Forests for Tomorrow Adaptive Management Initiative

Synthesis of Information on Selected Topics & Clarification of Key Uncertainties

EXCERPT:

Response of BC Conifers to Light Regimes Created by Overstory Removal

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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 booth 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 wv 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

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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 (Calveau 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

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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

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shape of the response curves is not sufficient to explain the successional dynamics in these forests.

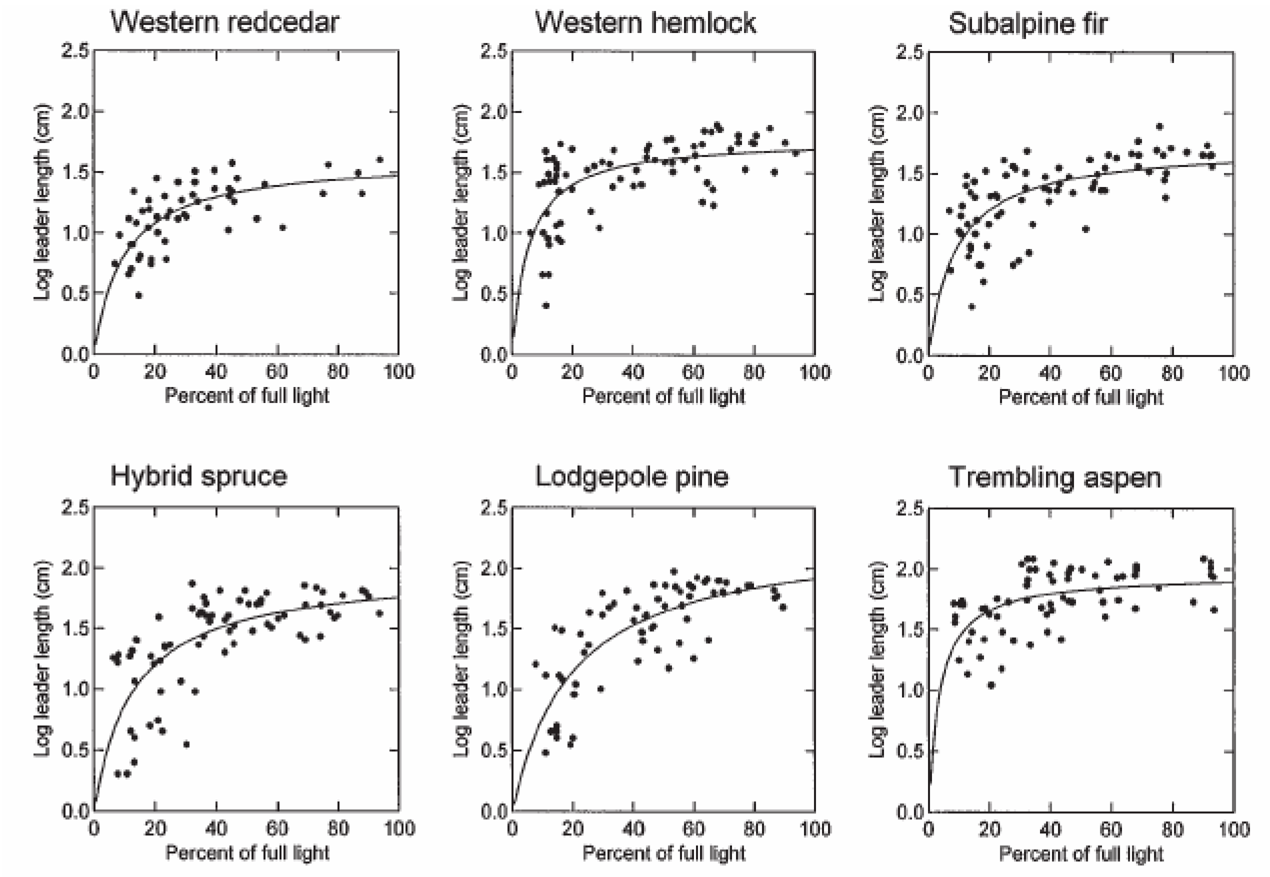

Figure 4. Light response curves for Interior BC Species by Climatic Region (Wright et al. 1998a).

