**EP1162 Discussion Literature outline**

**Proposed headings/themes for the discussion**

1. Introductory statements
2. Tree growth
   1. Introductory statements
      1. In order for partial cutting siviculture systems to achieve the objectives for a stand, requires forest managers to understand the likely range of effects on the stand and residual trees.
      2. From a silviculture perspective, the success of partial cutting is related to the growth response of residual trees (Thorpe & Thomas, 2007).
      3. This requires knowledge of stand-level changes that are introduced from partial harvesting, as well as species-specific responses.
      4. What does partial harvesting do to the stand?
         1. Thinning a stand by removing large dominant trees, as in this study, introduces a range of stand-level changes that include:
            1. Increased growing space for residual trees
            2. Increased light penetration
            3. Increased air temperatures due to increased light
            4. Increased soil temperatures
            5. Changes in soil moisture and nutrient availiability for residual trees
            6. Possible changes in wind throw and snow breakage due to lower canopy interception
            7. These changes will not be experienced equally by all residual trees however. A tree’s ability to respond to these stand-level changes will depend on a range of factors including:

Canopy position at the time of treatment

Diameter at the time of treatment

Autecological controls on plasticity

Distribution of residual trees

* + - 1. From (Thorpe et al., 2007): treatments dramatically increase the light available to residual trees and likely cause soil temperatures to rise as more sunlight reaches the forest floor. This will differ by tree size, however, as larger residual trees may continue to shade smaller trees, resulting in less light and temperature increases for smaller trees.
      2. In the cold, wet sites considered in this study, even small increases in soil temperature could have important implications for tree growth (Lajzerowicz et a;., 2004)
      3. . Nutrient flush- ing following harvest may also help to explain the pattern of growth response.
    1. Importance for forest managers to understand these differences, and how they interact with environment, autecology and other factors to control outcomes from silv. Treatments.
  1. Differences by stand treatment
     1. For the first three years after treatment (1992-1994), trees in both the HRTU and LRTU had lower growth rates than in the control. This suggests there was a lagged growth response to the treatment.
        1. Literature on growth response delays.
        2. When surrounding neighbours are removed, residual trees commonly display enhanced growth, but with a variable time lag following harvest (Thorpe et al., 2007; Thorpe & Thomas, 2007). This pattern has been found in a number of species and treatments, with peak residual-tree growth occurring 6–25 years after harvest (e.g., Youngblood 1991; Groot and Ho¨kka¨ 2000; Latham and Tappeiner 2002; Jones and Thomas 2004).
        3. Residual black spruce trees displayed a sizeable increase in growth following partial harvest. At their peak, radial growth rates were double those found before harvest. The mean observed peak was delayed, occurring 8–9 years after harvest, and the response pattern exhibited a 2-year delay period of no response followed by a 6- to 7-year period of increase after harvest (Thorpe et al., 2007)
        4. We hypothesize that [delayed growth response]S may be caused either by slow acclimation responses or by resource allocation to root and (or) shoot growth during the first 2 years after harvest (Thorpe et al., 2007).
           1. Individuals restore the root–shoot balance by greater initial investments to root growth to offset the increased transpiration losses associated with the greater light and higher temperature conditions and the relative changes in the photosynthetic versus nutrient uptake capacity following the canopy opening (Kneeshaw et al., 2002)
     2. From 1994 to 2009, growth was similar between all treatment units. From 2009-2020, the HRTU had the highest growth rates in terms of basal area and volumes.
        1. The HRTU now has the highest basal area increment, which was highest over the most recent measurement period.
           1. Annual volume increment, on the other hand, declined in all TUS over the 2009-2020 period, compared to 1997-2009.

In the HRTU, volume growth continued to exceed the other Treatment Units.

* + - * 1. These differences suggest that the HRTU will continue to accrue basal area and volume faster than the othe treatment units. At some point, we expect these growth rates to taper off and become similar to the other Tus.
      1. Literature on sustained growth rates after harvest.
  1. Differences by species
     1. Subalpine fir is one of the most shade tolerant species in BC (Klinka et al. 1992)
        1. Subalpine fir can tolerate long periods of suppression by dominant trees, and can respond to changes in canopy light transmission by changing leaf morphology, accelerating growth and aboveground biomass.
     2. At the tree-level spruce trees grew faster than fir trees, but those differences were only evident in the HRTU. In the other TUs, both species had similar growth rates.
     3. Spruce growth was found to be more sensitive to soil temperature than fir (Lajcerwicz et al. 2004).
     4. From Lajcerowicz et al. 2004: The greater temperature sensitivity of spruce than fir is consistent with differences in their natural distribution and supports the notion that shade-tolerant species (e.g., fir) are less respon- sive to improved environmental conditions than are less tol- erant (e.g., spruce) species (Venenklaas and Poorter 1998; Walters and Reich 1999).
     5. From Lajcerowicz et al. 2004: In open, high-light areas with rela- tively warm soil temperatures, spruce may outcompete fir for growing space via greater growth rates. In areas with in- tact forest cover and lower light and soil temperatures, fir does not have a growth rate advantage over spruce, but it has greater survival at low growth rates (Kobe and Coates 1997; this study). More generally, differences between our study species suggest that understory tolerance in subalpine forests is tolerance of both low light and low soil temperatures.
  2. Differences by tree diameter at age of harvest

