathead Region of south eastern British Columbia. Final Technical Report to FIA-FSP. Project Number: M085196.

Forest Practices Board. 2007. Lodgepole Pine Stand Structure 25 Years after Mountain Pine Beetle Attack Special Report FPB/SR/32.

Personal Communications

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Overstory Release in Response to Light

The Forests for Tomorrow (FFT) program was established by the BC Government in 2005 in response to the devastating impact of major fires and the mountain pine beetle (MPB) epidemic on the forest land base of the Province. The program is aimed at improving the future timber supply and protecting other forest values through the re-establishment of young forests on lands that would otherwise remain underproductive.

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An adaptive management workshop held on June 26, 2008 under the FFT program for key staff engaged in restoring forest cover to the mountain pine beetle area raised a range of uncertainties or questions from participants. This is one of the topics for which our team was asked to review and summarize information in the existing literature.

Executive Summary

When stands are attacked by mountain pine beetle, some overstory trees survive. Many of these surviving trees will 'release' to expand in crown size, diameter and height. This release may shade seedlings, but may also increase stand volumes and provide crop trees earlier than expected.

Overstory trees release in response to decreased competition for light, water, nutrients and space from neighbouring trees. Increased light to existing foliage allows rapid build-up of new foliage, and increased root space increases moisture and nutrient availability.

The degree of release depends on the attributes of the particular species, the length of time trees have been 'suppressed', and local site conditions. Usually the increase in diameter is more than the response of height. Some trees do not response to release. Either they are already in a dominant position, or have a poor root system and low live crown ratio that make it impossible to respond. Sometimes thinning shock (increased light to trees accustomed to shade) will retard release, prevent it altogether, or kill the tree. Generally tolerant species have quicker, more striking responses than intolerant species.

Thinning of trees can improve growing conditions for remaining trees. In effect, the volume of the stand is redistributed to the remaining trees. However, this is not always the case on all sites or species, and thinned volumes are often never recovered.

In stands killed by mountain pine beetle the overstory trees that remain alive may be pine, but could more likely be Douglas-fir or Engelmann spruce. Subalpine fir is more likely an understory species.

For lodgepole pine, Brockley (2007) reported that effects of post-thinning density on tree diameter at breast height (DBH) were strongly linear at both their study sites, with the largest increases in diameter being measured at the lowest stand density. An extreme case is noted by Mason (1915 in Daniel et al. 1979) where a lodgepole pine tree increased from 134 rings per inch to 8 rings per inch over a 4 year period after release. The Canadian Forest Service (2001) examined overstory growth after commercial thinning of lodgepole pine (done in an attempt to beetle proof stand). In the first 5 years after harvest, radial growth rate increased in spaced stands by about 40%, but declined in unspaced stands (by about 18%). In Sullivan et al.'s (2006) overall analysis of tree growth across the three regional replicates, lodgepole pine grew

significantly faster in mean diameter in the low-density than in either of the medium- or high-density stands. The Forest Practices Board studied stands attacked by mountain pine beetle during 1979 in Sub-Boreal Pine Spruce biogeoclimatic units. Survival rates of mature pine ranged from 10 to 50% for the areas sampled. Most overstory trees that survived the infestation grew in diameter significantly faster after the epidemic than before it. The range of response varied from 1.0 to 3.0 times the radial growth during the last 25 years when compared to the previous 25 years. The average increase was approximately 44% greater than the pre-infestation growth rate. Height response to thinning is much less than diameter response, supporting the contention that a limited degree of crowding is required to maximize the height growth of lodgepole pine. Responses of Douglas-fir and Engelmann spruce to increased light are likely more dramatic than for lodgepole pine because the more shade tolerant species often respond better to release (see the section on “Response of BC Conifers to Light Regimes Created by Overstory Removal”, beginning on p.32).

Summary: A qualitative assessment of the few studies we found suggests that lodgepole pine and interior Douglas-fir may increase in crown size by 30 to 40% over 5 years in post beetle attacked stands. Similar increases in stem diameter will occur, increases in height are likely not significant. We expect shading may be increased as much as 10% to 20% near live trees over 5 years as a result of those expanding crowns. At the same time, light levels are increasing due to dying twigs and branches, so the net light levels are not simple to estimate. The proportion of live trees in the stands will determine the net changes in light levels. Empirical studies to assess changes in light and crown closure over time for various combinations of proportion of live and dead stems in a stand would be informative.

The Issue

When stands are attacked by mountain pine beetle, usually some overstory trees survive. It is likely that these surviving trees will ‘release’ to expand in crown size, diameter and height. This release may shade seedlings, but may also increase stand volumes and provide crop trees earlier than expected. The amount and timing of the ‘release’ are of interest.

Basic Biology

Basic silvicultural understanding suggests that overstory trees will release in response to decreased competition for light, water, nutrients and space from neighbouring trees. Increased light to existing foliage allows rapid build-up of new foliage, and increased root space increases moisture and nutrient availability, fostering enhanced growth. The degree of release depends on the attributes of the particular species, the length of time trees have been ‘suppressed’, and local site conditions. Usually the increase in diameter is more than the response of height. An extreme case is noted by Mason (1915, cited in Daniel et al. 1979) where a lodgepole pine tree increased from 134 rings per inch to 8 rings per inch over a 4 year period after release (tree age unknown). Some trees do not readily respond to release. Either they are already in a dominant position, or they have a poor root system and low live crown ratio that make it difficult to respond in a timely manner. “Thinning shock” may occur when increased thermal and solar loading and high evaporative demand on needles accustomed to shade reduces needle function and net photosynthesis. Sometimes “thinning shock” will retard release, prevent it altogether, or kill the tree.

It is well known that thinning of trees can improve growing conditions for remaining trees and can result in stands of the same or even greater volume than the pre-thinned stand if it were left unthinned (e.g., Daniel et al. 1979). Moderate thinning is often found to be more effective than heavy thinning, but even very heavy thinning can result in the same or better stand volumes

than expected from unthinned stands if given enough time. The increase in volume (or even recovery of stand volume) does not always occur, depending on species and site conditions. Coates (2008) observed that in some plots in the Flathead, the volume was greater (approximately 20 years after the attack) than at the time of the mountain pine beetle infestation despite losses of lodgepole pine. In effect, increased diameter growth rates after the attack compensated, at least in part, for the volume lost to the attack, but did not bring the stand up to the volume it would have had without the beetle attack.

Species differ in their response to release. Generally shade-tolerant species have quicker and more striking responses than intolerant species. Capacity for release generally decreases with tree age (but ponderosa pine and Douglas-fir have shown accelerated growth in response to release even after 200 years). Thinning while trees are young (pre-commercial thinning, PCT) increases individual stem diameters Sullivan et al. (2006). PCT alone, or in combination with vegetation management treatments creates the conditions that allow for an increase in crown volume or size on the remaining trees and, because crowns are the production factory of a tree, this usually increases vigour and growth. The duration of accelerated growth depends on stand dynamics as the canopy closes and individual tree growth rate declines. Growth naturally declines after various ages (depending on species and site conditions). Usually, stands attacked by mountain pine beetle are older than stands typically pre-commercially thinned, so we are more interested in release of older overstory trees, but some young stands of pine are also attacked so remaining overstory trees can sometimes be quite young.

In stands killed by mountain pine beetle the overstory trees that remain alive may be pine, but could more likely be Douglas-fir or Engelmann Spruce. Subalpine Fir is more likely an understory species.

Release of Overstory Lodgepole Pine

Lodgepole pine has great potential to respond to various silvicultural practices designed to diversify structural heterogeneity and growth rates of crop trees within stands Sullivan (2006). For lodgepole pine, Brockley (2007) reported that effects of post-thinning density on tree DBH were strongly linear at both their study sites, with the largest increases in diameter being measured at the lowest stand density. These results are consistent with the results reported from other *Pinus* thinning studies (see summary in Johnstone and Cole 1988; Makinen and Isomaki 2004, both in Brockley 2007).

Other studies in British Columbia have documented increased diameter and volume growth of lodgepole pine after release. The Canadian Forest Service (2001) and Whitehead and Russo. (2005) examined overstory growth after commercial thinning of lodgepole pine (done in an attempt to beetle-proof stand). As illustrated in Figure 1, they reported that in the first 5 years after harvest, radial growth rate increased in spaced stands (by about 40%) but declined in unspaced stands (by about 18%). (Fertilization enhanced radial growth in all treatments). They suggested that with growth concentrated on larger stems in spaced units, larger piece size at the final cut should result in higher log values and lower logging costs because the same volume is on fewer pieces so costs associated with handling wood are decreased. There are concerns however over wood quality from more widely spaced stands (see below). As well, market conditions and milling systems affect gains or lack of gains from spacing. Dunsworth (pers. comm.) noted that the expected higher value for larger pieces did not seem to materialize during Weyerhaeuser's Forest Project.

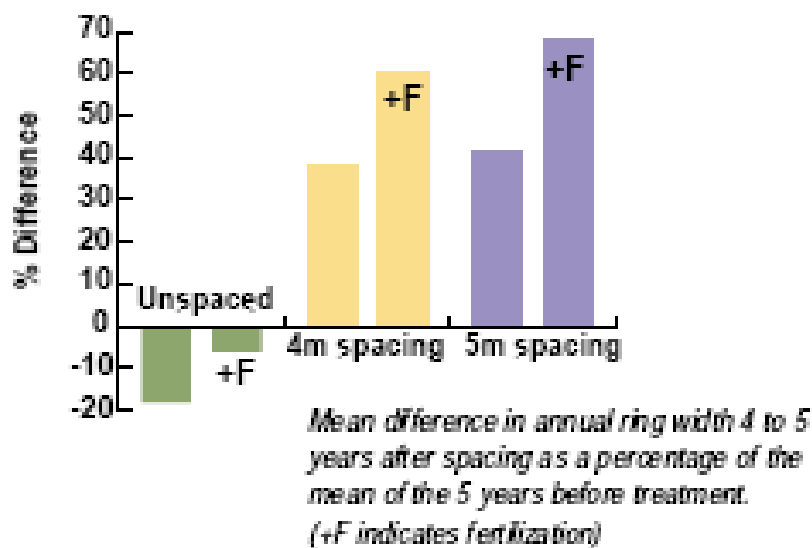


Figure 1. Mean difference in annual ring width 4 to 5 years after spacing (CFS 2001).

Live overstory trees remaining after beetle are not always old because young stands are also attacked. Although stands are rarely attacked at less than 20 or 30 years old, the results from studies below may still be applicable.

Lindgren et al. (2007) showed that thinning of young lodgepole pine (at 12 to 14 years old) resulted in significantly increased DBH and basal area (BA) growth over the 10 year period of their study. As well, 5 years following thinning, crown area, volume and live crown ratio all appeared to be enhanced by PCT and repeated fertilization; however, the differences were not statistically significant. Each study area (located near Summerland, Kelowna and Williams Lake) had nine treatments: four pairs of stands thinned to densities of ~ 250 (very low), ~ 500 (low), ~ 1000 (medium) and ~ 2000 (high) stems ha⁻¹, with one stand of each pair fertilized five times at 2-year intervals, and an unthinned stand. The usual prescription (>90 per cent of stands) for PCT of lodgepole pine in BC is 1200 – 2000 stems per ha, with variations from this range tending to be higher rather than lower density. The broad range of densities applied during this study (250 – 2000 stems per ha) was clearly testing extremes beyond standard operational prescriptions and, at the lowest densities, may give some insight to responses in beetle-killed stands. However, these stands are younger than stands typically killed by beetle. Results were consistent with those reported by several studies following PCT and fertilization treatments Lindgren et al. (2007). Height growth was not significantly enhanced by thinning treatments, volumes generally decreased.

Sullivan et al. (2006) designed a study to test the hypotheses that large-scale stand thinning to low densities, at a 15-year period after PCT, would enhance: (i) productivity and structural features (crown volume and dimensions, diameter, and height growth of crop trees (those dominant trees destined for harvest)); and (ii) coniferous stand structure (abundance, species diversity, and structural diversity of coniferous tree layers). There were five lodgepole pine stands located at each of three replicate study areas in south-central British Columbia: Penticton Creek, Kamloops, and Prince George. These areas were selected on the basis of having several thousand hectares of young lodgepole pine forest. Stands within these tracts of young forest had relatively uniform tree cover and comparable diameter, height, and density of

lodgepole pine trees prior to PCT. Original stands before thinning typically had over 10,000 stems of lodgepole pine, but that varied from site to site. Each replicate had four second-growth lodgepole pine stands (age range of 17–27 years); three of which were PCT to low (~500 stems/ha), medium (~1000 stems/ha) or high (~2000 stems/ha) density. The fourth stand was left unthinned. The second-growth stands had very few remnant trees and snags remaining from previous stands. There was also an old-growth lodgepole pine stand (age range 160–250 years) as part of the set of treatment stands at each study area.

In Sullivan et al.'s (2006) overall analysis of tree growth across the three regional replicates, lodgepole pine grew significantly faster in mean diameter in the low-density than in either of the medium- or high-density stands. However, there was no difference in mean height growth among stand densities over the 15-year period since PCT. The pattern of faster diameter growth in the low-density stands was also reflected in the significantly higher tree volume increment for lodgepole pine in the low than high-density stands across the regional replicates. Mean tree volume increments were different between the low- and high-density stands (but medium density stands were similar to both).

In Sullivan et al.'s (2006) study, trees in the low-density (52.8 m³) stands had a similar crown volume to the medium-density (42.9 m³) stands, but a greater volume than those in the high-density (27.8 m³), unthinned (11.7 m³), or pine component (30.9 m³) in the old-growth stands. Mean crown volume was also significantly lower in the unthinned than in each of the medium-density, old-growth, and high-density stands. This same analysis was conducted with crown volumes of all conifer species included as an overall mean value for the old-growth stands. Again, mean crown volume was significantly different among stands, with the low-density, medium-density, and old-growth stands all having greater crown volumes than those in the unthinned and high-density stands. Mean crown diameter at the widest point was also significantly different for lodgepole pine in these stands. The pattern of differences among stands essentially followed that of crown volume. Measurement of mean crown height indicated that there was a significant difference among stands with the low-density, medium-density, and old-growth stands having the greatest crown heights among stands. When total conifers were considered in the analysis, trees in the old-growth stands had the highest crown heights of all stands. Mean crown ratio (crown length/total height) of trees was also significantly different among treatment stands. Crown ratios were similar in the low-density (0.77), medium-density (0.72), and high-density (0.62) stands, and both the low- and medium-density stands had higher mean crown ratios than those in the unthinned (0.52) and pine component of the old-growth (0.40) stands. The mean crown ratio for overall conifers in the old-growth stands (0.57) was similar to the high-density and unthinned stands, but was lower than those in the low- and medium-density stands. In addition, mean crown volume was similar in the two heavily thinned stands and the overall conifer crown volume in the old-growth stands. Thus, even at an age of 32–42 years, these young stands have comparable crown volumes to those in the old-growth.

Sullivan et al.'s (2006) results at 15 years after treatment followed the same trajectory reported at 5-year and 10-year measurements in these same stands. Heavy thinning from dense stand (usually over 10,000 stems/ha) to 500 stems/ha (low-density) has consistently maintained faster diameter growth than in the medium- and high-density stands. A similar relationship was reported for western larch (Schmidt and Seidel 1988 in Sullivan et al. 2006) and for dominant and co-dominant trees in thinned 20–50-year-old stands (Long 1983, Bailey 1996, both in Sullivan et al. 2006). Height growth continued to be variable but was reasonably uniform at 5.5–6 m when the adjusted mean height increments were analyzed across the regional replicates. The less dramatic effects of thinning on height than diameter growth support the contention that some limited degree of crowding is required to maximize the height growth of lodgepole pine.

These growth patterns match those reported earlier from much smaller (<1 ha) research-scale installations (Sullivan et al. 2006) and from operational-scale installations.

Pre-commercial thinning of lodgepole pine stands is controversial because the treatment does not necessarily achieve the intended yield objectives and negatively affects wood quality. These concerns are related to heavy thinning which reduces the total volume of wood and the ratio of juvenile to mature wood, thereby affecting the structural integrity (load-bearing) of the final lumber products. However, at least in Sullivan et al.'s (2006) study, at 15 years post-thinning in stands 32–42 years of age, mean stand volume (ranging from 108.53 to 132.51 m³/ha) was similar in the medium and high thinning densities, albeit higher than that (72.88 m³/ha) in the low-density thinning. Density management regimes typically represent a compromise between maximization of volume production (m³/ha for a specified time interval) and maximization of individual tree growth and size. Usually, when stands are heavily thinned, the gains in individual tree size do not outweigh the loss of stand volume due to thinning.

The Forest Practices Board studied stands attacked by mountain pine beetle during 1979 in the Wentworth landscape unit, Quesnel forest district. These stands are much older than the ones studied by Sullivan et al, above. The area sampled was in the Sub-Boreal Pine Spruce biogeoclimatic units (SBPSxc, SBPSmk and SBPSdc). They reported mortality, "secondary structure" (seedlings, saplings and sub-canopy trees that survived the pine beetle attack), growth following release, and new regeneration for stands attacked by mountain pine beetle 26 years ago. Survival rates of mature pine ranged from 10 to 50% for the areas sampled. Most overstory trees that survived the infestation grew in diameter significantly faster after the epidemic than before it. Ten of the 14 sampled trees showed a significant growth response. The range of response varied from 1.0 to 3.0 times the radial growth during the last 25 years when compared to the previous 25 years (see Figure 2). The average increase was approximately 44% greater than the pre-infestation growth rate. A photo shows radial growth of approximately 70mm for the last 25 years compared to 40mm for the previous 25 years.

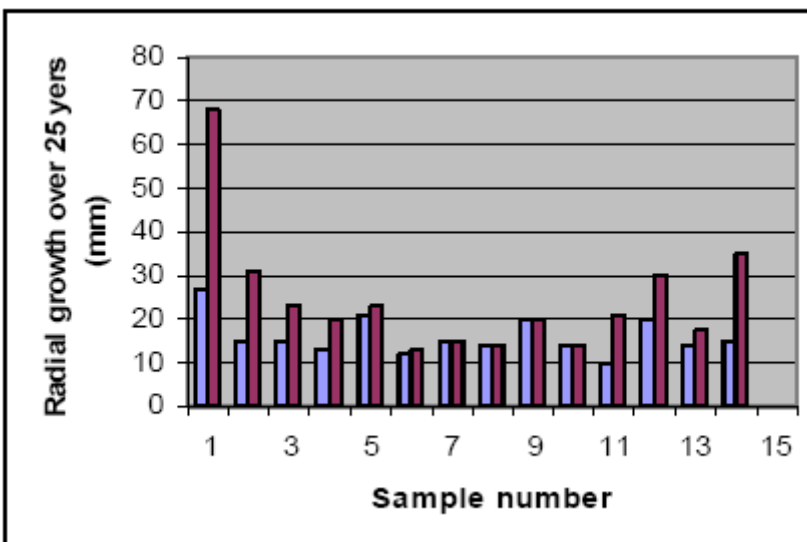


Figure 2. Release of surviving overstory pine trees following 1979 beetle attack over 25 years pre beetle (blue) and post attack (red).

Release of Other Overstory Species

Coates (2008) studied tree response after a 25-30 year old MPB attack in the Flathead region of south eastern BC. His study indicated that growth release of surviving overstory trees varied with species and size following high pine mortality (50-100%). Surviving lodgepole pine trees often exhibited a strong positive response after the attack. Western larch, interior spruce and Douglas-fir showed a similar responses but response in subalpine fir was weak. These results are supported by studies from other areas (Daniels et al 1979).

Douglas-fir will respond to release by increasing diameter growth. Pre-release tree variables that help predict post-release diameter growth include diameter growth rate, diameter, and height. Pre-release height and diameter growth rate are important indicators determining whether advance Douglas-fir should be retained. Trees with greater pre-release height and diameter growth respond more than slower growing trees. Slower growing trees may also respond, but over a longer period of time. Three factors found to be important in predicting post-release height growth are pre-release height growth rate, live crown ratio at time of release, and whether the 5-year pre-release annual height growth was decelerating, constant or accelerating.

Interior Douglas-fir may release in a similar fashion to coastal Douglas-fir. Chan et al. (2006) reported that in Douglas-fir in western Oregon, thinning increased overstory stem growth, crown expansion, and retained crown length. Thinning treatments ranged from light (from 550 original trees thinned to ~250 trees/ha), moderate (~150 trees/ha), and heavy (~75 trees/ha) thinning. Thinned overstory canopies began to close rapidly the third year after thinning, decreasing % skylight by approximately 2%/year, whereas % skylight in unthinned stands increased slightly.

Wood Quality after Release

There is a concern that wood quality will be compromised in open grown trees. More knots and wider rings lead to less desirable wood products. Wood density is often considered to be the most important indicator of clear-wood quality, with high-density wood being preferred to low density wood. Thinning and fertilization treatments are often associated with decreased wood density, primarily because of the disproportionately large increase in low-density earlywood production compared with high-density latewood. Juvenile wood is produced within and near the live crown and has several undesirable wood properties, including lower density, higher fibril angle and shorter cells compared with mature wood, which is produced along the branch-free portion of the lower stem. Because thinning and fertilization treatments tend to increase the size of crowns where juvenile wood is laid down, it follows that these silvicultural treatments would increase the juvenile to latewood ratio throughout the lower stem.

Pruning may mitigate some of the negative stem form and wood quality attributes associated with fast-growing trees without adversely affecting stem growth. However costs of pruning are high and the technique is rarely used on an operational basis in the interior or the coast.

Summary

For overstory lodgepole pine and Interior Douglas-fir we can expect crowns of trees surviving mountain pine beetle infestation to increase in size by 30 to 40% over 5 years in post beetle attacked stands. Similar increases in stem diameter will occur, while increases in height are likely to not be significant. Shading may be increased as much as 10% to 20% near live trees over 5 years as a result of those expanding crowns. At the same time, light levels are increasing due to dying twigs and branches, so the net light levels are difficult to estimate. The proportion of live trees in the stands will determine the net changes in light levels. Empirical studies to assess changes in light and crown closure over time, as well as stem diameter, height and volume, for various combination of proportion of live and dead in a stand would be informative.

Key Uncertainties

There is sufficient current information on overstory release to suggest that live trees will increase in size substantially after their neighbours die. This information can be used to predict general light levels underneath canopies of different levels of live stems.

Additional information can be gained in the longer term to increase the accuracy of the responses. Proposed experiments for Forests for Tomorrow will measure overstory plots including rates of crown expansion, height and diameter growth.

Short-Term Learning

The information gained through the experiments will add information over the long term (5 to 10 years and longer). These experiments will not help decisions over the next few years. We suggest that sufficient information exists to give a reasonable sense to responses of live stems after remaining stems have been killed by beetle attack.

Literature Cited

- Brockley, R., C.B. Statland, F. van Thienen, and P. Staffeldt. 2007. Development of Residual Trees and Regeneration Following Mountain Pine Beetle Attack in Thinned Lodgepole Pine Stands. FIA-FSP Project M075010, Executive Summary.
- Canadian Forest Service. 2001. Commercial Thinning of Mature Lodgepole Pine Results of "Beetle Proofing" Research in the East Kootenays. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, BC.
- Chan, S.S., D.J. Larson, K.G. Maas-Hebner, W.H. Emmingham, S.R. Johnston and D.A. Mikowski. 2006. Overstory and understory development in thinned and underplanted Oregon Coast Range Douglas-fir stands. *Can. J. For. Res.* 36(10): 2696–2711.
- Coates, D. 2008. Evaluation of stand dynamics after a 25-30 year old MPB attack in the Flathead Region of south eastern British Columbia. Final Technical Report to FIA-FSP. Project Number: M085196.
- Daniel, T.W., J.A. Helms and F.S. Baker. 1979. Principles of silviculture. 2nd ed. McGraw hill, NY.
- Hermann, R.K. and D.P. Lavender. 1990. *Pseudotsuga menziesii* Douglas-fir. In: Russell M. Burns and Barbara Honkala Silvics of North American Trees: volume 1 Conifers. USDA Forestry Service. Agric Handbook eds.
- www.na.fs.fed.us/pubs/silvics_manual/volume_1/pseudotsuga/menziesii.htm
- Lindgren P.M.F., T.P. Sullivan, D.S. Sullivan, R.P. Brockley and R. Winter. 2007. Growth response of young Lodgepole Pine to thinning and repeated fertilization treatments: 10-year results. *Forestry* 80(5) 587-611.
- Sullivan, T.P., D.S. Sullivan, P.M.F. Lindgren and D.B. Ransome. 2006. Long-term responses of ecosystem components to stand thinning in young Lodgepole Pine forest. III. Growth of crop trees and coniferous stand structure. *Forest Ecology and Management* 228 (2006) 69–81.
- Whitehead, R. J and G.L. Russo. 2005. Beetle proofed lodgepole pine stands have less damage from mountain pine beetle, Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre. Victoria, British Columbia. Information Report BC-X-402

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Managing Snowshoe Hare Damage

The Forests for Tomorrow (FFT) program was established by the BC Government in 2005 in response to the devastating impact of major fires and the mountain pine beetle (MPB) epidemic on the forest land base of the Province. The program is aimed at improving the future timber supply and protecting other forest values through the re-establishment of young forests on lands that would otherwise remain underproductive.