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 amablis 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

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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

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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 out-performed 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

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- 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 wv.
- 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.

<u>Species choice:</u> 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.

<u>Best chance for leaving overstory:</u> 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.

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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 a 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 overstory removal is unnecessary as overstory 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 sand 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 overstory 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.

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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 15-25M^2 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**

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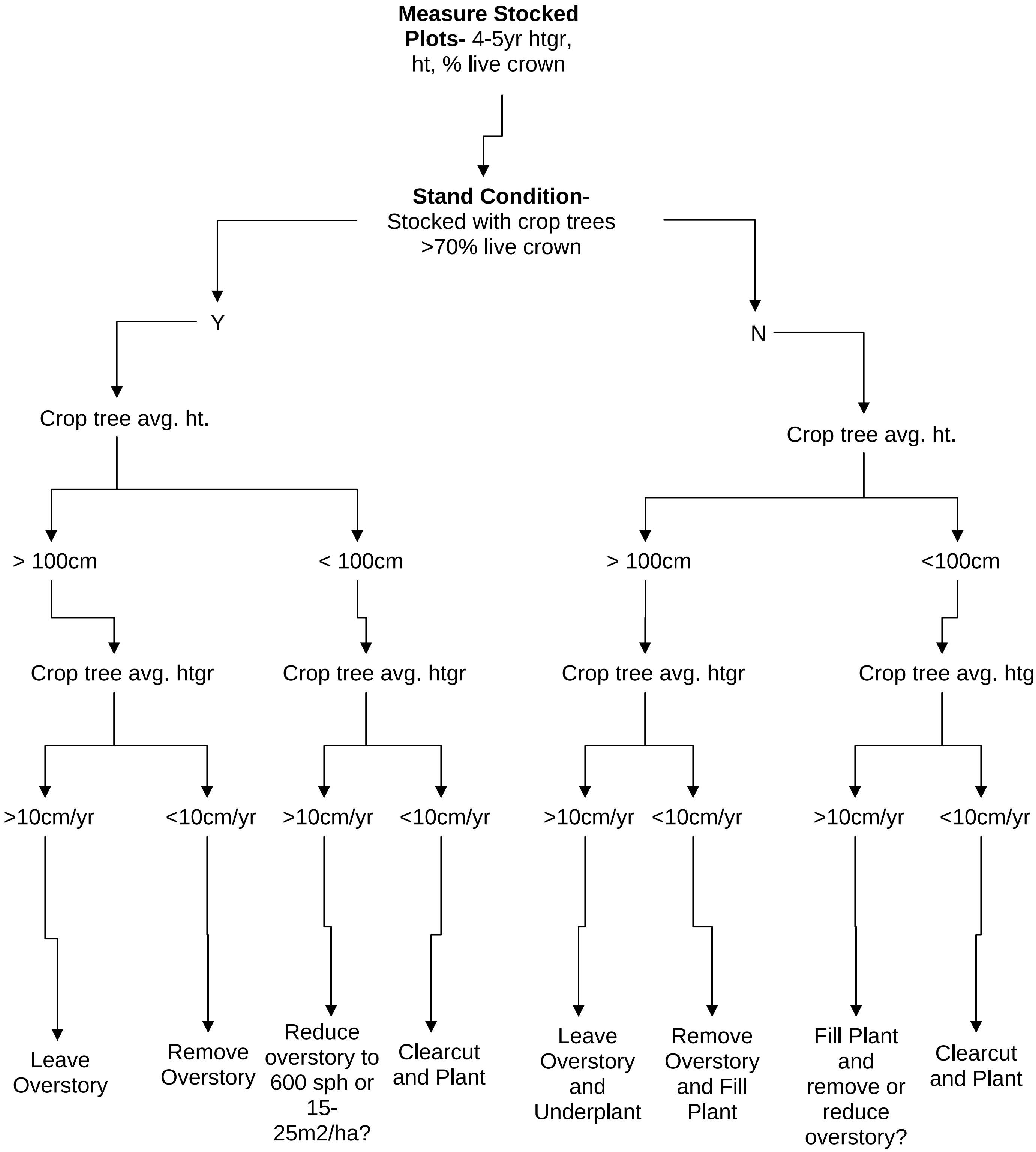