1. Stand structure over time
   1. Tree diameter class distributions
      1. Across all units and measurement periods, the stands maintained a negative exponential tree diameter distribution (the reverse-J), with more trees distributed among smaller size classes.
         1. At the species-level, fir trees displayed this diameter distribution, whereas spruce was more evenly distributed among diameter classes. In the smaller diameter classes, fir trees outnumbered spruce, whereas the largest trees in each treatment unit were spruce.
   2. Stand volume and basal area
      1. Over the four year periods, we see that the CTU maintained the highest volume per hectare.
      2. In the past 10 years, we also see that the HRTU and LRTU have converged in terms of volume and basal area. This is likely due to increased growth rates associated with higher removal, and suggests that the cumulative volume may be higher in the HRTU.
         1. What does literature say about cumulative volumes in thinned stands?
         2. Important to note, however, that the variation in volumes is higher in the HRTU than other units. Thus, while higher removal and subsequent growth rates might lead to similar yields than more retention, these treatments may also increase the range of stand conditions over time.
2. Implications for partial harvest silviculture systems in central BC
3. Other considerations for partial cutting in central BC
4. Conclusions

**Proposed points of discussion**

In the introductory statements paragraphs, I suggest we summarize important results from study.

# Tree growth

What are the interacting effects of residual basal area, species and tree diameter class on tree growth responses over time and over the entire post-harvest period (27 years)? How did different residual basal area treatments change resource availability to residual trees?

Partial cuts allow for manipulation of light conditions in the understory but it is important to determine how the advance regeneration existing under different levels of suppression may react to different levels of release (Wang et al., 2011).

## Was there a lag effect in growth response? What are some potential causes of a delayed growth response?

From: (Wang et al., 2011) Typically, smaller trees are less affected by the postrelease stress than larger trees (Boily and Doucet 1991; Murphy et al. 1999), which is also the case in our study. There are, however, observations contradicting the respira- tory stress hypothesis.

From (Kneeshaw et al., 2002): stock forests have been adopted in parts of the British Co- lumbia interior dry belt, primarily because shade-tolerant Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) has proven difficult to regenerate in clearcuts, because of high sum- mer temperatures and associated moisture stress (Newsome et al. 1990) and susceptibility to damage from frosts during the growing season (Steen et al. 1990). Furthermore, Douglas-fir is considered to have acceptable release potential for use with partial-cutting systems (Hopwood 1990; Weetman and Vyse 1990). However, a companion species, lodgepole pine (Pinus contorta Dougl. ex Loud.), which also occurs widely in this ecosystem, is generally believed to respond poorly to release.

From: Kneeshaw et al. 2002: Compared with open-grown seedlings, shaded seedlings show a number of acclimations that facilitate their survival in lower light. These acclimations include changes in photo- synthetic and respiratory rates (Björkman 1981; Evans 1987; Sims and Pearcy 1994; Larcher 1995), changes in the spe- cific leaf area (Kellomäki and Oker-Blom 1981; Niinemets and Kull 1995a; Beaudet and Messier 1998), changes in the seedling hydraulic architecture (Sellin 1997), and changes in the shoot and crown architecture (Oker-Blom and Smolander

1988; Niinemets and Kull 1995b). Also, many studies have shown considerable differences between above- and below- ground allocation in sun- and shade-grown seedlings (Messier and Puttonen 1995; Canham et al. 1996). Upon canopy release, the shade-acclimated seedlings need to mod- ify their functions and structure to survive in the new condi- tions.