The mountain pine beetle epidemic had affected over 10 million hectares of forest land by 2008 and is expected to expand further. This loss in forest cover is unprecedented in both scale and complexity. Many forest types have been affected across a range of ecological conditions from the dry Chilcotin to moist sub-boreal and high elevation zones. These twin factors of scale and complexity have, in turn, created numerous uncertainties for forest managers. Adaptive management strategies have been proposed as one approach for dealing with these uncertainties.

An adaptive management workshop held on June 26, 2008 under the FFT program for key staff engaged in restoring forest cover to the mountain pine beetle area raised a range of uncertainties or questions from participants. This is one of the topics for which our team was asked to review and summarize information in the existing literature.

Executive Summary

Snowshoe hare (*Lepus americanus*) damage seedlings by clipping the leader and lateral shoots. As well, they gnaw bark in small patches near the base of the stem or on the lower branches. Feeding damage may occur higher on the tree in deep snow years. Smaller seedlings are highly susceptible to mortality from clipping at the root collar. Larger seedlings, sapling and young trees suffer deformity, reduced growth rate, and occasional mortality from girdling. Feeding damage may: limit regeneration of appropriate tree species in certain forest ecosystems; increase cost of achieving Free Growing Status; decrease net productive forested area; and, result in loss of mean annual increment.

Northern populations of snowshoe hares undergo cycles that range typically 9 to 11 years between population peaks, but populations in different geographic areas of BC seem to be at quite different levels (Quesnel higher than Prince George, for example).

Snowshoe hares require dense, brushy, usually coniferous cover for thermal and escape cover. Heavy cover 3 m above ground provides protection from avian predators, and heavy cover 1 m tall provides cover from terrestrial predators. A wide variety of habitat types are used if cover is available. In northern regions snowshoe hares occupy conifer and mixed forests in all stages of succession, but early successional (<30 years old) forests foster peak abundance. Dense conifer understories support higher hare densities than hardwood understories because the former provide superior thermal and hiding cover. However, broadleaf cover is important to snowshoe hares in some areas.

The quantity of hare browse is linked to both the number of hares using the area, and to the percentage of available cover (>0.5m high), with increasing browse as cover increases. Sometimes even at low populations, hares can focus on fertilized seedlings (which are highly preferred forage) and seriously damage new plantations.

Potential solutions for reducing damage by hares:

- 1) Identifying problem areas and times: Gain knowledge of how extensive and severe attacks are expected to be. Of most concern are areas of high hare numbers at times when populations are increasing or peaking.

- 2) In areas of high hare numbers and peaking hare cycles clearcutting may be the best option. Delay underplanting until numbers drop, and time plantation establishment to occur during the low phase of the snowshoe hare population cycle.
- 3) Where populations are lower, and damage less severe or extensive, then there is more opportunity for underplanting dead pine stands, perhaps in combinations with some of the tools noted below.

Methods to reduce hare damage range from mechanical barriers, scent repellents, alternate food sources, and stand treatments to decrease the attractiveness of the stand to hares. Scent applications are not usually successful operationally, and mechanical barriers have a number of challenges (snow press, poor seedling form, clipping along edges of protector). Alternate food sources have been used successfully and are being tried experimentally in Prince George. Habitat management by removal of overstory and/or understory cover may be the best option. While thinning can reduce overhead cover it can also encourage denser growth of shrubs thus improving hare habitat, so subsequent brushing may be necessary. Other tools include using larger planting stock with a reduced fertilizer regime, and selection of tree species based on snowshoe hare preferences (*Abies*, Douglas-fir, hemlock and sometimes spruce seem less preferred than lodgepole pine). Ongoing local studies by Doyle, Deanna and Ransome should be followed closely.

The Issue

Snowshoe hare (*Lepus americanus* L.) damage seedlings by clipping the leader and lateral shoots. As well, they gnaw bark in small patches near the base of the stem or on the lower branches. Feeding damage may occur higher in deep snow years. The stem of trees less than 60 mm diameter at the root collar is occasionally girdled. Smaller seedlings are highly susceptible to mortality from clipping at the root collar. Larger seedlings suffer deformity, reduced growth rate, and occasional mortality from girdling. High-risk stands occur in areas near clearcuts with young seedlings, and high-density, second growth, pole-size lodgepole pine (*Pinus contorta*) stands with a dense brushy understory. Newly planted seedlings or trees that have recently been fertilized are most attractive. In terms of conservation and sustainability of temperate forests, feeding damage may: limit survival and growth of appropriate tree species in certain forest ecosystems; add costs to reforest these stands in time for Free Growing Status; decrease net productive forested area; and, result in loss of mean annual increment. There is more specific concern that in MPB-killed stands in the Northern Interior Forest Region (NIFR) underplanted seedlings may experience significant damage from snowshoe hares and this will limit the ability to re-establish forest cover quickly.

Young lodgepole pine that are not covered by snow are very susceptible to damage. Most damage occurs within several years of planting and follows a very regular 9 to 11-year population cycle. Ellsworth (2008) reported hares preferred lodgepole pine branches over all other conifers in the winter. In his trials, lodgepole pine was the most nutritious conifer, and it had the highest protein and energy content of all the species tested. In fact, hare consumption of browse in the field and in the laboratory directly reflected the amount of protein contained in the plant species. The two species with the lowest protein and energy values, hemlock and grand fir, were almost entirely avoided in the field, and in the lab they would only resort to feeding on these species when they had consumed all other browse species. It is possible hares can change the course of succession by altering stand composition.

Basic Biology

Northern populations of snowshoe hares undergo cycles that range from 7 to 17 years between population peaks Sullivan (1995). The average time between peaks is approximately 10 years but ranges between 9 and 11 years (Keith 1963, 1990 in Sullivan 1995). The period of abundance usually lasts for 2 to 5 years followed by a population decline to lower numbers or local scarcity. Concentrations of abundance tend to be scattered. Populations across North America do not peak simultaneously in all areas, although there is a great deal of synchronicity in northern latitudes. From 1931 to 1948 the cycle was synchronized within 1 or 2 years over most of Canada and Alaska, despite differences in predators and food supplies. The next anticipated peak in abundance of hares is 2009-2011.

Snowshoe hares utilize different areas of their home range at different times of the year in relation to food availability Watson et al. (1999). Hares switch from a diet of mainly woody browse during the winter to a diet of forbs, grasses, and leaves during the summer. They are adapted to feed within a small vertical band of vegetation 0-1.5 m high. During the winter, as snow accumulates, snowshoe hares utilize higher branches of trees and shrubs. After many years of heavy and consistent browsing, a browse line becomes established below which edible twigs no longer grow. Snowshoe hares seldom, if ever, dig in the snow for food.

Snowshoe hares require dense, brushy, usually coniferous cover. Thermal and escape cover (both provided by low vegetation) are important, especially for young snowshoe hares. Heavy cover 3 m above ground provides protection from avian predators, and heavy cover 1 m tall provides cover from terrestrial predators. Overwinter survival of snowshoe hares increases with increased cover. Visibility in good snowshoe hare habitat ranges from 2 percent at 5 m distance to 0 percent at 20 m. Travel cover is slightly more open, ranging from 14.7 percent visibility at 5 m to 2.6 percent at 20 m Sullivan (1995).

A wide variety of habitat types are used if cover is available. In northern regions snowshoe hares occupy conifer and mixed forests in all stages of succession, but early successional forests foster peak abundance. Dense conifer understories support higher hare densities than broadleaf understories because the former provide superior thermal and hiding cover (Watson et al. 1999). However, broadleaf cover is important to snowshoe hares in some areas. Dense stands of immature hardwoods were the preferred habitat of snowshoe hares in Alberta (Watson et al. 1999). In Alberta, the highest densities of hares during a low population period were in thickets of small black spruce and alder at the edges of bogs, in patches of beaked hazel, and in areas of dense trembling aspen and willow in all seasons (Watson et al. 1999). In mixedwood forests in Alberta, snowshoe hares were in young broadleaf dominated stands consisting of trees less than 20 cm diameter at breast height (DBH at 1.3 m), with high grass cover (during summer only) and high shrub/sapling and willow densities throughout the year. The pattern of habitat use by snowshoe hares is based primarily on understory density not on species composition (Watson et al. 1999), however, species composition may influence population density.

Effects of Forestry Practices

Several studies have examined impacts of forestry treatments on hare populations and on damage to crop trees. We note only those conducted in BC or close to BC.

Thinning of the overstory has been reported to both increase and decrease hare numbers. Ausband and Baty (2005) assessed snowshoe hare habitat use during winter on two precommercial thinning treatments in sapling stands (approximately 18 years old) in

northwestern Montana. One treatment type retained 0.2-ha patches of unthinned saplings, representing 8% of the total stand area, and the second retained 0.8-ha patches of unthinned saplings, representing 35% of the stand area. Snowshoe hare habitat use was also estimated within a nearby control sapling stand and mature conifer stands. Snow tracking and fecal pellet counts were used to estimate hare use before and after thinning treatments were applied. There was no conclusive trend in hare use of sapling stands after thinning, but use within the control stand and adjacent mature stands suggested there was considerable movement of hares to nearby untreated stands after thinning. Hares used retention patches regardless of size, even though large retention patches were four times larger than small retention patches. Because hares demonstrated an affinity for dense patches of residual forest, any retention of untreated saplings may be beneficial for hares during winter (and potentially damaging to susceptible crop seedlings and saplings). Hare use within thinned portions of the stand and unthinned remnant blocks suggests that over the winter hares may also benefit from a connectivity of dense cover. Results from other studies also suggest connectivity of dense cover may benefit hares (Ausband and Baty 2005).

Sullivan and Sullivan (1988), in a study located near Prince George BC, noted that population density and recruitment of snowshoe hares increased significantly in thinned stands of lodgepole pine during the first winter but declined thereafter. Their study focused on lodgepole pine stands (mixed with broadleaves and spruce) that started with stocking of 30000 to 40000 stems per ha and were spaced to 2300 stems in 1979. Grids of live traps and plots to monitor damage to crop trees were set up and monitored from March 1979 to November 1983. Trees were on average 540 cm tall. The study took place in the late stages of the hare abundance cycle when populations were high. After thinning, hare abundance on the treatments increased while those on controls decreased, presumably due to hares being attracted to increased food and cover provided by fallen pine stems. The peak only lasted a year or two before both thinned and control abundances began to decline. Crop tree damage increased in the controls from 35% in 1979 to 57% in 1980 and 69% in 1981, then decreased in 1982 and dropped again in 1983 to 23%. In the thinned stands crop tree damage decreased to 3% when hares were using the fallen pine as forage and cover, but jumped to 75% over the winter of 1980-81 when that food source dried up. After that, damage reduced to 18% due to declining hare populations and deep snow in the thinned stand. Further decreases to 14 percent occurred in the last year of study. Thinning overstocked lodgepole pine had little or no effect on reproduction or survival of snowshoe hares but reduced average body weights. Note that Sullivan and Sullivan (1988) did not include replicates of sampling grids, so their results are not as conclusive as they could be. The increased damage coincided with the increase, peak and decline phases of hare cycle. Supplemental food does not seem to stop the cyclic hare decline, so alternate food sources could be used as means of deflecting hare damage from crop trees. Sullivan et al. (2006) report results of a long term study on effects of thinning and fertilization on hare populations that confirm the trends in earlier studies. Hares benefit from fertilized stands and dense stands, with peak densities in unthinned stands or stands thinned to only 2000 stems. Stands thinned to 100, 500 and 250 stems had lower hare numbers (fertilization did not improve habitat significantly). In another study Sullivan (1994) noted that in areas dominated by conifers, herbicide treatment also did not reduce cover or forage to an extent that affected hare populations.

In a study dealing directly with underplanting and snowshoe hare, Doyle (2007) assessed the effects of removal of cover on hare damage. The study took place in the Skeena-Stikine and Kalum Forest Districts where approximately 40,000 ha of lodgepole pine plantations had been attacked to varying degrees by *Dothistroma*, resulting in a high loss and/or severe reduction in the growth of the young trees in close to 10% of that area. Subsequent underplanting of

different species within the most severely impacted stands has resulted in very high loss of these seedlings as a result of browsing, with the snowshoe hare believed to be the main species damaging the seedlings. In addition to the pine, other commercial tree species (planted and natural regeneration) are also present in the plantations.

Rather than clearcutting the entire plantation, selective pine removal trials were established to determine if the removal of these trees alone would result in higher survival of underplanted seedling trees, and to determine if, or when, the rate of browsing damage decreased in relation to the distance to a non-harvested edge. The MoF established trials (removal of various amounts of dead and dying pine) in four separate locations, to establish if the removal of cover and forage plants for potential browsers, would result in an increase in the survival of underplanted seedlings. Three seedlings species were planted in 2006; sub-alpine fir, western hemlock and interior spruce, and the study looked both at the impact of cover and distance to edge on the rates of browsing damage to these seedlings.

To confirm that hares were the main species browsing the seedling trees, seedlings were examined to identify species specific browsing attributes. In addition, fecal pellet quadrats were established to identify the species and relative density of herbivores using the trial areas. Vegetation type, percentage coverage and distance from forested cover were also measured to establish if these impacted the level of browsing on the seedlings. After the first year of monitoring, 35% of all seedlings were browsed throughout the trial areas (cleared and adjacent control areas combined). On three of the four trial sites most of the browsing was done by hares, while at a fourth site cattle were responsible. Browsing damage impacted ~90% of all seedling spruce underplanted within the un-cleared (control) *Dothistroma* impacted stand, and approximately 40% of all hemlock, and 30% of all the sub-alpine fir. Hares preferentially browsed spruce, while cattle were the main species damaging (browsing and/or trampling) the fir. Overall, 35% of all seedlings (962) planted were damaged by browsing, with spruce approximately three times as likely to be browsed by hares (42%), than western hemlock (14%) or sub-alpine fir (8%) seedlings. Cattle primarily damaged sub-alpine fir with 27% of all seedlings damaged, followed by 8 % of spruce seedlings.)

Clearing of the dying/dead *Dothistroma* trees significantly reduced browsing damage by >50%, in all areas except where the cattle were present. In addition, the probability of browsing declined with distance from cover. At the site with cattle the probability of browse/trampling damage increased the further the seedling was from the uncleared forest edge. Within cleared areas the quantity of hare browse was significantly linked to both the number of hares using the area, and to the percentage of available cover (>0.5m high), with increasing browse as cover increased.

Importance of Hares

Although snowshoes hare forage on conifers during winter, they are valuable components of the ecosystem. Hare are relied upon by many species as a source of food. Great horned owls (*Bubo virginianus*), coyotes (*Canis latrans*), fishers (*Martes pennanti*), and Canada lynx (*Lynx canadensis*) are just a few of the species that prey heavily upon hares. In particular, the Canada lynx, which is federally listed in the United States as a threatened species, preys almost exclusively on snowshoe hares, and lynx populations can be negatively affected by decreases in the hare population (Ausband and Baty 2005). Forest management practices and, in particular, precommercial thinning treatments in coniferous sapling stands and subsequent effects on snowshoe hare abundance have been a recent area of concern since the listing of the lynx. Only thinning below 2000 (or maybe even 1000) stems per ha seem to reduce habitat quality for hare for any significant period of time (Sullivan et al. 2006/07).

Potential Solutions – Reducing Damage by Hares

1) Identifying problem areas and times: The first step in managing hares is to gain knowledge of how extensive and severe attacks are expected to be. Two factors govern the level of expected attack: hare populations, and stand condition. At high population and in stands with good cover, underplanting is not recommended, unless various techniques to protect seedlings are employed. At low populations and low cover, underplanting is more likely successful. At intermediate condition (moderate populations, or suboptimal habitats, then underplanting could be considered, but again one or more of the techniques below would need to be implemented to help improve conifer survival. The effectiveness of different tools, at various times of the hare cycle, remains uncertain and should be addressed by applied research/adaptive management.

2) Reducing seedling damage: Reducing or eliminating seedling destruction by hares is a prerequisite to successful forest renewal in many forests at various periods. Solutions to hare damage range from mechanical barriers and scent repellents to alternate food sources and stand treatments to decrease the attractiveness of the stand to hares. Costs of these treatments depend on several factors, which should be explored while evaluating their utility.

Mechanical barriers: Zimmerling and Zimmerling (1998) examined the effectiveness of a mechanical barrier, a tubular, polyethylene/polypropylene mesh seedling protection device used to reduce overwinter feeding damage by snowshoe hares and meadow voles (*Microtus pennsylvanicus*) on spring planted, plug stock (1 + 0) lodgepole pine. Seedlings fitted with the seedling protection devices had significantly lower levels of feeding damage (3 and 9%) than control seedlings (25 and 41%) respectively on two study sites. Most of the feeding damage to treated seedlings was the clipping of the terminal leader or laterals that were not protected by the protection device. In two instances, a vole tunnelled under the seedling protection device to damage the stem of the treated seedling. This physical barrier can be effective in reducing feeding damage by small mammals on lodgepole pine.

Scent compounds: Certain mustelid scent compounds have suppressed feeding by snowshoe hares Sullivan and Crump (1984), presumably because of a predator-induced "fear response" in the prey species. Sullivan et al. (1985) reported that several predator odor preparations reduced feeding on coniferous tree seedlings by hares. Of the urines tested, red fox produced the most effective short-term suppression of feeding (Sullivan et al 1985).

Sullivan and Crump (1984) investigated the influence of the volatile constituents of red fox (*Vulpes vulpes*) urine in suppressing feeding by snowshoe hares on coniferous tree seedlings. Pen and field bioassays indicated that the odor of fox urine and its principal component, 3-methyl-3-butenyl methyl sulfide, had a negative effect on feeding behavior of hares. The other sulfur-containing compounds, 2-phenylethyl methyl sulfide and 3-methylbutyl methyl sulfide, as well as six other constituents, were not effective. Synthetic urine mixtures composed of eight and nine volatile constituents, respectively, did not suppress feeding in pen bioassays. Pen bioassays clearly demonstrated that 3-methyl-3-butenyl methyl sulphide was the functional compound responsible for altering hare feeding behavior.

Sullivan and Crump (1986) conducted spring field trials of red fox urine odours at Tabor Mountain, 25 km southeast of Prince George, B.C., during April to June 1984. The study area was in the Sub Boreal Spruce biogeoclimatic zone, overgrown with deciduous brush species, mainly willow (*Salix* spp.) and Sitka alder (*Alnus sinuata*), with some aspen (*Populus tremuloides*), black cottonwood (*P. trichocarpa*), and paper birch (*Betula papyrifera*); and had experienced coniferous plantation failure because of feeding damage by snowshoe hares. The hare population cycle peaked in this area in 1980-1981 but the peak was much more of a

plateau than that described elsewhere. Although field results were not as outstanding as those obtained with certain mustelid scent-gland compounds Sullivan and Crump (1984), suppression of feeding in the presence of real urine and 3-methyl-3-butenyl methyl sulfide was still highly significant when compared with a control. This study and that of Sullivan and Crump (1984) demonstrated the potential of mammalian-predator semiochemicals for use as area repellents to protect forest and agricultural crops.

Habitat management: Control of snowshoe hares by habitat management basically involves removal of overstory and/or understory cover. Silvicultural practices can be modified to reduce snowshoe hare use of an area by reducing brushy areas that attract snowshoe hares. While thinning can reduce overhead cover it can also encourage denser growth of shrubs thus improving hare habitat (second-growth stands with dense brushy understories and high sapling densities are optimum snowshoe hare habitat). Hence the effectiveness of removing live or dead overstory to reduce hares will in part depend on the response of understory shrubs. Larger blocks of open areas may reduce hare damage since most damage is found at edges of openings close to cover.

Reduced intensity of feeding has been noted by Sullivan in "open" plantation habitats compared with overgrown habitat. In a habitat manipulation study, Sullivan and Moses (1986) reported a dramatically reduced abundance of hares in a scarified habitat, but the amount of feeding damage to planted coniferous trees was still unacceptable. Sullivan (1994) in the SBS documented that use of herbicide to remove vegetation may reduce forage and cover for a few years, but, particularly in areas with high proportion of young (25 year old) conifer trees, herbicides did not have significant impacts on numbers of hares.

In her review Sullivan (1995) noted that in aspen-birch stands reduction of coniferous cover in cutover areas reduces use by snowshoe hares. Snowshoe hare damage is probably reduced where slash and brush are disposed of by burning. In quaking aspen (*Populus tremuloides*) stands in Alberta, intensive regeneration and periodic removal of competing brush promotes fast early growth and reduces snowshoe hare damage.

Other solutions: Possibly the most pragmatic recommendations include timing conifer plantation establishment during the low phase of the snowshoe hare population cycle, using larger planting stock with a reduced fertilizer regime, and selection of tree species based on snowshoe hare preferences.

The possibility of raising Douglas-fir stock or non-fertilized pine that is less palatable to snowshoe hares has been discussed. Douglas-fir is browsed in some areas, but to a much lesser extent than pine. Spruce may be less palatable than Douglas-fir, but results seem to vary geographically (spruce have been heavily browsed in Smithers area, Doyle pers. comm.). Douglas-fir may be browsed by ungulates so deciding if it is the best alternative also depends on ungulate pressures in the area.

Supplemental food does not seem to stop cyclic hare decline, so alternate food sources could be used as means of deflecting hare damage from crop trees.

Summary

Because hare populations are expected to peak in the next few years, underplanting may result in particularly low survival. Clearcutting may be the best option in areas of heavy attack. In areas where underplanting is desirable and some damage is expected but not prohibitive, potential solutions include planting trees that are less palatable to hares, or planting stock of palatable trees on sites with a sparse cover to support hares (Doyle 2007). As well, there is the

possibility of removing various amounts of dead overstory to reduce cover for hares (provided a flush of shrubs is not expected in response). Protective barriers around trees or chemical deterrents may have to be considered as the only potential way to ensure planting success. Two studies that are underway should be followed closely to help guide the next few years of treatments. 1) Currently Hanna and Doyle have established tree shelter trials (in *Dothistroma* attacked pine stands) to determine if this prevents browsing. (See Danskin 2007). Sullivan (pers. comm.), however, reported that Plantskydd has not been effective. 2) As well, Ransome (Sullivan et al 2006/07; Ransome and Sullivan 2007/08) is examining the effectiveness of removing shrub cover to reduce hare damage. Ransome's proposed study is outlined in Appendix 1. There will also likely be work soon to explore effects of removing dead pine overstory on hare numbers and damage.

This seems an opportune time to conduct field surveys to identify the spatial location of low risk and high risk stand conditions so that post 2011 an underplanting program can be implemented in low risk areas. Higher risk areas could be targeted for overstory removal in various amounts in concert with various tools to limit damage.

Key Uncertainties

Although hares will preferentially feed on planted seedlings even when at low populations, most damage is in areas where populations are high. Identifying population levels seems important, particularly as levels seem to vary place to place in relatively short distances. It may be that pellet counts in stands to be planted are the only way to get a sense of local hare populations

In areas of high hare numbers the options are to avoid underplanting until numbers are lower, or treat stands to reduce damage. Treatment options are areas of uncertainty. How well will alternate food sources work, how well will brushing work under a canopy? Would partial removal of the canopy be beneficial? What are the possibilities for planting larger stock? Less well fertilized stock? Alternate species of seedlings? Many options are worth testing.

Short-Term Learning

All these treatments are suitable for short-term research that will provide information to adapt practices over the next few years. With appropriate controls and replication, useful means of treatment can be assessed.

Literature Cited

Ausband, D.E. and G.R. Baty. 2005. Effects of precommercial thinning on snowshoe hare habitat use during winter in low-elevation montane forests. *Can. J. For. Res.* 35: 206–210.

Danskin, D. 2007. Plantskydd Application in underplanted MPB-killed pine stands: A brief summary. MoF. Prince George. Oct. 16.

Doyle, F. 2007. Appendix 5: The First Year Impact of Snowshoe Hare browsing on seedling trees planted in *Dothistroma* attacked Pine stands: Is browsing reduced by overstorey removal? Nadina Forest District Forest Health Strategy 2008-2009 Ministry of Forests.

Ellsworth, E. 2008. Stories of applied animal behavior. In BEHAVE, journal for graduate Foraging Ecology Class at the University of Idaho and Washington State University under the direction of Drs. Karen Launchbaugh and Lisa Shipley found at http://www.cnr.uidaho.edu/range556/Appl_BEHAVE/projects/hare_forage.html

Ransome, D. and T.P. Sullivan. 2007/08. Managing Damaging Agents in MPB-killed Stands & Protection of New Plantations: Annual Report Submitted to Forest Practices Branch, Forests for Tomorrow.