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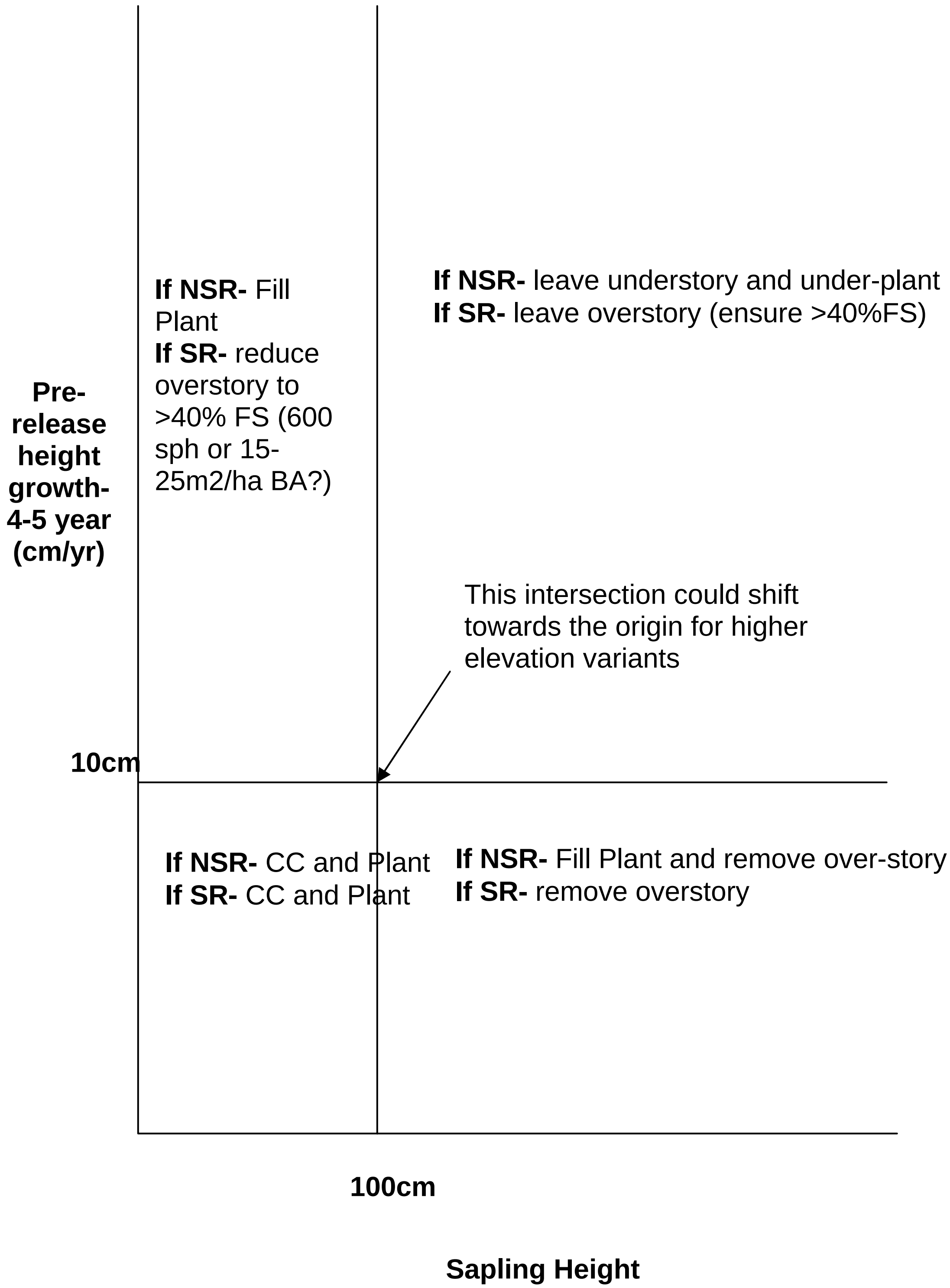

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