Sullivan, T.P. 1994. Influence of herbicide-induced habitat alteration on vegetation and snowshoe hare populations in sub-boreal spruce forest. *J. Appl. Ecol.* 31: 717-730.

Sullivan, J. 1995. *Lepus americanus*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.fs.fed.us/database/feis/> [2008, August 25].

Sullivan, T.P., L.O. Nordstrom, and D.S. Sullivan. 1985. Use of predator odours as repellents to reduce feeding damage by herbivores. I. Snowshoe hares (*Lepus americanus*). *J. Chem. Ecol.* 11: 903-919.

Sullivan, T.P., and Crump, D.R. 1984. Influence of mustelid scent gland compounds on suppression of feeding by snowshoe hares (*Lepus americanus*). *J. Chem. Ecol.* 10:1809-1821.

Sullivan, T.P. and D.R. Crump. 1986. Feeding responses of snowshoe hares (*Lepus americanus*) to the volatile constituents of red fox (*Vulpes vulpes*) urine. *J. Chem. Ecol.* 12: 729-739.

Sullivan, T.P. and R.A. Moses. 1986. Demographic and feeding responses of a snowshoe hare population to habitat alteration. *J. Appl. Ecol.* 23: 53-63.

Sullivan, T.P. and D.S. Sullivan. 1988. Influence of stand thinning on snowshoe hare population dynamics and feeding damage in juvenile lodgepole pine. *J. Appl. Ecol.* 25: 791-805.

Sullivan, T.P., D.S. Sullivan, P.M.F. Lindgren and D.B. Ransome. 2006. Influence of repeated fertilization on forest ecosystems: relative habitat use by snowshoes hare (*Lepus americanus* L). *Can. J For. Res.* 36:2080-2089.

Sullivan, T.P., P.M.F. Lindgren, D.B. Ransome, and D.S. Sullivan. 2006-07. Small mammal population monitoring and protection of new plantations. Annual Report Submitted to: Forest Practices Branch, Forests For Tomorrow.

Watson, J., B. Beck, J. Beck, M. Todd and R. Bonar. 1999. Snowshoe hare winter range habitat suitability index model version 4. Foothills Model Forest.

Zimmerling, T. and L.M. Zimmerling. 1998. Effectiveness of a physical barrier in deterring vole and snowshoe hare feeding damage to lodgepole pine seedlings. *West. J. Appl. For.* 13:12-14.

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Appendix 1: Ongoing studies in FFT areas

Ransome et al. are continuing a local study in the Northern Interior Forest Region near Prince George. Presently, they are monitoring hare populations and damage under a variety of overstory conditions with the intent to gain information on where hare populations are in their cycle. Since FFT are active in both merchantable and non-merchantable stands, the study is looking at both overstory conditions. On some of these monitored sites, treatments such as supplying alternate food sources, brushing understory, or trying less fertilized stock, will be

implemented (and the monitoring information used as baselines. They are addressing 3 objectives:

- (1) Install a network of monitoring sites and monitor vole and hare populations in representative MPB-killed non-merchantable lodgepole pine stands in the NIFR. Relate vole numbers to stand conditions, and potential for feeding damage to plantations. Monitor relative habitat use by snowshoe hares at the NIFR network of MPB-killed stands. Monitoring sites are located near Dunkley, Prince George, and Vanderhoof in the Prince George and Vanderhoof Forest Districts.
- (2) Install a network of monitoring sites and monitor habitat use by hares in representative MPB-killed merchantable lodgepole pine stands, in the NIFR. Monitoring sites are located near Quesnel, Fort Fraser, and Fort St. James in the Quensel Forest District, Vanderhoof Forest District, and Fort St. James Forest District, respectively.
- (3) Monitor the survival of seedlings planted in MPB non-merchantable stands. Monitoring sites for the survival trials are located between Quesnel and Prince George in the Prince George Forest District.

Ransome et al.'s Results and Management Recommendations for 2007/2008

Objective 1: Live trapping of voles and snowshoe hares was initiated in 2006 and was conducted from May to September in 2006 and 2007. Similarly, pellet plots for snowshoe hares were examined on all sites in 2006 and 2007.

- There appeared to be an increase in meadow voles in MPB-killed non-merchantable stands from 2006 to 2007.
- Abundance of red-back voles appeared similar in MPB-killed non-merchantable stands from 2006 to 2007. However, their numbers appear to be building to peak populations in non-pine mature forests.
- Abundance of hares appeared similar in 2006 and 2007 for Dunkley. However, there were more hares captured in 2007 than 2006 in Prince George and Vanderhoof. Similarly, there was a two-fold increase in number of pellets encountered in the pellet pots from 2006 to 2007 for Prince George and Vanderhoof. Although the data only represents two years of monitoring, the use of MPB-killed non-merchantable stands by hares is increasing.

Objective 2: Pellet plots for snowshoe hares were established and cleared in 2007.

- Abundance and habitat use of MPB-killed merchantable stands was greater in Quesnel than Fort Fraser or Fort St. James.
- One merchantable stand had approximately the same use by snowshoe hares as did the unthinned control (optimal habitat).

Objective 3: Four sites were monitored for clipping by snowshoe hares and voles on freshly planted seedlings in the NIFR. Sites were planted in mid to late July 2007 and assessed for damage the first week of August.

- Block 93G043-524 suffered a high level (36%) of damage within a few weeks after planting.
- Block 93G043-524 suffered lower levels of damage (6%) than the previous block. Remaining blocks suffered low damage (< 1%).
- 95% of the seedlings were clipped by snowshoe hare and 5% by voles.

Ransome et al.'s Recommendations for the 2008-2009 Monitoring Period

Management Recommendations: As both hares and meadow voles appear to be increasing in MPB-killed non-merchantable stands:

- (1) Continue interacting with FFT operational staff in NIFR of the Ministry of Forests and Range; annual report to FFT; and include an additional extension event (e.g. field tour September 2008, SISCO/NSC).
- (2) Continue monitoring of vole populations in MPB-killed non-merchantable stands, salvage clearcuts, and uncut forest stands.
- (3) Continue monitoring snowshoe hare populations and relative habitat use by hares in MPB-killed stands (both non-merchantable and merchantable stands) and live unthinned control stands.
- (4) Assess whether abundance of voles and hares is related to percent cover and/or volume of vegetation. If there is a relationship between these species and the vegetation, this information can be used to predict which sites are most susceptible to damage.
- (5) Plant those MPB-killed non-merchantable stands, not currently planted, that are being monitored for damaging agents, in order to:
 - Superimpose a survival trial on these stands, similar to that currently being conducted for Objective 3 (above).
 - Superimpose damage-reduction techniques on the current design to determine their effectiveness in reducing damage to planted seedlings.

Viability of Seed from Dead Lodgepole Pine

The Forests for Tomorrow (FFT) program was established by the BC Government in 2005 in response to the devastating impact of major fires and the mountain pine beetle (MPB) epidemic on the forest land base of the Province. The program is aimed at improving the future timber supply and protecting other forest values through the re-establishment of young forests on lands that would otherwise remain underproductive.

The mountain pine beetle epidemic had affected over 10 million hectares of forest land by 2008 and is expected to expand further. This loss in forest cover is unprecedented in both scale and complexity. Many forest types have been affected across a range of ecological conditions from the dry Chilcotin to moist sub-boreal and high elevation zones. These twin factors of scale and complexity have, in turn, created numerous uncertainties for forest managers. Adaptive management strategies have been proposed as one approach for dealing with these uncertainties.

An adaptive management workshop held on June 26, 2008 under the FFT program for key staff engaged in restoring forest cover to the mountain pine beetle area raised a range of uncertainties or questions from participants. This is one of the topics for which our team was asked to review and summarize information in the existing literature.

Executive Summary

How long does seed from dead pine remain viable and have acceptable germination success? How much seed remains in the cone bank of dead pine and how fast does it decline over time? These are questions that FFT recipients asked mainly due to concern that areas left to regenerate naturally may not do so due to non-viable seed. Seed viability affects both natural regeneration under stands attacked by mountain pine beetle and determines opportunity to collect seed from those stands. We do not explicitly address the impacts of the mountain pine beetle epidemic on seed availability for nurseries, but rather focus on how seed viability impacts decisions of FFT recipients. We mention cone collection only to suggest broad guidelines should recipients collect their own seed. We do not evaluate impacts to the provincial seed supply of the vast amount of dead pine. Seed viability is one of many factors affecting success of natural regeneration under dead pine stands.

Lodgepole pine is usually characterized by serotinous cones – those that remain closed on the tree when seed maturation is complete. In serotinous cones, the cone scales are sealed together with resin and require a temperature of between 45 and 60°C for the bond to be broken. Not all trees within a stand will possess serotinous cones, although stands may be predominantly serotinous or non-serotinous. Seed depends mostly on levels of cone serotiny.

Serotinous cones are generally considered to be discrete, closed units isolated from the tree and the environment as long as serotiny is maintained. There have been many observations of viable seed from serotinous cones more than 10 years old. During 2006, BC's Tree Improvement Branch looked at the viability of seed from trees that had been dead for 10 years and found viable seed in all collections investigated.

Concern for loss of viable seed arises when there is a lack of serotiny. Although most MPB-killed lodgepole pine stands may initially have a canopy seed bank, serotiny is being lost on many sites because of the increase in direct and indirect solar radiation reaching the defoliated crowns. Cones closer to the ground will achieve high temperatures sooner and, therefore, open first. Conditions within many of these killed stands are limiting the window of opportunity to secure the canopy seed bank. Whether the disseminated seed will form a stand is uncertain and highly variable by site. Considerations include the rate of seed release, degree of mineral soil exposure, predation of seeds, and the environmental conditions of the site.

There is also the potential for there to be a seed quality issue if a tree is dying and trying to develop cones at the same time. There may not be adequate reserves to try and prevent dying and transport sugar to the cones, resulting in poor quality or non-viable seed.

Another concern expressed pertains to the storage characteristics of lodgepole pine seed. The Tree Improvement Branch (2008) and Tree Seed Working Group (2007) observed and quantified excellent storage characteristics with this species and estimate an average linear decrease in germination capacity of only 0.05% per year or 1% in 20 years. There should not be any significant concerns regarding the longevity of the large-scale collections taking place today, although seed may be reduced in abundance in the future due to the smaller area of lodgepole pine producing seed post-beetle. (In terms of seed yield (kg of seeds per hl of cones), there has been a trend towards decreased yield in the 2006 and 2007 collection years. Average yield increased from 2001 to 2005, but has subsequently dropped. The most reasonable explanation for this apparent drop in seed yield is the greater proportion of class 3 and class 4 cones appearing in seedlots).

Solutions:

- 1) For natural regeneration, attempt to promote conditions conducive to seed germination. The probability of natural regeneration can be increased by removing dead pine stems, increasing mineral soil exposure and spreading the cone-bearing branches uniformly across the site. Coates (2008) noted little pine regeneration in the first 10 years in post-beetle attacked pine stands in the Flathead. This is not due to seed viability, but to site and light factors.
- 2) For seed collection, collect seed from dead trees only if no seed is available from seed orchards or from live natural stands. Follow standard cone collection procedures and be aware of cone classes. Class 4 and 5 are non-serotinous or damaged cones and these should not be collected. Class 1 are fully serotinous cones. Classes 2 and 3 are more subjective, as they are based on the proportion of the cone that is weathered. Class 2 cones have partial weathering (up to 66%) and class 3 cones have between 67 and 100% weathering.

The Issue

An outstanding regeneration question is how long seed from dead pine remains viable and has good germination success. This affects FFT recipients' decisions on whether to rely on natural regeneration or plant a stand. It also affects opportunities to collect seed.. Seed viability is one of many factors affecting success of natural regeneration under dead pine stands. Seed viability is maintained for extended periods in serotinous cones of lodgepole pine but seed may not be viable when cones are not serotinous or lose serotiny (see below).

Most of the concern regarding seed viability arises from observations of the lack of natural pine regeneration in stands killed by mountain pine beetle. Coates (2008) for example, noted little pine regeneration in the first 10 years in post-beetle attacked pine stands in the Flathead. *This lack of regeneration, however, is likely not due to seed viability, but to site and light factors. Studies reviewed below suggest that viable seed is present in the cones of beetle killed lodgepole pine trees for at least a decade after trees die.*

Basic Biology of Lodgepole Pine Seed Production

(From TIB 2008): Lodgepole pine cones require two growing seasons to mature after pollination (26–27 months after bud differentiation). Fertilization takes place in the season after pollination and is followed by growth and development of the embryo, seed coat and megagametophyte

(nutritive tissue). Lodgepole pine can begin to form seed cones at 10–15 years of age. The cones can contain between 100 and 130 cone scales. Not all scales are equally fertile. The basal cone scales are sterile – they do not reflex backwards, as there are no viable seeds to disseminate. With the potential for 2 seeds per scale, the average maximum seed potential is 40–60 seeds per cone.

Lodgepole pine is usually characterized by serotinous cones – those that remain closed on the tree when seed maturation is complete. There is variability in serotiny; not all trees within a stand will possess serotinous cones, although stands may be predominantly serotinous or non-serotinous. The coastal variety (var. *contorta*) of lodgepole pine produces mainly non-serotinous cones. In serotinous cones, the cone scales are sealed together with resin and require a temperature of between 45 and 60°C for the bond to be broken (see Tinker et al. 1994 for a thorough review). The seeds will remain viable within the cones until fire or high temperatures break the resin bond.

Once the serotinous bonds are broken, the cone scales can open and close with changes in atmospheric conditions. Flexing of the cone scales depends on the moisture content of the scales – the higher the moisture content, the greater degree of cone scale flexing and seed release (Hellum and Barker 1980). This is due to differential shrinkage of the top and bottom of the cone scale (Harlow et al. 1964). Depending on cone scale moisture content and atmospheric conditions, seed release may be instantaneous or may occur over several years. Cone serotiny and the associated traits of asymmetry and thickening of cones scales exposed to weathering (or fire) are considered to be more evolved characteristics of the genus *Pinus* (Tree Improvement Branch 2008). (It has been hypothesized that cone serotiny is controlled by a single gene.)

Without fire or extreme temperatures, the annual production of serotinous cones will contribute to the canopy seed bank. Decreased serotiny has been correlated with increased elevation and with increased latitude. A trend of decreased serotiny has also been observed moving from east to west within the interior of BC (M. Carlson, pers. comm., March 2008 in Tree Improvement Branch 2008). It has been observed by many that cone serotiny is rare in young stands, but far more common in older stands. The age of transition is variable, but has been estimated at between 15 and 30 years (Tree Improvement Branch 2008). Young stands produce less serotinous cones and seed is released annually to take advantage of gaps in stand stocking. As stands mature and stocking stabilizes, trees generally become more serotinous and start to build up the canopy seed bank for future regeneration following fire or other disturbance events. The proportion of serotinous cones in a stand has also been linked to the most recent disturbance type. Stands originating from severe fires showed a high proportion of serotinous cones, and those originating from other disturbances or mixed fire severity regimes show a higher proportion of non-serotinous cones.

With all of these interacting factors, it is difficult to define a consistent pattern of cone serotiny across the landscape. Cone serotiny is a highly evolved characteristic allowing the species to take advantage of a wide variety of sites and conditions.

Results of Past Studies

There is little concern about the seed viability of serotinous cones from dead lodgepole pine trees; the concern arises due to lack of serotiny. Serotinous cones are generally considered to be discrete, closed units isolated from the tree and the environment as long as serotiny is maintained. Viability of seed within old, serotinous cones was noted as early as 1880 when

Sargent (1880 in Tree Improvement Branch 2008) reported germination of seed from 10-year-old serotinous cones.

There have subsequently been many similar observations (see Tree Improvement Branch 2008 for refs.), and in 2006 the Tree Improvement Branch looked at the viability of seed from trees that had been dead for 10 years and found viable seed in all collections investigated. At the 2003 Forest Genetics Council Northern species committee meeting questions arose about collection of seed from dead lodgepole pine. This was primarily in response to the need for increased seed to regenerate beetle-killed stands. An invitation was extended to operators interested in determining whether stands of dead trees still had viable seed. Nine collections from the Nadina forest district were received at the Tree Seed Centre, cone evaluations performed and seed extracted and hand dewinged. The seed quantities were quite small and so germination tests were carried out on unprocessed seed and performed cutting tests on the ungerminated seed. This did not provide estimates of germination capacity for a seedlot collected from these stands, but provided information regarding whether viable seed is present in these dead stands of lodgepole pine. Results of germination tests were low (between 66 and 85% germinants), below the 95% level obtained by most lodgepole pine seedlots collected today, but in part this reflects unprocessed seed. Regardless of germination standards, results indicate that even ten years after tree mortality viable seed can still be found within the cones. This agrees with many studies on the long-term viability of seed on lodgepole pine trees. The reason for the longevity of viable seed is thought to be because following cone and seed maturity, the vascular connection between the cone and tree are broken and the cone functions independently (no further water or sugar exchange). The serotinous cone provides good insulation and protection for the seed. It is possible that in cooler areas seed may not be released from pine after mountain pine beetle attack because temperatures never reach levels to break serotiny. Even if serotiny is broken eventually then understory vegetation may have increased to levels that may outcompete small pine germinants.

Because serotinous cones house viable seeds, seed viability only becomes a concern when cone serotiny is lost. Although most MPB-killed lodgepole pine stands may initially have a canopy seed bank, serotiny is being lost on many sites because of the increase in direct and indirect solar radiation reaching the defoliated crowns, the higher solar energy breaks serotiny. Cones closer to the ground will achieve high temperatures sooner and, therefore, open first. These conditions are limiting the window of opportunity to secure the canopy seed bank. Whether the disseminated seed will form a stand is uncertain and highly variable by site. Considerations include the rate of seed release, degree of mineral soil exposure, predation of seeds, and the environmental conditions of the site.

There is also the potential for there to be seed quality concerns if a tree is dying and trying to develop cones at the same time. There may not be adequate food reserves to try and prevent dying and transport sugar to the cones, resulting in poor quality or non-viable seed. On the other hand, maybe the stresses result in allocation of available resources to reproduction; there is some anecdotal evidence on collections from red and green attack trees. The Tree Improvement Branch (2004) performed some seed evaluations and found no observable difference between seed collected from red and green attack trees. They did not process this seedlot and so do not know the relative proportions of the two tree types, but the final seedlot did achieve a germination of 96%. (The 2004 paper notes that there are also two more seedlots that were collected in 2004 from green and red attack trees that were currently being processed at a private extractor - results from those should be available by now).

Another concern is the loss of serotiny combined with slow release of seed over time, therefore decreasing seed yield. Loss of serotiny (breaking of bonds) and cone opening are two distinct

events that often, but not always occur at the same time, so that serotiny can be lost, but cones don't open fully or quickly and seed can degrade within the cone.

A final concern expressed pertains to the storage characteristics of lodgepole pine seed, however storage concerns seem unfounded. The Tree Improvement Branch (2008) and Tree Seed Working Group (2007) observed and quantified excellent storage characteristics with this species and estimate an average linear decrease in germination capacity of only 0.05% per year or 1% in 20 years. There should not be any significant concerns regarding the longevity of the large-scale collections taking place today.

Solutions

1) Rely more on natural regeneration where canopies after mountain pine beetle attack are open enough to allow light to the ground and break cone serotiny. Also choose areas where understory competition is not intense. For natural regeneration, attempt to promote conditions conducive to seed germination. Removing the overstory would help natural regeneration if light reaching the canopy floor is low (see point 2 below). The probability of natural regeneration can be increased by spreading the cone-bearing branches uniformly across the site (Tree Improvement Branch 2008). Bancroft (1996 in Tree Improvement Branch 2008) describes post-harvest survey procedures and drag scarification methods for naturally regenerating lodgepole pine stands. Most of these treatments, however, have not been attempted under dead canopies. Studies to assess the rate of pine germination are recommended. Coates (2008) noted little pine regeneration in the first 10 years in post-beetle attacked pine stands in the Flathead. This is likely not due to seed viability, but to site and light factors.

2) Where canopies limit light penetration to the ground (either by having dense dead stems or considerable density of live stems after beetle attack), or where cooler climate make release of seed doubtful, or where getting ahead of understory growth is important, then focus on planting rather than relying on natural regeneration.

3) When collecting lodgepole pine seed, collect from dead trees only if no seed is available from seed orchards or if there is no seed from live natural stands for the area. When collecting seed from dead pine, be aware of cone classes to estimate seed viability (Tree Improvement Branch 2008, see Figure 3 below) as this varies by class. Cones have been categorized into 4 or 5 classes based on the likelihood of having good amounts of viable seeds. Class 4 and 5 are non-serotinous or damaged cones and these should not be collected. Class 1 are fully serotinous cones. Classes 2 and 3 are more subjective, as they are based on the proportion of the cone that is weathered. Class 2 cones have partial weathering (up to 66%) and class 3 cones have between 67 and 100% weathering.

Cone crop ratings are quite general and subjective with regards to total cones on a tree and the proportion of trees having a good crop (Tree Improvement Branch 2008). The individual cone standard was 20 filled seeds per cone, but there are many crops being collected that do not meet this standard. The seed need, harvest cost, and whether orchard crops will become available for an area, will drive the decision for seed collection, but a sample evaluation will provide an indication of what can be expected from the crop and the total volume of cones required.

Key Uncertainties

There seems to be viable seed for at least a decade after trees die. No further investigations into seed viability seem warranted at this time. However, there still remains considerable uncertainty about the factors governing actual germination success. We investigate some of

those factors in other background papers (light reaching the understory, pine grass competition, hare damage, rust and mistletoes, and overstory release).

Class 1**Class 2**

Insets illustrate
cone weathering
variation on
opposite sides of
the same Class 2
and Class 3 cones

**Class 3****Class 4**

Figure 3. Lodegpole pine cone classes (Tree Improvement Branch 2008).

Literature Cited

Bancroft, B. 1996. Fundamentals of natural lodgepole pine regeneration and drag scarification. BC Min. For., Silv. Prac. Br., Victoria, BC. 30 pp.

<http://www.for.gov.bc.ca/hfp/publications/00096/NatPlregen.pdf>

BCMoF Tree Seed Centre Cone and Seed Improvement Program. 2004. Seed from Dead lodgepole pine trees. Dave Kolotelo Cone and Seed Improvement Officer from Seed and Seedling Extension Newsletter, Volume 15, December 2004

Coates, D. 2008. Evaluation of stand dynamics after a 25-30 year old MPB attack in the Flathead Region of south eastern British Columbia. Final Technical Report to FIA-FSP. Project Number: M085196

Harlow, W.M., W.A. Cote Jr., and A.C. Day. 1964. The opening mechanism of pine cone scales. Jour. For. 62:538–540

Hellum, A.K. and N.A. Barker. 1980. Cone moisture content influences seed release in lodgepole pine. Can. J. For. Res. 10:239–244.

Sargent, C.S. 1880. Vitality of the seeds of *Pinus contorta*. Bot. Gaz. 5:54.

Tinker, D.B., W.H. Romme, W.H. Hargrove, R.H. Gardner and M.G. Turner. 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. Can. J. For. Res. 24:897–903.

Tree Improvement Branch. 2004.. Seed from dead lodgepole pine trees. BC Min. For., Tree Tree Improve. Br., Victoria, BC. Seed and Seeding Ext. Newsletter, Vol. 15.
<http://www.for.gov.bc.ca/hti/publications/misc/DeadPLiSSEN.pdf>

Tree Improvement Branch. 2008. Lodgepole Pine Cone Collections Tree Improvement Branch Bulletin 05, March 2008.

Tree Seed Working Group. 2007. Conifer Seed Longevity by Dave Kolotelo. From Tree Seed Working Group News bulletin, Volume 45. Cone and Seed Improvement Program, BCMoF Tree Seed Centre.

Response of BC Conifers to Light Regimes Created by Overstory Removal

The Forests for Tomorrow (FFT) program was established by the BC Government in 2005 in response to the devastating impact of major fires and the mountain pine beetle (MPB) epidemic on the forest land base of the Province. The program is aimed at improving the future timber supply and protecting other forest values through the re-establishment of young forests on lands that would otherwise remain underproductive.

The mountain pine beetle epidemic had affected over 10 million hectares of forest land by 2008 and is expected to expand further. This loss in forest cover is unprecedented in both scale and complexity. Many forest types have been affected across a range of ecological conditions from the dry Chilcotin to moist sub-boreal and high elevation zones. These twin factors of scale and complexity have, in turn, created numerous uncertainties for forest managers. Adaptive management strategies have been proposed as one approach for dealing with these uncertainties.

An adaptive management workshop held on June 26, 2008 under the FFT program for key staff engaged in restoring forest cover to the mountain pine beetle area raised a range of uncertainties or questions from participants. This is one of the topics for which our team was asked to review and summarize information in the existing literature.

Executive Summary

Understanding conifer responses to light is key to making silvicultural decisions in stands in BC that have been attacked by mountain pine beetle. A large body of science has accumulated during the last 10 years on both leaf-level and whole-plant-level light responses for BC conifer species. This work indicates the following:

- All species grow best under full sunlight
- Shade-tolerant species (e.g. western hemlock, western redcedar, subalpine fir) grow well under low light and relatively poorly under high light
- Shade-intolerant trees, especially lodgepole pine, can grow (more so in height than diameter growth) under low light but will likely not survive well
- Shade-tolerant species have a strong capacity to adjust carbon assimilation, slow or stop growth and reallocate carbon to allow both persistence and rapid response to decreasing or increasing light conditions
- Size and vigour significantly effect light responses across species
- Shade-tolerance response appears to be relatively consistent across the regions in BC
 - There are relatively small differences in light response curves among species with the exception of *Pinus* species
 - Species choice for light response appears to be least important in the ICH Biogeoclimatic Ecosystem Classification (BEC) variant
 - The strongest response to increasing light was in moderate and moist climates like the ICHmc (particularly for hybrid spruce and subalpine fir)
 - Low light growth may be enhanced in cold climates such as the ESSFmc and ww for hybrid spruce and subalpine fir
- Underplanting is a useful option, but requires overstory manipulation and creation of light environments that balance the species tolerance needs with the competitive response of vegetation

Key Uncertainty: Data from historical studies on species' light responses suggest most species grow more rapidly under higher light levels, that shade-tolerant species grow less well under

high light, and that shade-intolerant species grow nearly as well under low light but experience greater mortality. These data were from many species at many sites, or many species at one to a few sites, and as a result the conclusions are not firm but can be used as a basis for generating hypotheses. The key uncertainty is whether these hypotheses hold across a broad range of sites and stand conditions. Currently there are no trials of comparative regeneration response of key tree species to the dynamic light and moisture levels found in mixed and pure lodgepole pine stands attacked by MPB.

The Issue

Stands infested with MPB consist of a variety of pre-attack regeneration conditions: stocked or non-stocked, with desirable or undesirable shade tolerant or intolerant species, whose growth is either impacted or not by the presence of competing vegetation. A fundamental issue for forest managers in considering MPB-attacked stands is how the existing understory will respond to the new changing light environment. Related questions are, under what conditions is response favourable, when should the overstory be removed, and when should stands be under-planted, fill-planted or clear-cut and replanted? In developing solutions to these questions we explored three closely related questions:

- 1) What are the expected seedling responses to light in general?
- 2) How do seedlings respond in terms of release (increased rates of growth) following overstory removal?
- 3) How do seedlings planted under existing overstory respond to varying light levels?

We reviewed the recent literature on conifer shade tolerance and release response to develop guidelines for prioritizing MPB-attacked stands for treatment in order to meet regeneration objectives and overcome potential short-term timber supply issues.

Question 1: Basic Eco-physiology Conifer Responses to Light

Light is likely the most important factor influencing tree growth in BC conifers (Claveau et al. 2002). Although a number of climatic variables are correlated with light, light drives photosynthesis and is a dominant climatic variable. Shade tolerance is an ecological concept that describes the ability of woody plants to persist under low light conditions (Grossnickle 2000, Spurr and Barnes 1980, Bazzaz 1979, Daniel et al. 1979). Shade tolerance indicates a basic genetic difference between species that is exhibited by their physiological responses to light at the leaf and whole-plant level. The variability in shade tolerance is fundamental to the amount and distribution of tree species in BC forests, and to the natural succession dynamics in these forests, particularly those that develop under gap-phase dynamics (McCarthy 2001, Messier et al. 1999).

Shade tolerance is a relative term and the expression of tolerance differs both between plant species of different sizes and between leaves and whole plants within species. It is the complex of plant responses to light and the associated photosynthetic environment that proffers adaptation to shade. The physiological responses linked to shade tolerance include stomatal control, photosynthetic efficiency, carbon assimilation and carbon distribution. Shade-tolerant tree species such as *Abies* typically produce flatter and shorter crowns to capture low light more efficiently (Claveau et al. 2002). This whole-plant response is similar for many conifer species but tolerant species are more plastic and adjust more quickly and effectively than intolerant species (McCarthy 2001). This response is expressed as a rapid shift of carbon within the plant that helps to balance the resource needs of photosynthetic and non-photosynthetic tissues. In forecasting established or planted seedling responses to changing light conditions it is important

to consider that leaf-level and plant-level responses may differ. There are several substantial reviews of shade tolerance in boreal species that reinforce this point (Messier et al. 1999, Wright et al. 1998a, Lieffers et al. 1999 and McCarthy 2001).

Messier et al. (1999) reviewed the functional ecology of conifers in relation to light in boreal forest species. They showed that at the leaf level, shade tolerance is conferred through reduced specific leaf mass, photosynthetic saturation point, live crown, and root-to-shoot ratio compared to shade-intolerant species. Shade-tolerant species have the capacity to reduce or suspend height or canopy growth, which is difficult for shade-intolerant species. McCarthy (2001) refers to this as the “crown growth type” in which photosynthate is allocated preferentially to lateral branches and foliage rather than to plant height growth. Pine species are affected in this way and can have height or radial growth rates comparable to shade-tolerant species but not persist, exhibiting low survival under extended periods of low light. It appears that the ability to stop height growth and redistribute assimilated carbon to stem and roots allows shade-tolerant tree species to persist under low light and to re-start growth under higher light conditions created by small gaps or larger openings. Messier et al. (1999) indicate that true firs (*Abies* spp.) compared to spruces (*Picea* spp.) have a greater ability to shed branches, grow laterally, stop growth when shaded, and grow quickly when suddenly exposed to increased light regimes. Newsome et al. (2003) have shown that lodgepole pine height growth is less impacted by low light than diameter growth under a wide range of aspen densities.

Wright et al. (1998a) in their assessment of growth responses to light in conifer species across a series of climatic regimes in north-western BC reinforced the point that the ecophysiological responses of shade tolerant species have a well established body of literature (Bazzaz 1979). Again this literature indicates that leaf level responses in stomatal control, gas exchange and carbon assimilation confer positive carbon gain under low light compared to shade-intolerant species. It is important to note that the leaf-level responses to light may not accurately reflect the whole-plant responses (Lieffers et al. 1999). Leaf-level responses suggest that photosynthesis increases sharply from no light up to 30-40% full sunlight but remains relatively flat above that level. Wright et al. (1998a) indicated that at the whole-plant level the tolerance differences are weaker due to the ability of the plants to shift carbon resources among leaves, stem and roots. This supports the work of Claveau et al. (2002) indicating that whole-plant or field compensation points (the light level point at which growth approximates zero) differ because of the ability of tolerant tree species to shift fixed and assimilated carbon from leaves to stems to roots, allowing these plants to slow or stop growth and persist until light regimes increase. This means that shade-tolerant and shade-intolerant species are not so different when comparing whole-plant responses.

The investigation by Wright et al. (1998a) was extensive and evaluated the height and diameter growth of seven species in 85 sites over nine biogeoclimatic variants across four climatic regions. Their results indicated that shade tolerance was generally expressed by species that grew well at low light and tended to grow poorly relative to shade intolerant trees at high light but that this response varied widely within species and among climatic regions. Their work indicated an amazing degree of similarity among the five major conifer species in their diameter growth response to percent full light across four forest zones (Figure 4). The greatest diameter growth responses to increasing light occurred in moderate climates like the Moist Temperate (ICHmc2), by hybrid spruce and subalpine fir. The best responses to low light (40-50% full sun) were in colder climates (ICHvc, ESSF, and BWBSdk1) and with true fir species. Although there were low- and high-light growth tradeoffs among species in the four zones, the differences in the shape of the response curves is not sufficient to explain the successional dynamics in these forests.

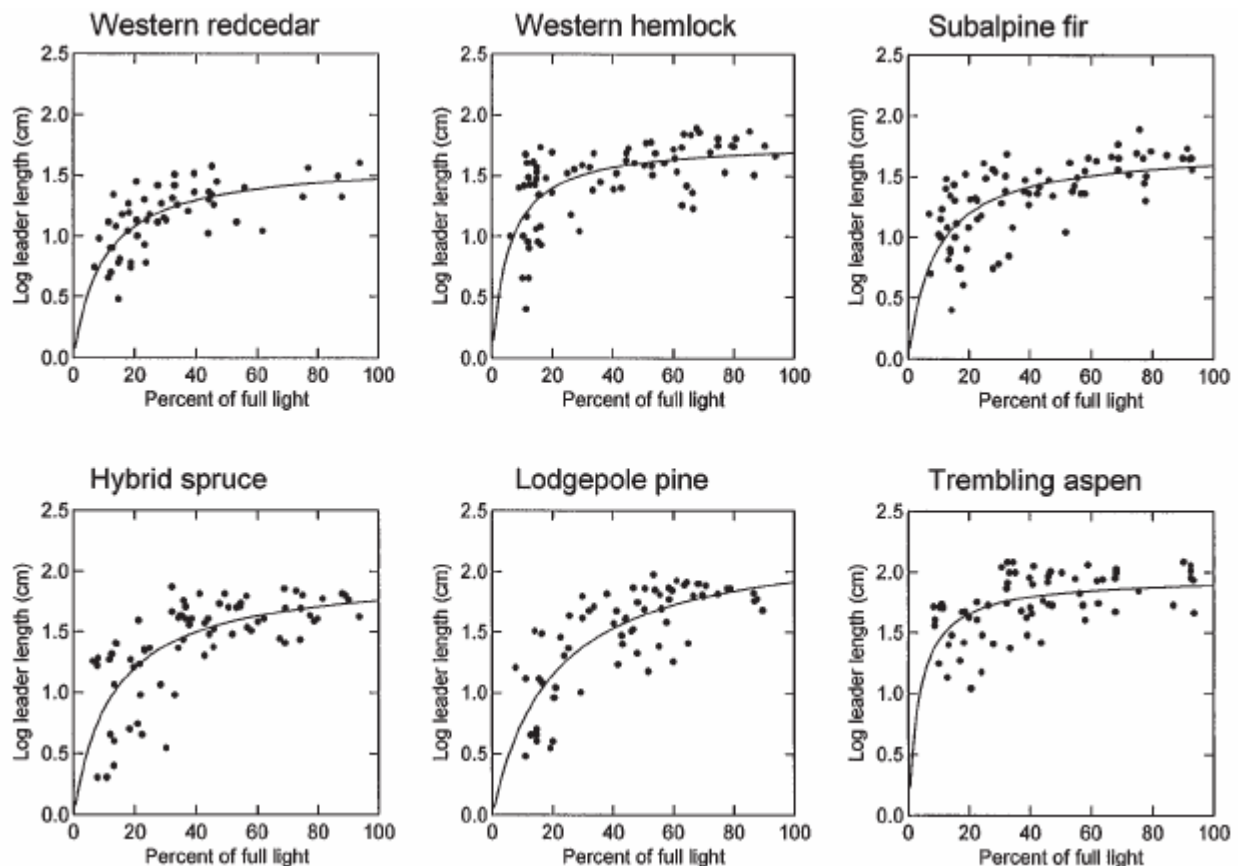


Figure 4. Light response curves for Interior BC Species by Climatic Region (Wright et al. 1998a).

It appears that variation among species regarding low-light survival in combination with high-light growth response more accurately reflects successional dynamics and suggests that low-light survival was more important than low-light growth in discriminating overall growth responses. Their evaluation suggests that;

- Western redcedar and western hemlock would be best under low-light, persistent overstory conditions,
- Hybrid spruce and subalpine fir have the best chance for release responses to canopy alteration, and
- Deciduous or pine species in the understory may be best treated by overstory removal and full light conditions.

Canham et al. (1999) in their assessment of responses to varying field light levels found continuous increases in planted seedling growth over a wide range of light regimes. Their field evidence from amabilis fir, interior spruce, lodgepole pine, red cedar and western hemlock seedlings on one site in the ICHmc in BC indicated whole-plant growth responses were mostly linear from 40% to 100% full sunlight. They also noted there was considerable variation in planted seedling growth response among species, also supported by Vyse et al. (2006). In general they found that shade-tolerant species had better growth at low light and relatively low growth at high light. But they also found that lodgepole pine could have relatively high height and diameter growth at low light but were unable to persist, exhibiting highest mortality at low

light levels. Hemlock, spruce and cedar seedlings had comparable growth responses over a range of light from 30-70% full sun. This suggests that light levels in the 20-40% range may be required to sustain most acceptable ICH tree species.

Claveau et al. (2002) investigated effects of tree size on response to light. They looked at three sites in BC (and three in Quebec) assessing advanced regeneration growth under a variety of light regimes in the ICHmk3 and SBSwk1 variants with sub-alpine and amabilis fir, interior and white spruce, and lodgepole and jack pine. They suggest that taller trees should have a competitive advantage above a given light level but may be at a disadvantage below that level. This involves a subtle interplay between ability to capture resources and resource needs to sustain plant growth. Selecting residual tree species and morphological types is directly affected by this tradeoff. This means that the selection of tall or short residuals needs to be done with an understanding of the expected future light regime. Their work suggests that the best approach to predicting response and selecting residual saplings is to assess sapling vigor (pre-release growth in the last four years) and sapling size. They show that in general for interior spruce, sub-alpine fir and lodgepole pine, saplings taller than 1m with historic growth of greater than 10cm/year show positive responses to increasing light levels.

Questions 2 and 3: Effects of Forestry Practices – Release and Under-planting

Responses of planted and natural seedlings to the specific condition of MPB-attacked stands (i.e. variable light regimes resulting from a range of standing dead stems) are not well documented but there is a significant body of evidence of responses to natural gaps or partial harvest. Wright et al. (2000) evaluated the sapling release responses of 11 tree species to a variety of light regimes in the northern interior of BC. Similar to the balsam fir responses documented in McCarthy's (2001) review of gap dynamics, they found that suppression of shade-tolerant species had relatively little effect on future response to changing light conditions. The modeling by Wright et al. (2000) indicates a more significant flattening of the light response curves after 20 years of suppression for shade-intolerant species than for tolerant species. Their diameter growth and percent full sun relationships allow evaluation of shade tolerance, suppression history and sapling response. They showed little effect of suppression history on current response to light for shade tolerant species. They indicated that 20 years after release lodgepole pine had the greatest growth above 60% full sun, hybrid spruce was dominant at intermediate light levels but aspen saplings had the slowest growth of all species at all light levels.

Kneeshaw et al. (2002) evaluated the response of sapling Douglas-fir and lodgepole pine in the IDFdc to partial harvest and showed that removal of the overstory led to increased root and stem diameter and root growth but that, as in Wright et al. (2002), these shade-intolerant species lagged 1 year in stem growth and 2-3 years in height growth. This is a result of having to rebuild their crowns and adjust their root-to-shoot balance to adapt to the new photosynthetic environment. They also found that much like Claveau et al. (2002), Douglas-fir and lodgepole pine height growth was strongly correlated with pre-release height growth. They established that taller, shade-intolerant trees showed greater reductions in growth during the first two years post-release than smaller saplings.

Comeau et al. (2003) found that following birch overstory thinning, interior spruce tended to respond better than subalpine fir over a range of light conditions. As indicated in Kneeshaw et al. (2002), tree size had a substantial effect on growth rates. This size effect was also evident in the thinning responses of subalpine fir in birch-dominated stands (Krasowski and Wang 2003). They showed that percent height growth response of intermediate size saplings (1.5-5m height) to overstory thinning was 2-3 times greater (74% vs 24%) than other size classes, and small

saplings (<1.5m height) had a similarly different response among size classes to overstory removal.

Claveau et al. (2006) evaluated Douglas-fir, white spruce, hybrid spruce, and subalpine fir and found similar sapling responses with deciduous canopy removal in the ICHwk2 in northern BC. They found that in general the seedlings reallocated carbon to stems and roots following overstory removal. This response was size-dependent, with taller saplings allocating more to root growth than to height growth in the first year. Taller trees needed more soil resources, higher light regimes and greater vigour to respond to release. This is consistent with the findings of Calveau et al. (2002).

The other source of guidance on seedling response to changing light environments comes from investigations into species responses from seeding or planting under canopies. Wright et al. (1998b) looked at favourable microsite conditions of seed germination and growth in forest gaps in the ICHmc in northern BC. They found emergence was related to light and substrate condition. They looked at lodgepole pine, western redcedar, western hemlock, hybrid spruce and subalpine fir and found that establishment and growth for all species benefited from ground cover disturbance. The most favourable of these disturbed conditions were shady, organic microsites with >20% full sunlight. These microsites tended to be on the south edge of gaps and had relatively high soil moisture.

Vyse et al. (2006) evaluated the response of underplanted Douglas-fir, lodgepole pine and ponderosa pine seedlings in the IDFxh. They found that six-year growth response was linear above 35% full sun with lodgepole pine outperforming Ponderosa pine, which outperformed Douglas-fir. They also found on these hot, dry sites that underplanting benefited from thinning to <15m² per ha basal area. In a similar study in the SBSmm in northeastern BC, Comeau et al. (2004) looked at the response of planted white spruce planted seedlings to aspen overstory thinning with and without fertilization. They found that reducing the overstory improved seedling performance but that the compensatory effects of vegetation response reduced seedling responses to high light (heavy thinning) or fertilization. They recommended that underplanting would benefit from thinning, but that residual basal areas should be > 25m²/ha. This differs from Vyse et al. (2006) but is likely a result of the cooler, moister BEC variant and the response of understory vascular plant vegetation to increased light.

A decision matrix and a decision tree which summarize expected responses to release are provided below.

Conclusions

In summary, understanding of conifer responses to light is key to making appropriate silvicultural decisions for MPB-attacked stands in BC. A large body of science has accumulated in the last 10 years on both leaf-level and whole-plant-level light responses for BC conifer species. This work indicates the following:

- All species grow best under full sunlight
- Tolerant species (e.g. western hemlock, western redcedar, subalpine fir) grow well under low light and relatively poorly relative to shade intolerant trees under high light
- Shade-intolerant trees, especially lodgepole pine, can grow (more so in height than diameter) under low light but will likely not survival well

- Shade-tolerant species have a strong capacity to adjust carbon assimilation, slow or stop growth and reallocate carbon to allow both persistence and rapid response to decreasing or increasing light conditions
- Across species, size and vigour significantly effect light responses. Large saplings (particularly shade-tolerant species) have a greater capacity to adjust because of their ability to capture resources. This is can be offset by a requisite need for greater resources to support the larger biomass and may mean they need higher light levels and greater pre-release vigour to respond to higher light levels quickly.
- Shade-tolerance response appears to be relatively consistent across the regions in BC
 - There are relatively small differences in light response curves among species with the exception of *Pinus* species
 - Species choice for light response appears to be least important in the ICH BEC variant.
 - The strongest response to increasing light was in moderate and moist climates like the ICHmc (particularly for hybrid spruce and subalpine fir).
 - Low-light growth may be enhanced for hybrid spruce and subalpine fir in cold climates such as the ESSFmc and vv.
- Underplanting is a useful option, but requires overstory manipulation and creation of light environments that balance the species tolerance needs with the competitive response of vegetation

Key Uncertainty

Historical light-response trial data suggest most species grow more rapidly under higher light levels, that shade-tolerant species grow less well under high light, and that intolerant species grow nearly as well under low light but experience greater mortality. The data were from many species at many sites, or many species at one to a few sites, and therefore the conclusions are not firm but form the basis for hypotheses. The key uncertainty is whether these hypotheses hold across a broad range of sites and stand conditions. There currently are no comparative trials investigating regeneration responses of key tree species to the dynamic light and moisture levels found in mixed and pure lodgepole pine stands attacked by mountain pine beetle.

Potential Solutions

The recent learning about conifer seedling responses to light in BC provides some consistent messages that can provide forest managers with advice on how to evaluate MPB-attacked stands for treatment. The following generalizations can be helpful.

Species choice: Matters least in ICH and matters most in IDF, or is not as important in wetter ecosystems as it is in drier ones. Hybrid spruce and subalpine fir have the best chance for release responses.

Best chance for leaving overstory: Tall or large saplings with >70% live crown and >10cm height growth/year for the last 5 years. Overstory should be reduced to sustain at least 20% FS (Full Sun) and preferably 40% FS.

Best chance for removing overstory: Tall or large saplings with >50 % live crown and relatively poor height growth in the last 5 years, particularly suppressed true firs.

In a more comprehensive way it may be possible to use two elements that were persistent in the literature on light responses as a framework for stand level decision-making. Both seedling/sapling vigour and size have clearly strong influence on release responses for BC conifers. Two important indicators of vigour are pre-release growth (as much as 5 years) and crown size (% live crown or crown volume). Two important measures of sapling size are height and diameter. Using these in a 2-dimensional graph with cut-offs we can create a set of quadrants that can help to partition the suite of stands for treatment. Within each quadrant we have identified a cohort of stands and regeneration conditions that would be favoured by a particular set of stand level treatments. This same approach can be developed into a dichotomous decision tree.

In Appendix 1 we illustrate an example based on the literature reviewed. The basic data would come from stocking surveys that would include crop trees with >70% live crown, crop tree height and crop tree height growth in the last 4-5 years. The two dimensions used would be average crop tree pre-release height growth (for crop trees with >70% live crown) and average crop tree height. The literature for BC conifers suggests that for the majority of species and BEC variants, a size cut-off of 100cm and an average growth cut-off of 10cm per year (or 100cm per decade) may be sufficient to discriminate good from poor crop tree and stand conditions for release. Using these we create four quadrants. The top right quadrant describes stand conditions where the crop trees are tall and growing well prior to release. Here if the stand is not stocked it should be underplanted to reach desired stocking but overstorey removal is unnecessary as overstorey conditions are likely sufficient to sustain the crop trees. Light conditions should be checked to ensure they are above 40% full sun.

The lower right quadrant represents stand conditions with a suppressed understory. Our review suggests that for shade-tolerant species successful release can be expected with overstorey removal given the large size and high % live crown. In addition to overstorey removal stand treatment should include fill planting if the stand is not stocked. The bottom left quadrant also represents this suppressed condition but here the crop trees are small and growing poorly. In these stand conditions the best option is to remove the stand and start again (i.e. clear-cut and plant).

For the upper left quadrant we have an anomalous condition where sapling crop trees are relatively small but growing well. Although it is uncertain how frequently this stand condition occurs, here the desired stand treatment is less clear and a variety of options may be possible. More work may need to be done to determine the reasons for short crop trees: it may simply reflect poor site productivity or shading from taller understory shrubs. If the stand is not stocked it should be fill-planted. The overstorey condition should be assessed to determine if it will provide a >40% full sun condition and if not it should be reduced to that level.

This approach to risk assessment and treatment priorities is generic and the cut-offs are generalized from the recent BC literature. It is possible that the height and growth cut-offs would need to be reduced for higher and colder BEC variants. However, this approach could provide consistent guidance to forest managers and a hypothetical framework for adaptive management design.

Literature Cited

Bazzaz, F.A. 1979. The physiological ecology of plant succession. *Annu. Rev. Ecol. Syst.* 10: 351–371.

- Canham, C.D., K.D. Coates, P. Bartemucci and S. Quaglia. 1999. Measurement and modeling of spatially explicit variation in light transmission through interior cedar–hemlock forests of British Columbia. *Can. J. For. Res.* 29: 1775–1783.
- Claveau, Y., C. Messier, P.G. Comeau and K.D. Coates. 2002. Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. *Can. J. For. Res.* 32: 458–468.
- Claveau, Y., P.G. Comeau, C. Messier and C.P. Kelly. 2006. Early above- and below-ground responses of subboreal conifer seedlings to various levels of deciduous canopy removal. *Can. J. For. Res.* 36: 1891–1899.
- Coates, K.D. and P.J. Burton. 1999. Growth of planted tree seedlings in response to ambient light levels in northwestern interior cedar–hemlock forests of British Columbia. *Can. J. For. Res.* 29: 1374–1382.
- Comeau, P.G., J.R. Wang and T. Letchford. 2003. Influences of paper birch competition on growth of understory white spruce and subalpine fir following spacing. *Can. J. For. Res.* 33: 1962–1973.
- Comeau, P.G., C.N. Filipescu, R. Kabzems and C. DeLong. 2004. Early growth of white spruce underplanted beneath spaced and unspaced aspen stands in northeastern British Columbia. *Can. J. For. Res.* 34: 2277–2283.
- Daniel, T.W., J.A. Helms and F.S. Baker. 1979. *Principles of Silviculture*. McGraw Hill, New York. 500p.
- Grossnickle, S. 2000. *Ecophysiology of Northern Spruce Species: The performance of planted seedlings*. NRC Research Press. Ottawa. 407p.
- Kneeshaw, D.D., H. Williams, E. Nikinmaa and C. Messier. 2002. Patterns of above- and below-ground response of understory conifer release 6 years after partial cutting. *Can. J. For. Res.* 32: 255–265.
- Kobe, R.K., and K.D. Coates. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Can. J. For. Res.* 27: 227–236.
- Krasowski, M.J., and J.R. Wang. 2003. Aboveground growth responses of understory *Abies lasiocarpa* saplings to different release cuts. *Can. J. For. Res.* 33: 1593–1601.
- Lieffers V.J., C. Messier, K.J. Stadt, F. Gendron and P.G. Comeau. 1999. Predicting and managing light in the understory of boreal forests. *Can. J. For. Res.* 29: 796–811.
- Messier, C., R. Doucet, J. Ruel, Y. Claveau, C. Kelly and M.J. Lechowicz. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. *Can. J. For. Res.* 29: 812–823.
- McCarthy, J. 2001. Gap dynamics of forest trees: A review with particular attention to boreal forests. *Env. Rev.* 9: 1–59.
- Spur, H.S., and B.V. Barnes. 1980. *Forest Ecology*. Third Edition. John Wiley and Sons, New York. 687p.
- Vyse, A., C. Ferguson, S.W. Simard, T. Kano and P. Puttonen. 2006. Growth of Douglas-fir, lodgepole pine, and ponderosa pine seedlings underplanted in a partially-cut, dry Douglas-fir stand in south-central British Columbia. *For. Chron.* 82: 723–732.

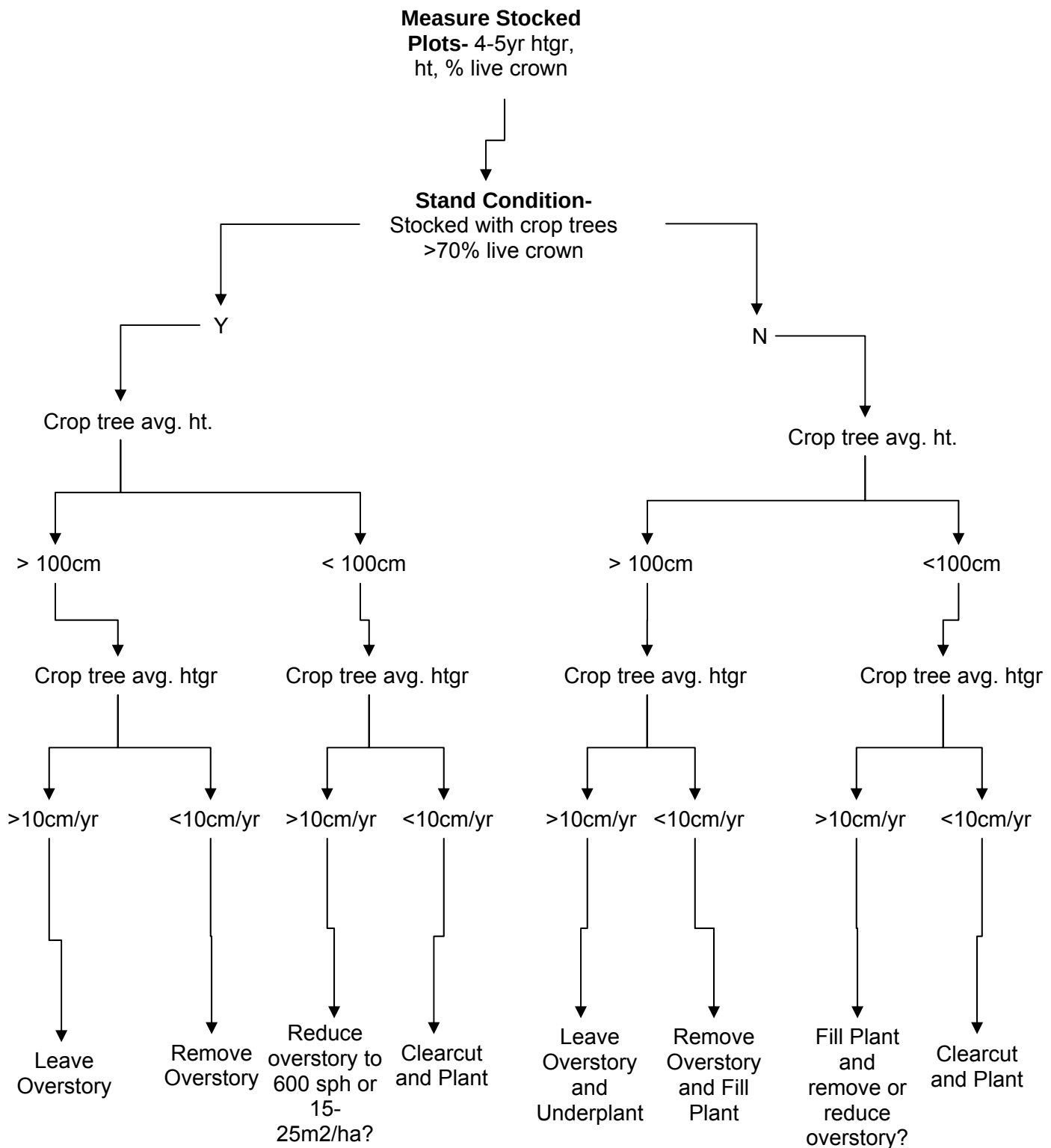
Wright, E.F., K.D. Coates, C.D. Canham and P. Bartemucci. 1998a. Species variability in growth response to light across climatic regions in northwestern British Columbia. *Can. J. For. Res.* 28: 871–886.

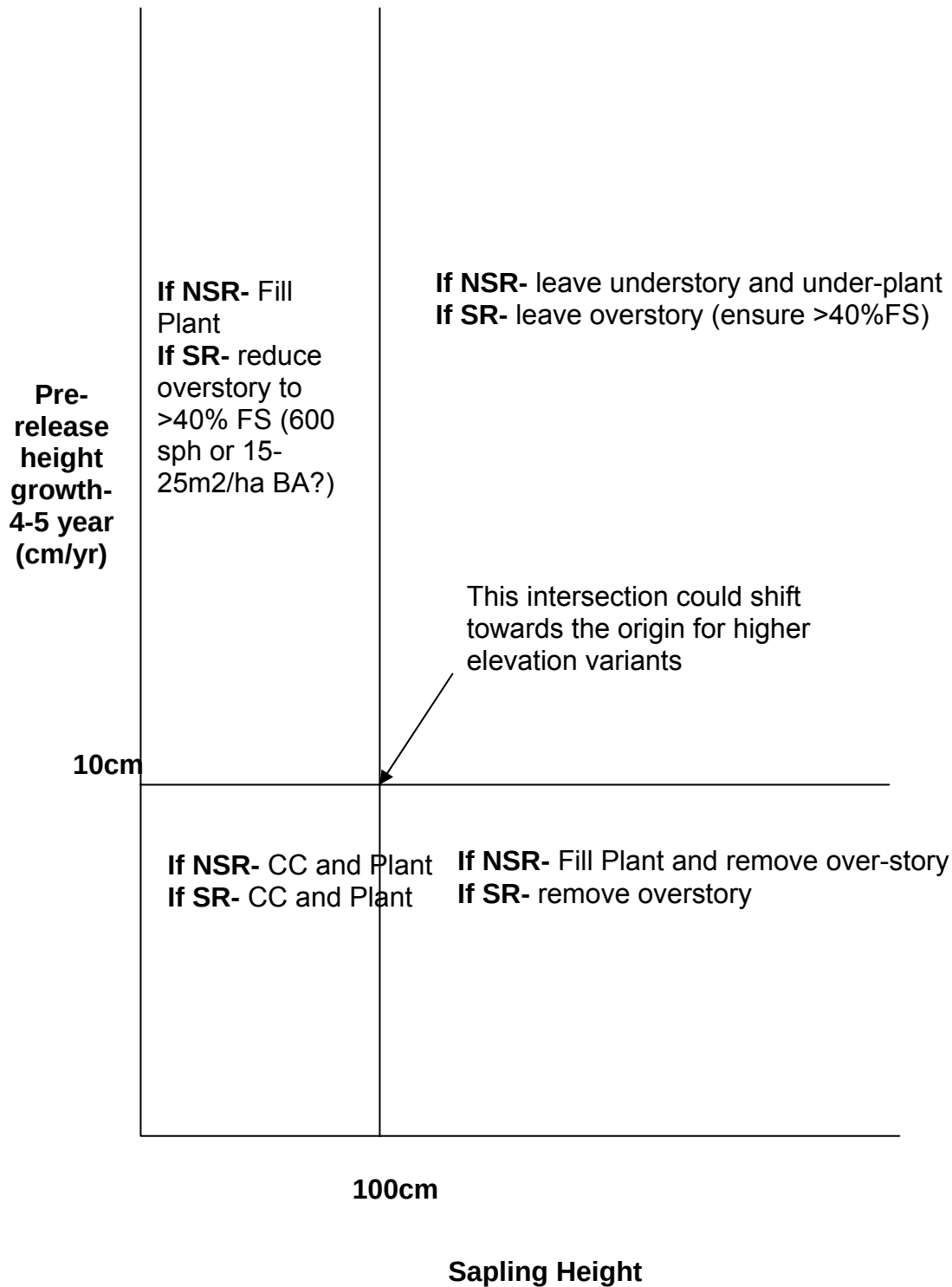
Wright, E.F., K.D. Coates and P. Bartemucci. 1998b. Regeneration from seed of six tree species in the interior cedar–hemlock forests of British Columbia as affected by substrate and canopy gap position. *Can. J. For. Res.* 28: 1352–1364.

Wright, E.F., C.D. Canham and K.D. Coates. 2000. Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. *Can. J. For. Res.* 30: 1571–1580.

Appendix 1. Decision Tree and Decision Graph for MPB-Attacked Stand Regeneration Planning

1a. Stand Condition- Stocked with crop trees >70% live crown	2A
2a. Average crop tree height >100cm	4A
2b. Average crop tree height <100cm	5A
4a. Average crop tree height growth > 10cm/year	LEAVE OVERSTORY
4b. Average crop tree height growth < 10cm/year	REMOVE OVERSTORY
5a. Average crop tree height growth > 10cm/year	REDUCE OVERSTORY TO 600SPH OR 15-25M² BA
5a. Average crop tree height growth > 10cm/year	CLEARCUT AND PLANT
1b. Stand Condition- Not stocked with crop trees >70% live crown	3A
3a. Average crop tree height >100cm	6A
3b. Average crop tree height <100cm	7A
6a. Average crop tree height growth > 10cm/year	LEAVE OVERSTORY AND UNDERPLANT
6b. Average crop tree height growth < 10cm/year	REMOVE OVERSTORY AND FILL PLANT
7a. Average crop tree height growth > 10cm/year	FILL PLANT AND REMOVE OR REDUCE OVERSTORY
7b. Average crop tree height growth > 10cm/year	CLEARCUT AND PLANT





Management of Pine Grass Competition

The Forests for Tomorrow (FFT) program was established by the BC Government in 2005 in response to the devastating impact of major fires and the mountain pine beetle (MPB) epidemic on the forest land base of the Province. The program is aimed at improving the future timber supply and protecting other forest values through the re-establishment of young forests on lands that would otherwise remain underproductive.

The mountain pine beetle epidemic had affected over 10 million hectares of forest land by 2008 and is expected to expand further. This loss in forest cover is unprecedented in both scale and complexity. Many forest types have been affected across a range of ecological conditions from the dry Chilcotin to moist sub-boreal and high elevation zones. These twin factors of scale and complexity have, in turn, created numerous uncertainties for forest managers. Adaptive management strategies have been proposed as one approach for dealing with these uncertainties.

An adaptive management workshop held on June 26, 2008 under the FFT program for key staff engaged in restoring forest cover to the mountain pine beetle area raised a range of uncertainties or questions from participants. This is one of the topics for which our team was asked to review and summarize information in the existing literature.

Executive Summary

Much of the background (and references therein) is condensed from Simard et al. (2003); Heineman et al. (2003) (Appendix 1), BC Forest Practices Branch (1997), and a BC Ministry of Forests website: <http://www.myacquire.com/spvegman/expertsystem/siteID.asp>

Pine grass (*Calamagrostis rubescens*) is a major competitor with conifer seedlings in the southern and central Interior, especially in the IDF and is one of several factors that make the dry, grassy Douglas-fir (*Pseudotsuga menziesii* (var. *glauca*) forests in interior British Columbia difficult to regenerate. There is concern that pinegrass will flourish in the increased light under stands killed by mountain pine beetle and make it difficult to successfully underplant these stands.

Pinegrass is an efficient competitor for soil water, partly because its growth peaks early in the growing season, well before conifer growth. Competition is most pronounced on drought-prone sites where roots compete for moisture which is the most critical factor for survival and early growth of planted tree seedlings. The grass increases the severity of summer drought and frost and reduces soil temperatures thereby contributing to poor seedling performance. On moister sites trees can establish through pine grass and competition is not as significant.

Pinegrass cover increases quickly and dramatically in response to greater light provided by harvested openings greater than one tree length in diameter. Following clearcutting, dense stands of pinegrass can develop within 2–4 years. Lightly disturbed areas can be completely invaded after one season. Severely disturbed areas are usually invaded after 4–5 years. The grass is increasing under the light levels found under dead pine stands but it is not clear how much competition occurs and how competition develops over time.

Solutions involve identifying where pinegrass is a severe competitor, and then removing pine grass and/or establishing seedlings before pinegrass invasion. Decisions about how to remove pinegrass then depend on the slope and amount of overstory retained. In the open, mechanical treatments (with ripper plows or disc trenchers) can control pinegrass for 3–4 years and, if intensive enough, increase Douglas-fir survival and growth. For lodgepole pine sites, only medium-impact mechanical site preparation is necessary where natural regeneration is expected. Chemical treatments to create planting spots about 150 cm in diameter are also options. On steep slopes, chemical treatments are usually better than mechanical treatments. Mechanical removal of forest floor material, particularly on steep slopes, improves pine growth

but can result in short-term negative effects on nutrient availability, the ECM community and soil physical properties. Under dead stands, treatments with herbicides or manual screefing are the most relevant options to explore. Other potentially useful approaches are early establishment of seedlings before the grass responses to increased light levels and using larger planting stock.

The Issue

Pine grass (*Calamagrostis rubescens* Buckl.) is a major competitor with conifer seedlings in the southern and central Interior, especially in the IDF and is one of several factors that make the dry, grassy Douglas-fir (*Pseudotsuga menziesii* (var. *glauca* (Beissn.) Franco) forests in interior British Columbia difficult to regenerate. There is concern that pinegrass will flourish in the increased light under stands killed by mountain pine beetle and make it difficult to successfully underplant these stands.

Basic Biology

Pinegrass is an efficient competitor for soil water, partly because its growth peaks early in the growing season, well before conifer growth (Nicholson 1989). Pinegrass continues to photosynthesize at reduced levels even when it is under moisture stress, which also provides it with a growth advantage over conifer seedlings and allows it to use an even greater share of soil water (Vogel 1985, cited by Haeussler et al. 1990).

Pine grass competition is most pronounced on drought-prone sites where roots compete for moisture which is the most critical factor for survival and early growth of planted tree seedlings (Örlander et al. 1998). Spittlehouse and Goldstein (1989) suggest that newly planted seedlings require about 4 weeks during which soil water potential does not drop below -0.1 MPa. Particularly in drier areas, such as the dry IDF, the grass increases the severity of summer drought and frost and reduces soil temperatures thereby contributing to poor seedling performance (Peterson and Maxwell 1987; Nicholson 1989; Stathers 1989; Fleming et al. 1998).

Following clearcutting, seedlings are able to establish in pine grass dominated understory throughout the IDF, but the probability of successful establishment increases with increasing moisture.

Pinegrass cover increases quickly and dramatically in response to greater light provided by harvested openings greater than one tree length in diameter. It spreads in response to light, medium soil disturbance associated with mechanical site preparation or prescribed fires (Haeussler et al. 1990, Huggard et al. 2005). The increased light levels and ground disturbance allow a continuous mat of pinegrass to develop from the loose open turf that occurs under forest stands. Treatments that favour the development of the pinegrass complex include:

- openings created by natural disturbances, clearcutting, group selection logging, or partial canopy removal
- removal of other non-crop vegetation (e.g., deciduous trees and shrubs)
- low to medium ground disturbance during logging
- low- to medium-impact mechanical site preparation (MSP)
- fires
- fertilization of conifers with nitrogen.

Following clearcutting, dense stands of pinegrass can develop within 2–4 years. Lightly disturbed areas can be completely invaded after one season. Severely disturbed areas are usually invaded after 4–5 years. Pine grass may diminish over time. At Opax, for example pine grass is no longer dominant on some sites and other species have established (Huggard et al. 2005).

Typical Treatments for Pinegrass

Usually, where pinegrass is thought to be a strong competitor it is removed to reduce moisture stress and increase soil temperatures early in the spring. Complete removal of pinegrass during site preparation is more beneficial than partial removal. Silviculture treatments that remove pinegrass with or without the forest floor in 1- to 3-m patches have been shown to inhibit the regrowth of pinegrass, and can influence soil water availability in the dry IDF and improve conifer performance (Nicholson 1989; Fleming et al. 1998). Removal of forest floor can sometimes have some negative effects on other soil properties (see section on ‘complicating factors’ below).

The pinegrass complex can be set back by creating plantable spots using mechanical treatments, manual screefing, or chemical broadcast or spot applications. High impact fires can also destroy the shallow roots and reduce pinegrass. Seeding disturbed sites with domestic grass/legume mixes can lead to the competitive exclusion of reduce pinegrass.

Appropriate treatments depend on if the overstory has been removed or not and the slope of the site. When overstories are removed, treatments usually involve disc trenchers and plow rippers, but these machines will not be suitable if pine grass needs to be treated under dead canopies of pine. Slope also affects appropriate treatments. Although mechanical and chemical treatments have improved short-term seedling microclimate, survival, and growth on flat sites (Nicholson 1989; Fleming et al. 1998), little is known about appropriate site preparation methods for steep slopes. The site preparation tools commonly used on flat pinegrass sites, such as disc trenchers and ripper plows (Newsome 1998), are not suitable on slopes steeper than 35%. In contrast, lower impact tools, such as screefers, excavators, mulch mats, and ground foliar chemical application, may be more appropriate on steep slopes.

Mechanical

While low- to medium-impact mechanical disturbance can increase pinegrass competition, intense mechanical site preparation retards pinegrass growth and provides 3–4 years of control. Dense pinegrass communities can increase the incidence and severity of summer radiation frost so mechanical treatments may be used to reduce pinegrass cover on frost-prone sites.

On Douglas-fir sites, intense mechanical disturbance is recommended. Ripper plow or disc trencher can control pinegrass for 3–4 years and increase Douglas-fir survival and growth. Patch scarifiers can remove pinegrass and expose 50 to 150 cm patches of mineral soil. Patch scarifiers have produced noticeable improvements in survival and growth of Douglas-fir at Opax and in the Cariboo Forest Region (Huggard et al. 2005, Vyse et al. 2006).

For lodgepole pine sites, only medium-impact mechanical site preparation is necessary where natural regeneration is expected. Any mechanical treatment that produces a continuous furrow (e.g., disc trencher, ripper, or ripper plow) is recommended for sites to be planted with lodgepole pine. Patch scarification has improved lodgepole pine survival compared to unprepared sites. Severe disturbance should be avoided on clearcuts with abundant lodgepole pine cones to minimize pine overstocking. A moderate pinegrass cover can help prevent pine overstocking.

Screefing

Patch scarification by planters (removing 30 cm diameter areas of surface grass) usually favours pinegrass and does not improve successful regeneration of seedlings. However, deep scalping, which removes the root mat, may help.

Prescribed Fire

Low- to medium-impact burning can cause a rapid increase in pinegrass after one growing season and is, therefore, rarely used.

Chemical

Herbicides provide the best pinegrass control option, and may be the only effective treatment option on steep slopes, soils that compact easily, or other sites where machines cannot be used. On hot, dry sites, dead vegetation may act as an effective mulch, but may cause problems on frostprone sites. Glyphosate trials in various biogeoclimatic zones (including the IDFdk, MSxk, and ICHmk1) consistently indicate good control of pinegrass for 2–3 growing seasons. Several trials indicate that glyphosate controls pinegrass when applied in the growing season, preferred times to apply glyphosate are May to June and later in August.

Limited research indicates that hexazinone effectively controls pinegrass but data are lacking on the length of control in B.C. forests.

Seeding

Seeding with domestic grasses following MSP can eliminate pinegrass. Since these domestic grasses can also be competitive, they may have to be grazed to minimize competition with crop trees.

Livestock Grazing

Although cattle graze pine grass, particularly early in the season, the effectiveness of using grazing for controlling pine grass has not been confirmed. Similarly sheep will graze pine grass. Livestock grazing tends to be for shorter duration than required for effective control. Repeated treatments of grazing may be effective, but may not be practical from an operational perspective

Complicating Factors

Long-term studies and modelling efforts have demonstrated that forest floor removal can have important effects on forest productivity (Skinner et al. 1989). Removal of the forest floor during harvesting and site preparation treatments can negatively affect both the quantity of nutrients and their availability. Forest floor materials contain large amounts of nutrients, and also provide habitat for organisms that convert those nutrients to forms available for uptake by conifers. IDF soils generally have medium to rich nutrient status due to the predominance of base-rich bedrock and low rates of leaching (Lloyd et al. 1990). The potential for scalping treatments to have long-term effects on overall nutrient content, on both gentle and steep slopes, is likely related to the size and depth of the scalps. Small scalps that remove only forest floor down to the mineral soil are likely to have little long-term effect because surface mineral horizons are relatively nutrient-rich in the IDF. Treatments that produce large, deep scalps (i.e., that remove surface mineral horizons) have greater potential to affect long-term productivity, but are not commonly applied in the southern interior IDF, except where they occur as landings and skid trails. On steep slopes, deep screefs have the potential to increase erosion hazard because of reduced soil structural stability. With medium- to fine-textured soils, any type of screefing on steep slopes can result in surface erosion following high-intensity rainstorms. Hope (1991) demonstrated on dry Douglas-fir sites, that scalping resulted in a reduction of 40% total N, 20% extractable P, and <10% extractable S in the forest floor and mineral soil. After 3

years, the scalping treatment resulted in reductions of most foliar nutrients, particularly B, and after 5 years the imposed nutrient deficiencies resulted in a decline in seedling growth (T.A. Black, unpublished data, in Simard et al. 2003).

Effects of pine grass removal on soil productivity can also occur though impacts on soil organisms. The forest floor and mineral soil are home to a variety of microorganisms, including ectomycorrhizal (ECM) fungi, which play important roles in forming and maintaining soil structure, improving uptake of soil water and nutrients, and maintaining the health of the plant-soil system (Perry et al. 1989). Protecting rhizosphere microorganisms is particularly critical in dry, cold environments (Smith and Read 1997), such as in the dry Interior Douglas-fir (IDF) Biogeoclimatic Subzone in interior British Columbia (Lloyd et al. 1990). The inoculum of ECM fungi tend to be concentrated in the forest floor (Harvey et al. 1979), and this layer can be removed in the mechanical treatment. Thus, it is not surprising that the diversity of ectomycorrhizae was lower in mechanical patches than in chemical patches. Although glyphosate inhibits growth of ECM fungi in pure culture (Chakravarty and Chatarpaul 1990; Kaps and Kuhns 1987), it does not appear to inhibit colonization of trees by ECM fungi in the field (Chakravarty and Chatarpaul 1990; Sidhu and Chakravarty 1990; Schoenholtz et al. 1987). It may also be used as a food source (Hurd et al. 2001). In Simard et al.'s (2003) study, glyphosate treatment enhanced mycorrhizal diversity, most likely by reducing pinegrass competition and stimulating pine growth. Heineman et al. (2003) also found that both mechanical and chemical site preparation treatments caused short-lived increases in richness (number of species) and diversity (a measure of the relative abundance of individual species) of ectomycorrhizal species at Murray Creek. However, 28 months after planting, ectomycorrhizal diversity was significantly reduced from untreated control levels in the mechanical treatment but not in the chemical treatment. Some grass species can inhibit ECM formation on conifer seedlings (Amaranthus and Perry 1987; Timbal et al. 1990).

Other factors besides pine grass may limit seedling establishment. These include summer drought, summer frost, winter temperature extremes, inadequate seed supply, seed predation and poor quality planting stock (Newsome 1998).

Presence of pinegrass is not always a detriment. Pinegrass can provide several benefits to crop trees including:

- reducing soil surface erosion
- contributing organic matter to surface soil layers
- recycling nutrients that might otherwise be lost to leaching
- excluding more competitive species
- reducing or preventing overstocking of lodgepole pine.

Recommended Approaches

Solutions involve identifying where pinegrass is a severe competitor, and then removing pine grass and/or establishing seedlings before pinegrass invasion. Decisions about how to remove pinegrass then depend on the slope and amount of overstory retained.

Identifying areas where pinegrass is a severe competitor

Pinegrass is a severe competitor on drier sites where openings have been created by natural disturbances, clearcutting, group selection logging, or partial canopy removal. When considering underplanting of stands killed by mountain pine beetle, effects of increased light

through the dead overstory need to be considered. Increased light seems to have allowed dramatic increases in pine grass in some areas of Prince George (Dow pers comm.), and in some open areas in Kamloops, but not under partial cuts in Opax (Huggard et al. 2005, Vyse pers. comm.). Evaluations should be site specific. .

Where pinegrass is deemed a potential problem then remove pinegrass

For Open Sites on Steep slopes: Results suggest that mid-elevation, steep (>35%), dry, grassy sites in interior British Columbia should be prepared for Douglas-fir or lodgepole pine seedling regeneration by removing pinegrass in large (>150 cm diameter) patches using ground foliar application of glyphosate. This contrasts with earlier research on flat sites, where it was necessary to remove the forest floor along with pinegrass in large patches to reduce damaging frosts and increase seedling survival.

On steep slopes, chemical treatments are usually better than mechanical treatments, but permits for chemical treatments require considerable paperwork. Mechanical removal of forest floor material improves pine growth, but can result in short-term negative effects on nutrient availability, the ECM community and soil physical properties. Mechanical treatments also run the risk of site degradation through compaction or operator error. There are many other advantages to chemical vs. mechanical treatments: they are cheaper, easier, and safer to apply; they improve the possibility of using advance regeneration; and they are visually less intrusive. Conversely, there is greater social opposition to the use of herbicides in general, but soil disturbance is also a concern, especially on steep slopes where erosion potential is high. Compared with patch treatments, broadcast herbicide treatments do not appear necessary for improved survival or growth of lodgepole pine on grassy sites and may have negative implications for range and wildlife values (Simard et al. 1998) as well as nutrient leaching (Nilsson and Örlander 1999). Thus, on steep slopes, large chemical patches that retain the forest floor are best for relieving the multiple environmental stressors. Ground foliar chemical application has resulted in good control of pinegrass and improved conifer performance, even where frost risk is high (Nicholson 1989).

For Open Sites on Flatter areas: On flat areas (less than 30% slope), chemical control is also likely effective but mechanical treatments will likely have less impact on soil nutrients than on steep slopes, and are thus a sound alternative. Mechanical and boot screefing in small patches is sometimes sufficient, particularly if trees are planted early before pine grass competition responds to the increased light.

If overstories are completely removed then mechanical treatments can be done with machines. For Douglas-fir sites, intense mechanical disturbance is recommended. The ripper plow or disc trencher can control pinegrass for 3–4 years and increase Douglas-fir survival and growth. For lodgepole pine sites, only medium-impact mechanical site preparation is necessary where natural regeneration is expected. Any mechanical treatment that produces a continuous furrow (e.g., disc trencher, ripper, or ripper plow) is recommended for sites to be planted with lodgepole pine. Severe disturbance should be avoided on clearcuts with abundant lodgepole pine cones to minimize pine overstocking. A moderate pinegrass cover can help prevent pine overstocking.

Under more closed canopies and where underplanting occurs under dead pine: Chemical treatment of patch scarification or screefing in large (>150 cm diameter) patches would be the best alternatives. Again, mechanical treatments have the advantage of less paperwork than chemical treatments. Patch scarification has improved lodgepole pine survival compared to unprepared sites.

Other Considerations

Any treatment of pine grass should be done considering other possible factors important to regeneration and tree growth and other resources. Several practices should be considered in concert to reduce erosion and minimize impacts on soil flora and fauna and minimize costs. Early planting may allow trees to establish before grasses flush and eliminate the need for site preparation.

Key Uncertainties

The issue is how best to reduce pine grass competition under canopies and to identify areas where that competition is severe enough to need intervention. Treatments with herbicides or manual screening are the most relevant options to explore. In some areas the need for treatment should be assessed by also trying early establishment of seedlings before the grass responds to increased light levels. Potential for trying larger stock also is an option.

Short-Term Learning

All the treatments noted under key uncertainties are suitable for replicated, short duration experiments that will achieve results over a few years. Experiments should have controls (untreated sites), and one or more treatments, replicated at least three times. Seedling survival, growth (diameter and height), should be recorded yearly after treatment.

Literature Cited

- Amaranthus, M.P., and D.A. Perry. 1987. Effect of soil transfer on ectomycorrhizae formation and the survival and growth of conifer seedlings in disturbed forest sites. *Can. J. For. Res.* 17: 944–950.
- BC Ministry of Forests website: <http://www.myacquire.com/spvegman/expertsystem/siteID.asp>
- BC Forest Practices Branch. 1997. Operational summary for pinegrass complex. ISBN 0-7726-3165-4.
- Chakravarty, P., and L. Chatarpaul. 1990. Non-target effect of herbicides: Effect of glyphosate and hexazinone on soil microbial activity, microbial population, and in-vitro growth of ectomycorrhizal fungi. *Pestic. Sci.* 28: 233–241.
- Fleming, R.L., Black, T.A., Adams, R.S., and Stathers, R.J. 1998. Silvicultural treatments, microclimatic conditions and seedling response in southern interior clearcuts. *Can. J. Soil Sci.* 78: 115–126.
- Haeussler, S., Coates, D., and Mather, J. 1990. Autecology of common plants in British Columbia: a literature review. Forestry Canada and British Columbia Ministry of Forests, Victoria, B.C. For. Res. Dev. Agree. Rep. 158.
- Harvey, A.E., M.J. Larsen and M.F. Jurgensen. 1979. Comparative distribution of ectomycorrhizae in soils of three western Montana forest habitat types. *For. Sci.* 25: 350–358.
- Heineman, J.L., G.D. Hope, S.W. Simard, A. Vyse, D.L. Lloyd and D.J. Miège. 2003. The effects of site preparation and harvesting practices on planted seedling productivity and microenvironment in southern interior dry, grassy IDF forests. Res. Br., B.C. Min. For., Victoria, B.C. Tech. Rep. 009. www.for.gov.bc.ca/hfd/pubs/Docs/Tr/Tr009.htm
- Hope, G.D. 1991. Effects of mechanical site preparation on soil and foliar nutrients in the drier subzones of the IDF, MS and ESSF zones — project 3.50. Forestry Canada and British Columbia Ministry of Forests, Victoria, B.C. For. Res. Dev. Agree. Res. Memo 193.

- Huggard, D.J., A. Arsenault, D. Lloyd, A. Vyse and W. Klenner. 2005. The Opax Mountain Silviculture Systems Project: preliminary results for managing complex, dry interior Douglas-fir forests. Ministry of Forests Research Program Extension Note 72. 16 p.
- Hurd, C., M. Tu, C.R. Robison and J.M. Randall. 2001. Chapter 7e. In: Tu, M., Hurd, C. & J.M. Randall. 2001. Weed Control Methods Handbook, The Nature Conservancy, <http://tncweeds.ucdavis.edu>, version: April 2001.
- Kaps, M.A., and L.J. Kuhns. 1987. The effect of glyphosate on the growth of two mycorrhizal fungi in pure culture. *Hortscience*, 22: 1058.
- Lloyd, D., K. Angove, G. Hope and C. Thompson. 1990. A guide to site identification and interpretation for the Kamloops Forest Region. British Columbia Ministry of Forests, Victoria, BC Land Manage. Handb. 23.
- Newsome, T.A. 1998. Site preparation on dry grassy sites in the Cariboo Forest Region. In *Managing the Dry Douglas-fir Forests of the Southern Interior: Workshop Proceedings*, 29–30 April 1997, Kamloops, B.C. *Edited by* A. Vyse, C. Hollstedt, and D. Huggard. BC Ministry of Forests, Victoria, B.C. Work Pap. 34. pp. 53–61.
- Nicholson, A. 1989. Water relations, survival, and growth of Douglas-fir seedlings at a pinegrass dominated site in south-central British Columbia Project No. 3.1. For. Can. and B.C. Min. For., Victoria, B.C. FRDA Memo No. 121.
- Nilsson, E., and G. Örlander. 1999. Vegetation management on grass-dominated clearcuts planted with Norway spruce in southern Sweden. *Can. J. For. Res.* 29: 1015–1026.
- Örlander, G., G. Hallsby, P. Gemmel and C. Wilhelmsson. 1998. Inverting improves establishment of *Pinus contorta* and *Picea abies* — 10-year results from a site preparation trial in northern Sweden. *Scand. J. For. Res.* 13: 160–168.
- Perry, D.A., M.P. Amaranthus, J.G. Borchers, S.L. Borchers and R.E. Brainerd. 1989. Bootstrapping in ecosystems. *BioScience*, 39: 230–237.
- Peterson, T.D. and B.D. Maxwell. 1987. Water stress of *Pinus ponderosa* in relation to foliage density of neighbouring plants. *Can. J. For. Res.* 17: 1620–1622.
- Schoenholtz, S.H., J.A. Burger and J.L. Torbert. 1987. Natural mycorrhizal colonization of pines on reclaimed surface mines in Virginia. *J. Environ. Qual.* 16: 143–146.
- Sidhu, S.S., and P. Chakravary. 1990. Effect of selected forestry herbicides on ectomycorrhizal development and seedlings growth of lodgepole pine and white spruce under controlled and field environment. *Eur. J. For. Pathol.* 20: 77–94.
- Simard, S.W., J.L. Heineman and P. Youwe. 1998. Brushing and grazing effects on lodgepole pine, vascular plants, and range forage in three plant communities in the southern interior of British Columbia: nine-year results. British Columbia Ministry of Forests, Victoria, B.C. Land Manage. Handb. 45.
- Simard, S.W., M.D. Jones, D.M. Durall, G.D. Hope, R.J. Stathers, N.S. Sorensen and B.J. Zimonick. 2003. Chemical and mechanical site preparation: effects on *Pinus contorta* growth, physiology, and microsite quality on grassy, steep forest sites in British Columbia. *Can. J. For. Res.* 33: 1495–1515.
- Skinner, M.F., G. Murphy, E.D. Robertson and J.D. Firth. 1989. Deleterious effects of soil disturbance on soil properties and the subsequent early growth of second-rotation radiata pine. Forest Research Institute, New Zealand Forest Service. FRI Bull. For. Res. Inst. N.Z. For. Serv. 153: 210–211.

- Smith, S.E. and D.J. Read. 1997. Mycorrhizal symbiosis. 2nd ed. Academic Press Ltd., London.
- Spittlehouse, D.L. and M.J. Goldstein. 1989. Modeling soil water availability for seedling establishment. *In*: Climate Applications in Forest Renewal and Forest Production. D.C. MacIver, R.B. Street, and A.N. Auclair (editors). Proc. Forest Climate '86, Nov. 17–20, 1986, Orillia, Ont.
- Stathers, R.J. 1989. Summer frost in young forest plantations. Forestry Canada and British Columbia Ministry of Forests, Victoria, B.C. For. Res. Dev. Agree. Rep. 73.
- Timbal, J., J. Gelpe and J. Garbaye. 1990. Preliminary study of the depressive effect of *Molinia caerulea* L. Moench on early growth and mycorrhizal status of *Quercus rubra* seedlings. Ann. Sci. For. 47: 643–649.
- Vogel, S.A. 1985. Influence of canopy cover and simulated grazing on water relations, stomatal conductance and photosynthesis of pinegrass and elk sedge. M.Sc. thesis. Univ. Montana, Missoula, Mont.
- Vyse, A., C. Ferguson, S.W. Simard, T. Kano and P. Puttonen. 2006. Growth of Douglas-fir, lodgepole pine, and ponderosa pine seedlings underplanted in a partially-cut, dry Douglas-fir stand in south-central British Columbia. *Forestry Chronicle*. 82:723-732.

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Appendix 1: Details of Local (BC) Results:

Both the studies in this Appendix concern sites that were clearcut and then left for some years before reforestation was attempted ... the worst case for pine grass. Vyse et al. (2006) is the only study where there is pine grass in understory, but even there some site prep was used; Huggard et al (2005) report on planting in openings at Opax where small patch site prep was highly successful in reducing pine grass.

1) Simard et al. (2003) planted lodgepole pine in pinegrass controls and small (90 × 90 cm) and large (180 × 90 cm) patches where (i) only pinegrass was removed using glyphosate or (ii) both pinegrass and the forest floor were removed using an excavator. Treatments were replicated three times in east- and west-facing clearcuts and effects were followed for 9 years.

Two-year pine survival was 78% in the control and >97% in large patches. All patch treatments improved pine growth, but it was greatest in large chemical patches during the initial 6 years and in both large patch treatments thereafter. Seedlings grew larger following any site preparation treatment than with no treatment. Seedlings were larger in large patches than in small patches. Seedlings were larger where the forest floor was retained than where it was removed along with pinegrass in the short term, but this forest floor effect was no longer apparent after 1995. Although seedlings grew larger following removal of pinegrass using either mechanical or chemical treatments, there was no added benefit of removing the forest floor along with pinegrass.

Removal of the forest floor reduced foliar and soil nutrients, increased bulk density and soil water availability, decreased porosity and aggregate stability, and reduced ectomycorrhizal

diversity and richness. These changes were not observed in chemical patches. Mechanical removal of the forest floor, either in large or small patches, resulted in significant decreases in foliar Al, B, and Mn concentrations compared with the control or chemical patches, where forest floor was left intact ($p < 0.05$). Planned contrasts also showed that mechanical forest floor removal significantly reduced foliar Fe compared with the control ($p < 0.05$). Foliar Al, B, Mn, and Fe concentrations were 43, 15, 48, and 18% lower in the mechanical patches than in the control, respectively. Foliar N and S were slightly lower (by 7 and 4%, respectively) in the chemical patches than in the control ($p < 0.05$). None of the other foliar nutrients were significantly affected by site preparation 5 years after the treatment application.

Mechanical site preparation treatments that removed the forest floor in small or large patches significantly reduced mineral soil N concentration and capital compared with the control after 5 years ($p < 0.05$). Concentrations of C, $\text{NH}_4\text{-N}$, and $\text{NO}_3\text{-N}$ were also substantially reduced by mechanical site preparation, but differences between the treatments were not significant ($p > 0.05$). Conversely, the mechanical treatments resulted in greater mineral soil cation exchange capacity, exchangeable Ca^{2+} , exchangeable Mg^{2+} , and pH compared with the control ($p < 0.05$). In contrast with the mechanical treatments, the chemical treatments had no significant effect on mineral soil nutrients ($p < 0.05$).

In Simard et al.'s study, all treatments that removed patches of pine grass increased soil temperatures and reduced frost relative to controls, but more so in the large patches than in the small ones. All site preparation treatments increased average daily soil temperature as well as minimum (nighttime) air temperature at seedling height.

None of the site preparation treatments consistently reduced the number of days where soil water potentials fell below -0.1 MPa, and the chemical treatments actually resulted in a greater number of stressful days (< -0.1 MPa) in most years.

Those results are consistent with those of other studies of grass interference and conifer establishment on dry, harsh sites in mid-latitude regions where a reduction in soil water availability was the primary mechanism of grass competition (references in Simard et al 2003). In this study, early survival of lodgepole pine seedlings in the undisturbed pinegrass community appeared to be reduced by inadequate water uptake, which probably resulted from low soil water availability (particularly in the droughty year of planting), low night-time air temperatures, and slow pine root egress.

Simard et al.'s results also agree with results from Heineman et al. 2003 (below) who studied the effects of site preparation on water availability in the seedling root zone at Fehr Mountain and Murray Creek, BC. Mechanical site preparation treatments that removed the forest floor resulted in short-term reductions in soil and/or foliar nutrient concentrations. However, 11 years after treatments were applied at Fehr Mountain, lodgepole pine showed no evidence of deficiencies. Likewise, pine at Murray Creek showed no evidence of deficiencies 5 years after treatment.

2) Heineman et al.'s (2003) review reported that one year after the scalping treatment was applied at Fehr Mountain, total soil nitrogen (N) content was reduced to 60% of the untreated control, extractable phosphorous (P) to about 80% of the control, and extractable potassium (K) and sulphur (S) to 85–90% of the control. The effect on exchangeable cations was small and presumably biologically insignificant. When comparisons were made among biogeoclimatic zones within the Kamloops Forest Region, the effect of forest floor removal on soil nutrient status was less in the IDF zone, where the forest floor is relatively thin, than in either the Montane Spruce (MS) or Engelmann Spruce–Subalpine Fir (ESSF) zones (Hope 1991). For Douglas-fir and lodgepole pine at Fehr Mountain, concentrations of most foliar nutrients had

decreased somewhat in the scalping treatment compared with the untreated control after 3 years, and boron (B) was reduced to possible deficiency levels. However, the presence of B is highly variable year-to-year, and depends on variations in weather conditions (R. Brockley, pers. comm., 2000). Nitrogen was somewhat deficient in both the control and treatments. By the time lodgepole pine seedlings were 11 years old, significant differences in foliar nutrient levels between treatments remained. Foliar aluminum (Al) and manganese (Mn) concentrations were significantly lower in the scalping treatment than in the control, but were still well above deficiency levels. Foliar sulphur (S) levels were low enough in both the control and scalping treatment to suggest a possible deficiency (G. Hope, unpublished data). Douglas-fir at Fehr Mountain was not sampled at age 11 because of low survival rates (due to frost). At Murray Creek, the effects of scalping and chemical site preparation treatments on soil and lodgepole pine foliar nutrient concentrations were assessed 5 years after site preparation. The removal of forest floor materials in both large and small patches significantly reduced total soil carbon (C) and N capital in comparison with the untreated control, whereas chemical treatments did not reduce quantities significantly. Nutrient levels were affected only within the screefed patches and not across the entire treatment plot, however, because forest floor materials were displaced but not removed from the site. Removal of the forest floor in large and small patches resulted in significant decreases in foliar Al, B, and Mn compared with the control.

Mechanical and chemical treatments improved water availability equally well at Fehr Mountain, maintaining potentials above -0.1 MPa throughout the growing season. For both Douglas-fir and lodgepole pine, increases in the availability of root-zone water improved stomatal conductance, which is known to be positively correlated with photosynthetic rates and growth rates. At Murray Creek, soils were measurably drier on east than on west aspects, a result that was attributed to the east aspect having 100 m lower elevation, steeper slope, and coarser soils than the west aspect. Soil water potential was commonly higher in large mechanical and chemical patches than in the control, suggesting that those treatments had greater potential for increasing water availability to seedlings. However, none of the site preparation treatments consistently reduced the number of days where water potentials fell below -0.1 MPa, and the chemical treatments appeared to increase the number of days with moisture stress. Chemical and mechanical treatments increased soil water availability equally well by reducing the presence of pinegrass, and nighttime air temperature at seedling height also increased as a result of both types of treatment. Removal of forest floor materials in mechanical treatments resulted in short-term reductions in soil and foliar nutrient concentrations at both Fehr Mountain and Murray Creek, but there was no evidence of long-term deficiencies. At Murray Creek, however, ectomycorrhizal diversity was significantly lower in the mechanical treatment than the untreated control 28 months after planting.

2) Vyse et al. (2006) examined the effects of partial cutting on seedling growth of three conifer species at a very dry, hot interior Douglas-fir site near Kamloops, British Columbia. Douglas-fir, lodgepole pine, and ponderosa pine seedlings were planted in mechanically (with a backhoe) prepared $50\text{ cm} \times 50\text{ cm}$ patches under different canopy conditions created by harvesting 60% of the original stand volume. The prepared areas were selected to represent canopy closures from open to closed, slopes from 0 to 60%, and all aspects. After six years, survival of Douglas-fir, lodgepole pine and ponderosa pine was 78%, 76% and 70%, respectively. Light level had a strong influence on survival and condition and the screefing treatment seemed to be effective at allowing trees to establish before pine grass competition. All species survived well in the most open conditions which was where there was the greatest understory grass, herb and shrub abundance. As well as noting that partial cutting can allow enough light for seedling growth, they also note that preparing small, vegetation-free planting spots is sufficient to achieve adequate understory stocking.

Effect of the Dwarf Mistletoe, *Arceuthobium americanum*, on Regeneration in Beetle-Killed Lodgepole Pine Stands

The Forests for Tomorrow (FFT) program was established by the BC Government in 2005 in response to the devastating impact of major fires and the mountain pine beetle (MPB) epidemic on the forest land base of the Province. The program is aimed at improving the future timber supply and protecting other forest values through the re-establishment of young forests on lands that would otherwise remain underproductive.

The mountain pine beetle epidemic had affected over 10 million hectares of forest land by 2008 and is expected to expand further. This loss in forest cover is unprecedented in both scale and complexity. Many forest types have been affected across a range of ecological conditions from the dry Chilcotin to moist sub-boreal and high elevation zones. These twin factors of scale and complexity have, in turn, created numerous uncertainties for forest managers.

Adaptive management strategies have been proposed as one approach for dealing with these uncertainties.

An adaptive management workshop held on June 26, 2008 under the FFT program for key staff engaged in restoring forest cover to the mountain pine beetle area raised a range of uncertainties or questions from participants. This is one of the topics for which our team was asked to review and summarize information in the existing literature.

Executive Summary

Dwarf mistletoe species *Arceuthobium americanum* poses a potential risk to lodgepole pine regeneration in beetle-killed pine stands. Foresters are concerned that mistletoe occurring on, or infecting live pine stems in the overstory of unsalvaged beetle-killed stands can proliferate in the overstory and infect seedlings leading to growth losses. Estimates of damage caused by mistletoe are based on individual tree studies comparing stems with differing levels of infection on similar sites. At the highest levels of infection, stands may lose up to 35% of their growth potential.

Mistletoe is perhaps the most treatable of all of the pests of lodgepole pine. Several biological and ecological features make mistletoes especially amenable to silvicultural treatment (Muir and Geils 2002): *Obligate parasitism, host specificity, extended life cycles, limited seed dispersal, slow intensification within tree crowns, and easy identification.*

A Forest Practices Code guidebook provides advice on the control of all species of mistletoe in BC and more detailed prescriptions are available for lodgepole pine in Muir and Geils (2002). Treatment prescriptions are based on infection ratings based on a 6 point scale (BC Ministry of Forests 1995b). Stands with ratings of 3 or higher should not have overstory retained. Regenerating stems that are infected are not considered acceptable stems in free growing surveys and should be removed.

Stand modelling in the Rocky Mountains has suggested that lodgepole pine can be partially cut or thinned without the risk of damage from future mistletoe infections if the overstory infection level is low. The DM guidebook (BC Ministry of Forests 1995a) recommends against the use of partial cutting in stands where the proportion of lodgepole pine is greater than 50% and more than 20% of the pine trees are infected. However, these recommendations are based on stands with high densities of overstory stems.

The key decision points in Mountain pine beetle attacked stands with mistletoe is how many live overstory trees exist and how high infection levels are on those trees or tall (>1 m) understory. A simple decision tool could be applied using the 6 point infection rating scale. For example, if the residual density was higher than 50 stems per hectare (sph) and the average infection level was 3 or higher, and if lodgepole pine in the understory is at 50% or more of the stocking target, the stand should be replaced (clearcutting the overstory or applying a prescribed burn could be

recommended). If infection level is low, and sufficient secondary structure is present or expected, no action would be a suitable option or partial cutting to retain live overstory would be acceptable. Planting of pine could take place outside pockets of infection. More detailed recommendations could be based on the detailed mistletoe spread and damage models that are available (see Robinson et al. 2002 for review).

The Issue

The dwarf mistletoe species *Arceuthobium americanum* poses a potential risk to lodgepole pine regeneration in beetle-killed pine stands. Foresters are concerned that mistletoe occurring on, or infecting live pine stems in the overstory of unsalvaged beetle-killed stands can proliferate leading to growth losses. Also, there is concern that mistletoe can infect pine seedlings in the understory and reduce their future growth potential.

Basic Biology

Dwarf mistletoes (*Arceuthobium spp*) are parasitic vascular plants that affect the growth and mortality of conifer species in many parts of the world. They are particularly pervasive and damaging in the western North America. Long standing infections cause growth loss and may result in tree mortality directly or in association with other mortality agents. Well developed infections lead to prolific branching and the characteristic “witches brooms”. The plants spread from tree to tree primarily by means of seed dispersal, in which the seeds are “shot” from the plant, traveling up to 30m. Animals, including several species of birds and small mammals, provide a more far-reaching dispersal mechanism. The plants and the brooms provide food and habitat for a wide variety of animal species which in turn contribute to the spread of the plant (Geils et al. 2002).

Species of dwarf mistletoe are relatively host specialised. One species *A. americanum* (hereafter A.a.) establishes on lodgepole pine and is regarded as a major pest of this species throughout western North America (Baranyay and Safranyik 1970, van der Kamp and Hawksworth 1985), but it also damages jack pine and ponderosa pine.

A.a. is found throughout the range of lodgepole pine but infections are most intense and damaging on drier sites where lodgepole is the dominant species. In wetter areas, where lodgepole pine is an early seral species, the dominance of pine is highly variable. The level of infection is also a function of fire history. Stands of pine that develop following high-severity fires have low levels of mistletoe, but stands that have experienced low-severity fires often have very high levels of infection. High-severity fires leave few if any residual stems of pine and infection of the subsequent regeneration proceeds from infected pine on the fire edge. Low-severity fires leave many survivors and if these survivors are infected with mistletoe, the regenerating stand beneath may become heavily infected. This circumstance is frequently found in the drier portions of the Chilcotin region of BC.

Geographic Distribution of Lodgepole Pine Mistletoe

Lodgepole pine mistletoe is found throughout the southern portion of the host species from 56 degrees north to the US border. The intensity of infections varies widely. It is lowest in mixed species stands in the wetter portions of the range and most intense in the dry Chilcotin region.

Damage

Estimates of damage caused by mistletoe are based on individual tree studies comparing stems with differing levels of infection on similar sites. At the highest levels of infection, stands may

lose up to 35% of their growth potential (van Sickle and Wegwitz 1978). These estimates have been scaled up to the provincial level and growth losses of 2.5 million m³ per year have been calculated for the province (van Sickle and Wegwitz 1978). However these estimates are not based on detailed surveys of mistletoe infection levels in the province and must be considered with caution. Nevertheless, there is no doubt that A.a. can cause serious damage and high levels of infection can and should be avoided.

Managing Risk

Mistletoe is perhaps the most treatable of all of the pests of lodgepole pine. Several biological and ecological features make mistletoes especially amenable to silvicultural treatment (Muir and Geils 2002):

Obligate parasitism. Mistletoes require a living host to survive and reproduce. When an infested tree or branch dies (or is cut), the attached mistletoe plants die as well.

Host specificity. Mistletoes generally infect only a single, susceptible host species or group of related species. Mixed species stands with less susceptible hosts reduce spread.

Extended life cycles. Life cycles of mistletoes are relatively long compared to other tree disease agents; a generation ranges from 2 to 10 or more years. Mistletoe spread from tree to tree, and increase within tree crowns is relatively slow. Because numerous infections are required to cause serious damage, the effects accumulate slowly.

Limited seed dispersal. Mistletoe seeds are dispersed a maximum horizontal distance of only 10 to 15 m; gravity and foliage limit effective spread in the vertical and horizontal planes; animal vectoring of mistletoe (with one or two exceptions) is rare enough to be ignored other than from ecological and evolutionary perspectives. Consequently, mistletoe tends to occur as pockets of infestation and small, young understory trees are targets for infection in these pockets. Planting lodgepole pine in these pockets is not recommended but there is an opportunity to regenerate pine outside of these pockets of infection.

Slow intensification within tree crowns. Mistletoe infection typically begins in the lower tree crown. Vertical spread is slow enough that trees with rapid height growth can outgrow or at least keep pace with mistletoe intensification. Opening the stand through thinning can provide more light to mistletoe infections. Thus, density management could allow silviculturists to influence the balance between growth of the host and the pathogen.

Easy identification. The plant can be seen and identified relatively easily. Incidence and severity ratings can generally be used to characterize dwarf mistletoe infections (Muir and Moody 2002). Severely infected stands can be detected by aerial surveys but incidence and severity usually must be determined by ground surveys or inventory sampling (Muir and Moody 2002). The ease of detection in beetle-killed stands has not been tested to our knowledge.

A Forest Practices Code guidebook (BC Ministry of Forests 1995a) provides advice on the control of all species of mistletoe in BC and more detailed prescriptions are available for lodgepole pine in Muir and Geils (2002). Most treatment prescriptions are based on surveys of the pine overstory to establish infection ratings based on a 6 point scale (BC Ministry of Forests 1995b). Stands with ratings of 3 or higher are considered unsuitable for silvicultural systems which retain overstory stems during the regeneration phase because of the risk of infecting the understory. Regenerating stems that are infected are not considered acceptable stems in free growing surveys and may require treatment.

Stand modelling work in the Rocky Mountains (cited by van der Kamp and Hawksworth 1985) has suggested that the partial cutting or thinning in lodgepole pine stands can be carried out without the risk of damage from future mistletoe infections if the overstory infection level is low (a low rating). The Dwarf Mistletoe guidebook (BC Ministry of Forests 1995a) recommends against the use of partial cutting in stands where the proportion of lodgepole pine is greater than 50% and more than 20% of the pine trees are infected. However, these recommendations are based on stands with high densities of live overstory stems.

The Risk and the Unknowns

Where stands of lodgepole pine have been attacked by mountain pine beetle, the risk of mistletoe infections are considerably reduced because when the tree dies and the mistletoe infection also dies. Mistletoe infections in residual stems will increase with the reduction in competition and increase in light. The risk of mistletoe infection in the stand depends on the density and infection level of surviving overstory stems of lodgepole pine, the proportion of pine in the understory, and its size and the existing infection level.

The primary unknown is the density of surviving lodgepole pine stems in pine beetle attacked stands planned for treatment and the level of mistletoe infection in those stems. This is part of the broader issue of a general lack of knowledge about the density of surviving stems of all species.

Ideally this uncertainty should be resolved by a province wide inventory of dead pine stands that identifies remaining live overstory and basic understory structure. In the absence of such an inventory, project planners will have to make do with low cost, local inventory approaches. Once the species and density of live stems is known, and levels of infection are known, then treatments for mistletoe are straightforward.

Risk Management Considerations and Options

Management options range from doing nothing, to removing the overstory and destroying the understory, to retaining the overstory and various combinations of sanitation thinning and supplementary underplanting. Prescribed burns have also been proposed as a method of eliminating mistletoe infections (Hessburg et al. 2008).

Results from recent surveys in pine beetle attacked stands have shown that the density of surviving lodgepole pine stems across a wide range of the epidemic area is low and the proportion of pine in the understory across the same area is also low (Vyse et al. 2007; Astrup et al. 2008; although Forest Practices Board 2007 among others have reported high levels of pine regeneration in the Chilcotin region). Prescribing foresters must be aware of the potential for future damage and record mistletoe infections in surveys before preparing prescriptions. They should also be aware that mistletoe infestations can create desired habitat features (Muir et al. 2004).

Risk Management Recommendation

A simple decision tool could be applied using the 6 point infection rating scale. For example, if the residual density was higher than 50 stems per hectare (sph) and the average infection level was 3 or higher, and if lodgepole pine in the understory is at 50% or more of the stocking target, replacing the stand (clearcutting the overstory or applying a prescribed burn could be recommended). If infection level is low, and sufficient secondary structure is present or expected, no action would be a suitable option. The same tool could be applied in developing a prescription for underplanting lodgepole pine. More detailed recommendations could be based

on the detailed mistletoe spread and damage models that are available (see Robinson et al. 2002 for review).

Key Uncertainties

The density of surviving lodgepole pine stems in pine beetle attacked stands planned for treatment. This is part of the broader issue. There is a lack of knowledge about the density of surviving stems of all species.

Short-Term Learning

Ideally this uncertainty should be resolved by a province wide inventory of dead pine stands. In the absence of such an inventory, project planners will have to make do with low cost, local inventory approaches.

Literature Cited

- Astrup, R., K.D. Coates and E. Hall. 2008. Recruitment limitation in forests: lessons from an unprecedented pine beetle epidemic. *Forest Ecol. Manage.* In press.
- Baranyay J.A. and L. Safranyik. 1970. Effect of dwarf mistletoe on growth and mortality of lodgepole pine. Canadian Forest Service, Canada Dept. Fisheries and Forestry. Pub 1285. 19p.
- British Columbia Ministry of Forests. 1995a. Dwarf mistletoe management guidebook. Forest Practices Code of British Columbia. 20p.
(<http://www.for.gov.bc.ca/tasb/legsregs/fpc/fpcguide/dwarf/dwarftoc.htm>)
- British Columbia Ministry of Forests. 1995b. Forest health surveys guidebook. Forest Practices Code of British Columbia. 56p.
- Geils, B.W., J. Cibrián Tovar and B. Moody (technical coordinators). 2002. Mistletoes of North American Conifers. Gen. Tech. Rep. RMRS–GTR–98. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 123 p.
- Forest Practices Board of British Columbia, 2007. Lodgepole pine stand structure 25 years after mountain pine beetle attack. Victoria, B.C. Forest Practices Board of British Columbia. Special Report 32. 16p.
- Hessburg, P.F., N.A. Povak and R.B. Salter. 2008. Thinning and prescribed fire effects on dwarf mistletoe severity in an eastern Cascade Range dry forest, Washington *Forest Ecology and Management* 255: 2907-2915.
- Muir, J.A. and B.W. Geils. 2002. Management strategies for dwarf mistletoe: silviculture. *In* Mistletoes of North American conifers. B.W. Geils, J. Cibrián Tovar, and B. Moody (technical coordinators). U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Ogden, Utah. General Technical Report RMRS-GTR-98, pp. 83–94.
- Muir, J.A. and B. Moody. 2002. Dwarf mistletoe surveys. *In* Mistletoes of North American conifers. B.W. Geils, J. Cibrián Tovar, and B. Moody (technical coordinators). U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Ogden, Utah. General Technical Report RMRS-GTR-98, pp. 67–73.
- Muir, J.A., D.C.E. Robinson and B.W. Geils. 2004. [Characterizing the effects of dwarf mistletoe and other diseases for sustainable forest management](#). *BC Journal of Ecosystems and Management* 3(2):88-94.

Robinson D.C.E., B.W Geils and J.A. Muir. 2002 . Spatial statistical model for the spread of dwarf mistletoe within and between stands. In: Crookston, N.L. and Havis, R. N. (Comps). 2002. Second Forest vegetation Simulator Conference. USDA Forest Service. RMRS-P-25. P178-185.

van Sickle, G.A. and E. Wegwitz. 1978. Silvicultural control of dwarf mistletoe in young lodgepole pine stands in Alberta and British Columbia. Canadian Forest Service, Victoria, BC. Report BC-X-180. 11p.

van der Kamp, B.J. and F.G. Hawksworth. 1985. Damage and control of the major diseases of lodgepole pine. In: D.M Baumgartner, et al. (eds). Lodgepole pine: the species and its management. Washington State University, Cooperative Education. Pp 125-131.

Vyse, A. 1981. Managing Lodgepole pine dwarf mistletoe in the Cariboo Forest Region. Cariboo Research Brief 17.

Vyse, A., C. Ferguson, D.J. Huggard and B. Zimonick. 2007. Regeneration beneath lodgepole pine dominated stands attacked or threatened by the mountain pine beetle in the south central Interior, British Columbia. Report to southern Interior region Forest Stewardship Section.

Effects of Stem Rusts and Stem Canker on Regeneration in Mountain Pine Beetle-Killed Lodgepole Pine Stands

The Forests for Tomorrow (FFT) program was established by the BC Government in 2005 in response to the devastating impact of major fires and the mountain pine beetle (MPB) epidemic on the forest land base of the Province. The program is aimed at improving the future timber supply and protecting other forest values through the re-establishment of young forests on lands that would otherwise remain underproductive.

The mountain pine beetle epidemic had affected over 10 million hectares of forest land by 2008 and is expected to expand further. This loss in forest cover is unprecedented in both scale and complexity. Many forest types have been affected across a range of ecological conditions from the dry Chilcotin to moist sub-boreal and high elevation zones. These twin factors of scale and complexity have, in turn, created numerous uncertainties for forest managers. Adaptive management strategies have been proposed as one approach for dealing with these uncertainties.

An adaptive management workshop held on June 26, 2008 under the FFT program for key staff engaged in restoring forest cover to the mountain pine beetle area raised a range of uncertainties or questions from participants. This is one of the topics for which our team was asked to review and summarize information in the existing literature.

Executive Summary

Several species of rust (particularly Western gall rust (*Endocronartium harknessii*), Comandra blister rust (*Cronartium comandrae*), and Stalactiform blister rust (*Cronartium coleosporioides*)) and one species of canker (Atropellis stemcanker (*Atropellis piniphilla*)) pose a risk to lodgepole pine regeneration in beetle-killed pine stands. Trees with rust infections or cankers are likely become crop trees because they do not die quickly. These trees compete with surrounding trees for resources and contribute little to stand productivity. Those trees that do reach rotation often suffer a serious degradation in wood quality. Foresters are concerned that these organisms infecting live pine stems in the overstory of un-salvaged beetle-killed stands might infect pine seedlings in the understory and reduce their future growth potential beyond the level that normally occurs in regenerating stands of pine. The levels of damage affect decisions about using underplanting or removing the overstory to gain successful regeneration.

Treatments for rusts include the selective removal of live host trees during spacing, removing infections (pruning infected branches and excising cankers), or through stand density management or combinations of these activities. However, the impact of rusts can be accentuated by premature stand entry and by spacing to low stand densities. A longer-term approach is to develop rust-resistant seedlings through an intensive tree improvement program (Wu and Ying 1998). A system of assessing thresholds for rust infection treatments is provided in the Stem Rust Guidebook. However, establishing and maintaining a high stand density for 2–30 years is probably the most effective form of management if pine stands are created.

In stands killed by mountain pine beetle and underplanted, the proportion of pine is likely to be low and the risk of rust infections also low. In stands where overstory is removed, risk of rust infection is likely not different than in non-beetle stands because the rust organisms die when the tree dies. Extensive areas of beetle kill might reduce future impacts from *Endocronartium*, because the regenerating pine stems would be some distance from spore sources but this is uncommon.

The risk of stem canker infection in beetle attacked stands is low and is not likely to differ from regeneration established in the absence of mountain pine beetle. Special management for stem canker measures are not recommended (van der Kamp and Hawksworth 1985).

The Issue

Several species of rust and one species of canker pose a risk to lodgepole pine regeneration in beetle-killed pine stands. Foresters are concerned that these organisms infecting live pine stems in the overstory of un-salvaged beetle-killed stands might infect pine seedlings in the understory and reduce their future growth potential beyond the level that normally occurs in regenerating stands of pine. If this is the case, the case for stand replacement would be strengthened.

Basic Biology

The pine stem rusts of importance (Allen et al. 1996) are:

- Western gall rust (*Endocronartium harknessii*)
- Comandra blister rust (*Cronartium comandrae*)
- Stalactiform blister rust (*Cronartium coleosporioides*)

One stem canker is also of significance:

- Atropellis stemcanker (*Atropellis piniphilla*)

Pine stem rusts are widespread throughout most forested ecosystems in British Columbia, occurring on pines and alternate herbaceous hosts. They can reduce tree growth, lower wood quality, and cause early mortality. They often play a significant role in early stand development, acting primarily as a natural thinning agent. Pine stem canker is most common in northern regions.

Although trees of all ages can be affected by pine stem rusts, most infection occurs in the initial stages of stand development. Pine stem rusts infect live hosts (as obligate parasites) and have a very selective host range. White pine blister rust affects soft pines (5 needle pines) only, whereas all other pine stem rusts in B.C. affect hard pines (2 and 3 needle pines) only. Pine stem rusts have a complex infection biology which, in most cases, depends on an alternate (herbaceous) host plant for part of the life cycle.

The biology of these rusts is well described in Ziller (1974). The *Cronartium* rusts require alternate hosts in order to complete their life cycles. Only the spores from an infected alternate host may infect a lodgepole pine. The spores produced by the rust on an infected lodgepole pine may only infect an alternate host and cannot directly infect another lodgepole pine. The cankers caused by a rust infection continue to release spores each year in late spring until the infected branch or stem dies. Western gall rust does not require an alternate host; spores released from a gall rust infection may directly infect the expanding candles of the same or another pine tree.

Rust spores can travel hundreds of kilometres making sanitation difficult, if not impossible. However, spores from the alternate hosts are relatively fragile and may only spread up to several kilometres. Presence of alternate hosts in large part determines risk and levels of infection. A severe rust infection in a stand usually places nearby stands at a higher risk of becoming infected.

Humid weather is required for successful infection, and it doesn't take many humid days to allow infection on an otherwise dry summer. Optimal conditions for infection are temperatures about 10 degrees Celsius for a 1 to 2 day period accompanied by high humidity. Infection by pine stem rusts tends to occur in "wave years." These are years of high infection that occur at

irregular intervals. Many stands are not exposed to wave years of rust infection when they are young and most susceptible. In these stands damage due to rusts is minor. In the stands that do experience wave years, and in certain areas where risk is high, damage can be considerable. Infection can lead to severe damage or death and young stands severely infected with any one or a combination of these rusts may fail to reach minimum stocking levels. The level of infection in a stand peaks before age 10. By age 10 to 12, most trees have a low risk of infection and stands older than this that are free of infection have likely escaped infection. By that age they have been exposed to spores multiple times.

The main impact of hard pine rusts occurs primarily in young stands, although mature trees may be infected. Stem rusts cause mortality when the rust mycelium girdles and kills the stem. The impacts of rusts are believed to be the greatest on the most vigorous trees. Since rusts are obligate parasites, good conditions for tree growth are also good for rust growth. Lower branches are the most susceptible infection sites and infection rates decline rapidly following crown closure, when lower branches are killed due to suppression. Crown closure also reduces the light available to the alternate host species.

Occurrence of lodgepole pine stem rusts

The stem rusts are found throughout the range of lodgepole pine in the province but the risk is greatest in the moister portions of the range. Planting of inappropriate provenances or susceptible families has aggravated the problem in some locations. A table has been appended which shows the most susceptible subzones (Table 1).

The occurrence of rusts depends in part on the abundance and location of alternate hosts, especially in the case of hard rusts and white pine blister rust. For Comandra blister rust, trees even a few meters away from the alternate host tend to have lower levels of infection. BC MoF has assessed 4 year old trees during 3 years of infection of Comandra blister rust that shows this pattern. The cumulative effects of infection over time are not yet known, but at least initially, trees a few metres away have lower levels of infection. The pattern is not as clear for stalactiform or western gall rust because they have multiple alternate hosts.

The distribution of stem rusts throughout young stands is often somewhat aggregated. Thus, mortality due to rusts may result in the stocking of some areas dropping below recommended minimum levels while other areas in the same stand remain overstocked.

Atropellis canker occurs in older pole sized stems and like the rusts, distribution is patchy.

Damage caused by stem rusts

Trees with rust infections or cankers are likely become crop trees. However, they do not die quickly. These trees continue to compete with surrounding trees for resources while contributing little to stand productivity. Those trees that do reach rotation often suffer a serious degradation in wood quality.

Managing the risk of rust infection

Regeneration and stand management activities can change the course of pine stem rusts in stands. Treatments include the selective removal of live host trees during spacing, removing infections (pruning infected branches and excising cankers), or through stand density management or combinations of these activities. However, the impact of rusts can be accentuated by premature stand entry and by spacing to low stand densities. A longer-term approach is to develop rust-resistant seedlings through an intensive tree improvement program (Wu and Ying 1998).

Risk of infection differs by zone. Generally as elevation rises, risk decreases. At high elevation (as in most of the ESSF) it is usually too cold for rust spores to cause infection before temperature and humidity drop to low to allow infection to be completed. The SBS zone has the highest risk. Dry zones and subzones are also at risk because even though they are generally dry they tend to have humid, warm days quite frequently.

Dealing with rusts in beetle-killed stands

Risk of rust infections is high only where pine is a large proportion of the regenerating stand. This would usually be the case when FFT removes the overstory and plants predominantly pine back on the site. In underplanting situations, pine is likely to be a smaller component of the planted stock and as such risk of infections should be lower.

The impact of rust infections on future rehabilitated stand potential in mountain pine beetle-killed stands is unlikely to differ from that in regular stand management. Increased risk is unlikely because the rust organisms die when the tree dies. Extensive areas of beetle kill might reduce future impacts from *Endocronartium*, because the regenerating pine stems would be some distance from spore sources. But such conditions are rare because patches of younger pine stands have been created by past logging and regeneration practices. Infected alternative hosts of the *Cronartium* hosts are likely to be close at hand.

Risk must be assessed at landscape level and stand basis. At the stand level, it is difficult to assess risk to new stands by looking at levels of rust in old stands. By the time stands mature the infected stems have largely died out and fallen. Rather, it is easier to look at nearby age class 2 and 3 stands and assess those stands by identifying cankers. Experts find more rust and recognize the multiple alternate hosts better than most operational foresters, so in areas of high risk, professional assessment would be useful. At the landscape level, assessments should include an examination of young stands within a 1- to 2-km radius for rust incidence. Suggestions for survey procedures are provided in the Stem Rust guidebook (BC Ministry for Forests 1996) on in mature stands.

In areas of high risk and where alternate hosts are present, then resistant tree species should be chosen (note that Ponderosa pine is also susceptible to these rusts). Non-pine species or lodgepole pine seedling that are resistant to rusts can be used. Kalamalka nursery has seedlings resistant seedling to Western gall rust. Prince George area also screens families for resistance. There may be a 3000 fold difference in susceptibility of families to western gall rust, and about a two fold difference in susceptibility to Comandra rust.

Where pine is the dominant species, more stems could be left to allow for damage by infection while still producing enough acceptable stems by rotation age. Establishing and maintaining a high stand density for 2—30 years is probably the most effective form of management if pine stands are created. A system of assessing thresholds for rust infection treatments and details on density management in these stands are provided in the Stem Rust Guidebook (BC Ministry of Forests 1996).

The risk of stem canker infection is low and is not likely to differ from regeneration established in the absence of mountain pine beetle. Special management measures are not recommended (van der Kamp and Hawksworth 1985).

Key Uncertainties

The risk of rust and canker infections in stands developing under dead pine is thought to be low, but this prediction is highly uncertain.

Short-Term Learning

Rust and canker infection levels should be monitored in all FFT programs.

Literature Cited

Allen, E.A. D. Morrison and G.Wallis. 1996. Common tree diseases of British Columbia. Canadian Forest Service. Victoria B.C. 178p.

B.C. Ministry of Forests 1996. Pine Stem Rust Management Guidebook. Forest Practices Code of British Columbia.

<http://www.for.gov.bc.ca/tasb/legsregs/fpc/fpcguide/PINESTEM/pine1.htm#intro>

van der Kamp, B.J. and F.G. Hawksworth. 1985. Damage and control of the major diseases of lodgepole pine. In D.M Baumgartner, et.al. eds. Lodgepole pine: the species and its management. Washington State University, Cooperative Education. Pp 125-131.

Wu, H.X. and C.C. Ying. 1998. Stability of resistance to western gall rust and needle cast in lodgepole pine provenances. Canadian Journal of Forest Research 28:439–449.

Ziller, W. 1974. Tree rusts of western Canada. Pacific Forest Centre. Victoria B.C. Can. For. Service Publication 1329.

Stem Rust Hazard and Risk by Forest Region (from Stem Rust Guidebook)

Table 1 identifies regional high hazard biogeoclimatic subzones that have a high probability of pine stem rust occurrence.

Table 1. Stem rust hazard and risk by forest region (B.C. Ministry of Forests 1996).

Forest region	BEC zone	BEC subzone	Rusts of hard pine (DSG, DSS, DSC)
Cariboo	IDF	all	H
	SBPS	all	H
	SBS	all	H
Kamloops	ICH	mk1	H
		dc1	H
	ESSF	dc2	H
		dk1	H
	IDF	dk2	H
		dm1	H
	MS	dm1	H
		dm2	H
		xk	H
		dc	H
Nelson	ICH	mk1	H
	ESSF	dc1	H
	IDF	dk1	H
		dk2	H
	MS	dm1	H
Prince George	BWBS	all	H
	ICH	mm	H
	SBS	all	H
Prince Rupert	SBS	all	H
Vancouver	IDF	ww	H

"H" denotes pine stem rust is considered a high hazard in this subzone and, as such, requires attention in any prescription.

Risk of Fire after Mountain Pine Beetle

The Forests for Tomorrow (FFT) program was established by the BC Government in 2005 in response to the devastating impact of major fires and the mountain pine beetle (MPB) epidemic on the forest land base of the Province. The program is aimed at improving the future timber supply and protecting other forest values through the re-establishment of young forests on lands that would otherwise remain underproductive.

The mountain pine beetle epidemic had affected over 10 million hectares of forest land by 2008 and is expected to expand further. This loss in forest cover is unprecedented in both scale and complexity. Many forest types have been affected across a range of ecological conditions from the dry Chilcotin to moist sub-boreal and high elevation zones. These twin factors of scale and complexity have, in turn, created numerous uncertainties for forest managers. Adaptive management strategies have been proposed as one approach for dealing with these uncertainties.

An adaptive management workshop held on June 26, 2008 under the FFT program for key staff engaged in restoring forest cover to the mountain pine beetle area raised a range of uncertainties or questions from participants. This is one of the topics for which our team was asked to review and summarize information in the existing literature.

Executive Summary

As a result of pine mortality from beetle attacks, concern has been expressed that uncontrollable wildfires similar to those experienced in Yellowstone National Park in 1988 would soon follow. As well, Forests for Tomorrow has expressed concern about the loss of seedlings planted beneath dead stands as a result of wildfire when compared to stock planted in clearcuts. While there is no question that the quantity and spatial distribution of fuels is changed in stands with a high proportion of mortality caused by mountain pine beetle, there is a lack of understanding about how these changes affect the risk of fire and the predictability of fire extent.

Several recent studies have shown that time-since-beetle outbreak is critical in understanding the relationship between beetle outbreaks, stand structure, fuel dynamics and fire risk. Nonetheless, empirical studies remain relatively few. The modeling and empirical studies reviewed here with respect to the question of how the quantity and spatial distribution of fuel change due to beetle attack affects fire behaviour and the predictability of fire extent, intensity and behaviour, suggest that:

- The majority of the studies undertaken in the spruce-fir forests did not support the hypothesized increase in fire occurrence, extent, or severity following insect outbreaks,
- Some results for the lodgepole pine-dominated forests indicate there is an increase in *surface* fire intensity in 0-5 years post-outbreak stands (caused by a pulse of surface fine fuels from dead trees) and in 5-60 years post-outbreak stands (caused by an increase in wind speed in the more open stands)
- BC fire experts expect that dead 20 to 30 year old stands will support intense fires that crown because of ladder fuels and abundance of ground fuels.

The degree to which dead boles increase fire hazard or severity is theoretical but not empirically known. The risk of underplanted seedling being killed in fires compared to the risk of seedlings in clearcuts is also unknown. But seedlings in clearcuts are frequently destroyed in major fires. Options to reduce fire hazard while maintaining attributes important for biodiversity over the landscape have not been well-explored.

The Issue

As a result of mortality of pine from beetle attacks, concern has been expressed that uncontrollable wildfires similar to those experienced in Yellowstone National Park in 1988 would soon follow. As well, Forests for Tomorrow has expressed concern about the loss of seedlings planted beneath dead stands as a result of wildfire when compared to stock planted in clearcuts. While there is no question that the quantity and spatial distribution of fuels is changed in stands with a high proportion of mortality caused by mountain pine beetle, there is greater uncertainty as to how these changes affect the risk of fire and the predictability of fire extent compared to non-beetle attacked stands.

Theoretical Basis

We have a basic understanding of how fire that follows beetle attacks can affect ecosystems based on historical experience. Insect outbreaks that are followed by fire have been shown to disrupt or redirect succession in forest systems. For example, interactions of mountain pine beetle, lodgepole pine, and fire largely determine composition of subsequent stands. Outbreaks of mountain pine beetle in dead or dying lodgepole pine stands result in large fuel buildups (Stuart et al. 1989). If outbreaks are followed by intense wildfire that opens serotinous lodgepole pine cones, eliminates overstory vegetation, and exposes mineral soil then the sites return to a vigorous young stand of lodgepole pine (Amman and Schmitz 1988). However, when no fire occurs after an outbreak, lodgepole may be replaced by ponderosa pine at low elevation sites or by Douglas-fir at high elevation sites (Ahlgren 1974, Mitchell 1990).

Most literature from BC (Shore et al. 2006) promotes the theory that risk of fire after beetle attacks depends on time since attack. During first 2 to 3 years while most dead needles are retained on the tree there is a greater likelihood of a crown fire. Foliar moisture may be as low as 7% compared to live needle moisture content of just over 100%. Moisture in fine branchwood may be 20%, which is much lower than in live branches. Both changes lead to increased chance of combustion and more complete combustion during crown fires.

After needles drop to the forest floor, usually 2 to 3 years after death, risk of crown fires actually drop below those of live stands. Branches left in canopy will have lower moisture content but will not support crown fire because needles play a large role in crown combustion. Increased distances between crowns should reduce the likelihood of spread of crown fires. Fallen dead trees will increase surface fuel loadings increasing intensity and flame length and may cause standing residual dead and live trees to burn.

Loss of needles also means that more solar radiation and wind reach forest floor. The forest litter layer dries out more than under live canopy. More and drier fuel on the ground means higher intensity ground fires. About 10-15 years after the trees die, the large branches begin to fall and the tree stems break off creating a large accumulation of fuels that could support a more intense ground fire but still may not support crown fires.

Manning et al. (1982) described three primary periods of increased fire hazard in lodgepole pine stands following mountain pine beetle outbreaks. These periods again, are based on the changes in fuel quality noted in the paragraph above and theoretical understanding of ecosystem dynamics.

1. Immediately following an outbreak, when needles and small branches are retained on standing dead trees, stand susceptibility to crown fires may be increased. Understory response to the outbreak will also affect stand

susceptibility during this period by altering the potential for simultaneous ground fire.

2. 10 years after an outbreak - an elevated fire hazard also occurs when tree bark begins to slough off.
3. 20 to 50 years after the outbreak - the most extreme hazard occurs after beetle-killed trees have fallen, approximately, and fuel-loading is at its maximum. Fuel quantity and arrangement may produce extremely high intensity fires.

Within the CFS (Taylor pers. comm., Hawkes pers. comm.) there is the belief that red needle stage is certainly at higher risk of ignition and the low foliar moisture will cause more spotting and crowning. Although they do not expect higher risk of ignition in grey attack stands they expect these stands to support higher fire intensities and higher rates of spread. Blackwell (pers. comm.) echoes these theoretically-based progressions.

Modeling and Empirical Studies

The BC literature notes that empirical evidence is very limited and Shore et al. (2006) reported only one empirical study, that of Turner et al. (1999) study in Yellowstone. Other empirical studies have been done by CFS, Pacific Forestry Centre. Hawkes (2008) noted that only a small number of escaped fires occurred in mountain pine beetle outbreak areas and fire sizes are confounded by fire suppression. Also, year to year variation in ignition events and weather confound separating effects of beetle on fire hazard and risk. In the few empirical measurements, the mean annual burn rate following mountain pine beetle outbreak is less than 0.02%. Hawkes also recorded fuel and overstory changes from some mountain pine beetle attacked areas (Table 2)

Table 2. Fine and coarse woody fuel loading and percent of overstory trees that have fallen over by study area (Hawkes et al. 2004 plus additions).

Location	Years Since MPB attack	<=7cm fine wood fuel load	>7cm coarse wood fuel load (t/ha)	%overstory trees that have fallen
Current outbreak				
Manning Provincial Park	0	4.3(t/ha)	45(t/ha)	No fall down
Tetachuck Lake	4	5.6(t/ha)	24(t/ha)	No fall down
Past MB Outbreaks				
Kootenay National Park	10	3.5(t/ha)	44(t/ha)	24
Chilcotin Plateau	16	5.3(t/ha)	28(t/ha)	52
Waterton Lakes National Park	19	6.8(t/ha)	42(t/ha)	52
Flathead study (Coates 2008)	20	Not reported	Not reported	100
F P B Chilcotin study (FPB 2007)	25	Not reported	32 to 166 m3/ha	0 to 80 depending on plot. Average 45
Chilcotin (Waterhouse and Armleder 2004)	15 to 20	?	?	70
Vanderhoof SBS (Lewis 2007)	5			5
Py study in Kamloops (Vyse pers. comm.),	4	Not reported	Not reported	25 for larger stems
Oregon thinned (Mitchell and Preisler 1998)	8 12			50 90

Oregon unthinned Mitchell and Preisler 1998)	9			50
	14			90
Oregon Py (Keen 1955)	5			15
	25			90

An important conclusion from BC studies is that differing disturbance histories and ecological conditions cause substantial variation in fine and coarse surface woody fuels both before and after beetle attacks, making generalizations difficult.

Researchers from the University of Wisconsin (Simard et al. 2008) have recently summarized the literature pertaining to fire-bark beetle interactions. Their summary incorporates some literature from BC and agrees with the small amount of other empirical literature from BC. We repeat their summary, largely verbatim, below.

Simard et al. (2008) note that the potential effect of bark beetle outbreaks on fire hazard has been discussed for a long time (reviewed by McCullough et al. 1998, Parker et al. 2006, Lynch 2006), but only recently have studies presented empirical data to detect and quantify this relationship. Some authors have claimed that beetle outbreaks set the stage for catastrophic wildfires (Hopkins 1909, Brown 1975, Geiszler et al. 1980, Parker and Stipe 1993), whereas others have stressed the importance of time since beetle outbreak (Gara et al. 1985, Schmid and Amman 1992, Romme et al. 2006) and have theorized that crown fire risk might be increased only during the first year or two after an infestation because of dead needles still on the trees. After the dead needles fall to the ground, the risk of crown fire might actually be lower than pre-outbreak conditions because of reduced canopy continuity and bulk density, two important predictors of crown fire rate of spread. One to several decades after the outbreak, when beetle-killed snags fall on the ground and understory tree growth creates ladder fuels, the risk of crown fire may again be increased (Gara et al. 1985, Romme et al. 2006).

Recently published empirical studies have used two approaches to quantify the effect of bark beetle outbreaks on fire risk. Some studies have used a retrospective approach, comparing observed with expected patterns of area burned in a landscape that was previously affected by bark beetle outbreaks, whereas others have looked at potential fire behavior based on behaviour models and populated by fuel loadings sampled in the field (Table 2). Retrospective studies were done in spruce-fir (*Picea engelmannii*-*Abies lasiocarpa*) forests in Colorado (Bebi et al. 2003, Kulakowski et al. 2003, Bigler et al. 2005, Kulakowski and Veblen 2007) and in lodgepole pine (*Pinus contorta* var. *latifolia*) forests in Wyoming (Turner et al. 1999; Lynch et al. 2006), and looked at the change in fire occurrence and/or severity.

The majority of the empirical studies undertaken in the spruce-fir forests did not support the hypothesized increase in fire occurrence, extent, or severity following spruce beetle or MPB outbreaks at any of the time-since-beetle intervals (range = 0-60 years) that were studied (Bebi et al., 2003, Kulakowski et al., 2003, Kulakowski and Veblen, 2007). One study (Bigler et al. 2005) found a slightly elevated probability of high severity burns 60 years after a SB outbreak. However stand structure was by far a better predictor of fire severity than occurrence of previous beetle outbreaks *per se*, suggesting that stand structure, not tree mortality, was the driver of fire severity (Bigler et al. 2005).

Results for the lodgepole pine-dominated forests are less clear. Turner et al. (1999) found that probability of severe fire increased with severe MPB damage and in late-successional stands, whereas it decreased with light or moderate beetle damage and in mid-successional stands; however since beetle damage occurs primarily in late successional stands, and because these two variables were analyzed independently, it is not possible to untangle their respective

effects. Using historical data in Yellowstone National Park, Lynch et al. (2006) found that the 1988 fires were slightly more likely (+11%) to occur in areas that were damaged by the mountain pine beetle in the 1970s, but there was no change in fire risk associated with the outbreaks of the 1980s. Lynch considered presence or absence of fire and not fire severity, which might explain why successional stage was not a significant variable in her analyses, contrary to the findings of other researchers (Renkin and Despain 1992, Turner et al. 1999).

Studies that have looked at potential fire behavior (Page and Jenkins 2007a, 2007b; Jenkins et al. 2008) have compared undamaged stands to stands that were damaged recently (0-5 years post outbreak) or decades ago (5-60 years post-outbreak, the range is broad but is as specific as reported in Simard et al. 2008's paper, and see Table 3 below) in three beetle/forest systems: DFB/Douglas-fir, MPB/lodgepole pine, and SB/Engelmann spruce (Table 3). These studies have found a consistent increase in *surface* fire intensity (fireline intensity and rate of surface fire spread) in 0-5 years post-outbreak stands (caused by a pulse of surface fine fuels from dead trees) and in 5-60 years post-outbreak stands (caused by an increase in wind speed in the more open stands). Probability of *crowning* (that is, the probability that a surface fire ignites tree crowns) was not tested in 0-5 years post-outbreak stands but was predicted to increase in 5-60 years post-outbreak stands because of lower crown base heights (that is, more ladder fuels allowing fuel continuity between forest floor and forest canopy) and higher surface fire intensity. However, *rate of crown fire spread* was **reduced** in 5-60 years post-outbreak stands because the density of the canopy (which needs to be above a certain threshold to allow active crown fires) was reduced by the beetles, which thinned the forest. This predicted reduction (or at least lack of increase) in active crown fire risk in post-outbreak stands support retrospective studies (see above) that have shown no effect of bark beetle outbreaks on occurrence of stand-replacing fires.

Table 3. Published empirical studies on bark beetle effects on fire activity.

Reference	Type of study	State	Forest Types	Bark beetle species (*)	Time since beetle (yrs)	Effect of bark beetle outbreaks on:	
						Fire occurrence or extent	Fire severity or behavior
Kulakowski and Veblen 2007	Retrospective	CO	Spruce-fir	SB, MPB	5	No effect	No effect
Bebi et al. 2003	Retrospective	CO	Spruce-fir	SB	0-50	No effect	NA
Kulakowski et al. 2003	Retrospective	CO	Spruce-fir	SB	0-50	No Effect	NA
Bigler et al. 2005	Retrospective	CO	Spruce-fir	SB	60	NA	Minor increase in severity †
Lynch et al. 2006	Retrospective	WY	Lodgepole pine	MPB	7,17	7=No effect;15= minor increase	NA
Turner et al. 1999	Retrospective	WY	Lodgepole pine	MPB	7-15	NA	Increase in severity †
Page and Jenkins 2007a, 2007b	Fuel sampling + potential fire behavior modeling	UT, ID	Lodgepole pine	MPB	5,20	NA	5 = increased surface fire intensity and rate of spread; crowning and crown rate of spread not tested; 20 = increased surface fire intensity and rate of spread; increased risk of crowning; reduced crown rate of spread

Reference	Type of study	State	Forest Types	Bark beetle species (*)	Time since beetle (yrs)	Effect of bark beetle outbreaks on:	
						Fire occurrence or extent	Fire severity or behavior
Jenkins et al. 2008	Fuel sampling + potential fire behavior modeling	UT, ID	Douglas-fir, Lodgepole pine, Spruce-fir	DFB, MPB, SB	0-5, 5-60	NA	0-5 = increased surface fire intensity and rate of spread; crowning and crown rate of spread not tested 5-60 = increased surface fire intensity and rate of spread; **

* DFB, Douglas-fir beetle; MPB, mountain pine beetle; SB: spruce beetle

** Data not shown in paper

† possible confounding of stand age and succession

N.A., not applicable

Conclusion

Studies have shown that time-since-beetle outbreak is critical in understanding the relationship between beetle outbreaks, stand structure, fuel dynamics and fire risk. The modeling and empirical studies reviewed here suggest that with respect to the question of how beetle attacks affect fire behaviour and the predictability of fire extent, intensity and behaviour, the following general conclusions are possible;

- In the spruce-fir forests the hypothesized increase in fire occurrence, extent, or severity did not take place,
- In lodgepole pine-dominated forests there is an increase in *surface* fire intensity in 0-5 years post-outbreak stands (caused by a pulse of surface fine fuels from dead trees) and in 5-60 years post-outbreak stands (caused by an increase in wind speed in the more open stands)
- 20- to 30-year-old stands killed by MPB will support intense crown fires because of ladder fuels and abundance of ground fuels.

Studies that will be Informative in the Future

Some studies are underway that will help assess fire risk in MPB killed stands. Initiated in 2005, the Carrott Lake Mountain Pine Beetle Experimental Fire Study is being conducted jointly by the B.C. Forest Service and the Canadian Forest Service with assistance from Canadian Forest Products. The study involves the experimental burning of research plots that contain lodgepole pine killed by mountain pine beetle. The experimental plots are relatively small and range in size up to 200x200m (4ha). Two plots have been ignited to date, and a number of ignition point source test burns have taken place. The behaviour of fire in these plots was monitored to assess the hazard associated with beetle-killed stands. There is also some work being done by CFS in Alberta looking at ignition of fires in dead stands. CFS is also involved with researchers at University of Victoria to try and untangle the effects of weather, suppression, and post-beetle fire events (Taylor pers. comm.).

The Canadian Forest Service (Beukema and Robinson 2004) has modelled stand structure and fuel changes after mountain pine beetle using Prognosis and FFE (Fire and Fuels Extension) models. Their simulations showed that the models do not accurately reflect build up of large fuels (underestimated) or fine fuels (overestimated), and do not capture snag dynamics well. These models need further calibrating before they are useful for predicting fire risk or potential.

Management Options

If risk of surface fires increases a few years after pine beetle attack and again 10 or 20 years after as trees fall, then some fuel management maybe appropriate to protect areas of high investments in planting. Hot fires in August will burn areas regardless if they have had fuel management, but in less severe fire situations fuel management can affect spread and intensity of fires. The location of activities to reduce fuels should be planned to consider focal areas of planting. Interspersing planted stands (in either underplanted or clearcut situations) in areas with dead pine will place those stands at greater risk of burning than if they were concentrated in areas where fuels have been controlled. Young stands can be effective fuel breaks, but not if they have considerable ground fuels and not if they are scattered throughout unmanaged stands. There needs to be a balance between risk of fire, the values being protected and the costs of protection treatments. Treatments to reduce fuels should be targeted to protect areas of considerable regeneration investment.

Key Uncertainties

The degree to which dead boles increase fire hazard or severity is theoretical but not empirically known. The risk of underplanted seedling being killed in fires compared to the risk of seedlings in clearcuts is also unknown. Options to reduce fire hazard while maintaining attributes important for biodiversity over the landscape have not been well-explored.

Literature Cited

- Ahlgren I.F. 1974. Effect of fire on soil organisms. In *Fire and Ecosystems*, ed. TT Kozlowski, CE Ahlgren, pp. 67–72. New York: Academic Press.
- Amman G.D. and R.F. Schmitz. 1988. Mountain pine beetle-lodgepole pine interactions and strategies for reducing tree losses. *Ambio* 17:62–68.
- Bebi, P., D. Kulakowski, and T.T. Veblen. 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. *Ecology* 84:362-371.
- Beukema S. and D. Robinson. 2004. Modelling Mountain Pine Beetle Effects on Growth and Fuel Loading. Prepared for Brad Hawkes, Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre
- Bigler, C., D. Kulakowski, and T.T. Veblen. 2005. Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. *Ecology* 86:3018-3029.
- Brown, J.K. 1975. Fire cycles and community dynamics in lodgepole pine forests. Pages 430-456 In: D. M. Baumgartner, editor. Symposium proceedings: Management of lodgepole pine ecosystems. Washington State University Cooperative Extension Service, Pullman, WA.
- Coates, D. 2008. Evaluation of stand dynamics after a 25-30 year old MPB attack in the Flathead Region of south eastern British Columbia. Final Technical Report to FIA-FSP. Project Number: M085196.
- Forest Practices Board. 2007. Lodgepole Pine Stand Structure 25 Years after Mountain Pine Beetle Attack Special Report FPB/SR/32.
- Gara, R.I., W.R. Littke, J.K. Agee, D.R. Geiszler, J.D. Stuart and C.H. Driver. 1985. Influences of fires, fungi, and mountain pine beetles on development of a lodgepole pine forest in south-central Oregon. In: D. M. Baumgartner, editor. Lodgepole pine: the species and its management. Symposium proceedings. Washington State University Conferences and Institutes, Pullman, WA., pp. 153-162.

Geiszler, D.R., R.I. Gara, C.H. Driver, V.F. Gallucci and R.E. Martin. 1980. Fire, fungi, and beetle influences on a lodgepole pine ecosystem of South-Central Oregon. *Oecologia* 46:239-243.

Hawkes, B.C., S.W. Taylor, C. Stockdale, T.L. Shore, R.I. Alfaro, R.A. Campbell, and P. Vera. 2004. Impact of mountain pine beetle on stand dynamics in British Columbia. In Mountain pine beetle symposium: Challenges and solutions, October 30–31, 2003, Kelowna, B.C. T.L. Shore, J.E. Brooks, and J.E. Stone (editors). Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C. Information Report bc-x-399. pp. 177–199. url: <http://warehouse.pfc.forestry.ca/pfc/25048.pdf>

Hawkes, B. 2008. Effects of the mountain pine beetle on fuels and fire behaviour. In Mountain Pine Beetle: From Lessons Learned to Community-based Solutions Conference Proceedings, June 10–11, 2008. *BC Journal of Ecosystems and Management* 9(3):77–83. url: http://www.forrex.org/publications/jem/ISS49/vol9_no3_MPBconference.pdf

Hopkins, A.D. 1909. Practical information on the Scolytid beetles of North American forests. I. Bark beetles of the genus *Dendroctonus*. USDA Bureau of Entomology Bulletin 83, U.S. Government Printing Office, Washington, D.C., USA.

Jenkins, M.J., E. Hebertson, W.G. Page and C.A. Jorgensen. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *Forest Ecology and Management* 254:16-34.

Keen, F.P. 1955. The rate of natural falling of beetle-killed ponderosa pine snags. *Journal of Forestry* 53(10):720–723.

Kulakowski, D. and T.T. Veblen. 2007. Effects of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. *Ecology* 88:759-769.

Kulakowski, D., T.T. Veblen and P. Bebi. 2003. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. *Journal of Biogeography* 30:1445-1456.

Lewis, K.J. and I.D. Hartley. 2006. Rate of deterioration, degrade, and fall of trees killed by mountain pine beetle. *BC Journal of Ecosystems and Management* 7(2):11–19. URL: http://www.forrex.org/publications/jem/ISS35/vol7_no2_art2.pdf

Lynch, H.J. 2006. Spatiotemporal dynamics of insect-fire interactions. Ph.D. dissertation. Harvard University, Cambridge, MA.

Lynch, H.J., R.A. Renkin, R.L. Crabtree and P.R. Moorcroft. 2006. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. *Ecosystems* 9:1318-1327.

Manning, G.H., L. Safranyik, G.H. van Sickle, R.B. Smith, W.A. White and E. Hetherington. 1982. A Review of Mountain Pine Beetle Problems in Canada. Environment Canada, Canadian Forestry Service, Victoria, BC.

McCullough, D.G., R.A. Werner and D. Neumann. 1998. Fire and insects in northern and boreal ecosystems of North America. *Annual Review of Entomology* 43:107-127.

Mitchell R.G. 1990. Effects of prescribed fire on insect pests. In *Natural and Prescribed Fire in Pacific Northwest Forests*, ed. JD Walstad, SR Radosovich, DV Sandberg. Corvallis, OR: Oregon State Univ. Press.

Mitchell, R.G. and H.K. Preisler. 1998. Fall rate of lodgepole pine killed by the mountain pine beetle in central Oregon. *Western Journal of Applied Forestry* 13(1):23–26.

- Page, W.G. and M.J. Jenkins. 2007a. Mountain pine beetle-induced changes to selected lodgepole pine fuel complexes within the intermountain region. *Forest Science* 53:507-518.
- Page, W.G., and M.J. Jenkins. 2007b. Predicted fire behavior in selected Mountain pine beetle infested lodgepole pine. *Forest Science* 53:662-674.
- Parker, D.L., and L.E. Stipe. 1993. A sequence of destruction: Mountain pine beetle and wildfire, Yellowstone National Park. USDA For. Serv., Southwestern Region.
- Parker, T.J., K.M. Clancy and R.L. Mathiasen. 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.
- Renkin, R.A., and D.G. Despain. 1992. Fuel moisture, forest type, and lightning-caused fire in Yellowstone National Park. *Canadian Journal of Forest Research* 22:37-45.
- Romme, W.H., J. Clement, J.A. Hicke, D. Kulakowski, L.H. MacDonald, T. Schoennagel and T.T. Veblen. 2006. Recent forest insect outbreaks and fire risk in Colorado forests: a brief synthesis of relevant research. Colorado Forest Restoration Institute, Colorado State University, Fort Collins, CO. URL: http://www.cfri.colostate.edu/docs/cfri_insect.pdf
- Schmid, J.M., and G.D. Amman. 1992. *Dendroctonus* beetles and old-growth forests in the Rockies. In: M. R. Kaufmann, W. H. Moir, and R. L. Bassett, editors. Old-growth forests in the Southwest and Rocky Mountain regions. Proceedings of a workshop. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-213, Fort Collins, CO.
- Shore, T.L., L., Safranyik, B. Hawkes, and S. Taylor. 2006. Effects of the mountain pine beetle on lodgepole pine stand structure and dynamics. Ch 3 in Safranyik, L. and B. Wilson. 2006. The mountain pine beetle a synthesis of biology management and impacts on lodgepole pine. NRC CFS.
- Simard, M. E., N. Powell, J.M. Griffin, K.F. Raffa and M.G. Turner. 2008. Annotated Bibliography or Forest Managers on Fire-Bark Beetle Interactions. Prepared for USFS Western Wildlands Environmental Threats Assessment Center January 18, 2008. *Revised February 25, 2008*.
- Stuart J.D., J.K. Agee and R.I. Gara. 1989. Lodgepole pine regeneration in an old, self-perpetuating forest in south Oregon. *Can. J. For. Res.* 19:1096–104.
- Turner, M.G., W.H. Romme and R.H. Gardner. 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. *International Journal of Wildland Fire* 9:21-36.
- Waterhouse, M. and H. Armleder. 2004. Windthrow in partially cut lodgepole pine forests in west-central British Columbia. B.C. Ministry of Forests, Research Branch, Victoria, B.C. Extension Note 70.

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