Height growth was re- stored only after considerable root growth had taken place. This tends to suggest that aboveground reductions in growth rate are not caused by decreasing productivity, but are in- stead a result of allocational changes in seedlings (Kneeshaw et al., 2002)

Observed periods of reduced height growth (growth shock) in seedlings and saplings following overstory re- moval appear to be linked to moisture-related stress (Kneeshaw et al 2002). observation that understory seedlings are limited because of insufficient capacity to take up and trans- port water (Kneeshaw et al. 2002). Therefore, these smaller trees might allocate more resrouces to root response after canopy opening in order to capitalize on increased soil moisture availability and to restore a functional balance between above- and below-ground systems (Kneeshaw et al. 2002).

From: Kneeshaw et al. 2002: It is speculated that changes in growth allocation patterns from aboveground tis- sues to belowground tissues should vary with climate and degree of overstory removal. Delays in aboveground growth response should be longer in drier sites and stands with greater overstory removal than in moister sites or those har- vested using partial cutting techniques. Forest

## Is growth accelerating in certain tree sizes? Have other studies identified that post-treatment growth response is stronger in certain size/ages?

Younger trees are likely to display larger growth increases than old trees, while larger trees may reach faster growth rates than their smaller coun terparts (Thorpe et al., 2007; Thorpe & Thomas, 2007). Suppression may also affect individuals’ ability to respond to harvest, and thus, slow preharvest growth rates may be associated with more modest growth increases.

Suppressed trees are likely to be smaller ones, therefore, one might expect that larger trees would release faster (my thought).

(Thorpe et al., 2007) found that Tree age had a strong influence on the magnitude of predicted responses . Older trees displayed modest growth responses compared with their younger counterparts, and very old trees (>200 years old) showed little or no positive growth response to harvest.

The intermediate trees responded best to a partial cut, while small trees responded well to a complete over- story removal, which caused growth losses in large trees and, to a lesser extent, in intermediate trees (Wang et al., 2011).

Many studies have demonstrated the significance of tree size in predicting variation in growth (e.g., Canham et al. 2004; Jones and Thomas 2004) but size was not an important pre- dictor of growth in the present study. This is likely due in part to the small range of residual-tree sizes, but tree age does appear to be a much stronger predictor of growth in this system (Thorpe et al., 2007).

From: Kneeshaw et al. 2002: partial canopy removal normally influences light more than temperature levels (Larcher 1995), which should lead to an increase in the seedling carbon balance. However, if acclimation to shade prevents the seedling from fully re- sponding to increased light (e.g., low light saturation, insuf- ficient water uptake and transport capacity, pigment injury) and if the respiration rates are simultaneously increased (in- creased repair demand, higher temperatures), seedlings may experience or approach a negative carbon balance as sug- gested by Staebler (1954). If this were true, larger individuals with greater non-photosynthetic biomass would be expected to respond more slowly to openings than would smaller indi- viduals.

We, however, observed no pre- and post-harvest differences in growth between size classes in terms of relative growth. However, temporally the larger individuals experi- ence a greater growth shock in the first post-harvest growing period than do the smaller individuals (Kneeshaw et al., 2002)

Studies examining the release of advance regeneration have observed conflicting patterns in trees at different developmental stages. Superior release responses in advance regeneration were observed in smaller trees (Givnish 1988; Oliver and Larson 1996; Claveau et al. 2002), larger trees (McCaughey and Schmidt 1982; Peterson and Pickett 1995; Webb and Scanga 2001), younger trees (Oliver and Stephens 1977; Ferguson and Adams 1980; Helms and Standiford 1985), or without any age dependence (Johnstone 1978; Boily and Doucet 1993; Puttonen and Vyse 1998).

FromGriesbauer and Green 2006: The age and size distribution within the advance-regeneration cohort may vary widely in any given stand, resulting in non-uniform release responses following mpb attack. Consequently, some stands developing from advance regeneration following mpb attack may be characterized by structures and distributions that become increas- ingly complex and uneven-sized over time.

## How did spruce and fir respond to release in this study? Do silvical characteristics explain differences between species?

1. Our study found that spruce trees responded to thinning with faster diameter growth rates than fir, with the strongest differences in the high-removal treatment unit. This suggests that where thinning treatments in this region retain both spruce and fir, high-removal treatments may favour spruce release. This is also supported by our analyses of stand-level volumes, which showed that spruce increased its composition relative to fir by volume and basal area more in the HRTU compared to the other treatment units.
   1. Other studies have shown that spruce growth responds favourably to heavy thinning.
   2. A 10-year analysis of white spruce growth underneath an aspen canopy found that a complete overstory removal and heavy basal area removal resulted in immediate and significant spruce radial and height growth responses, compared to control and partial cutting treatments (Smith et al. 2016).
   3. In a white spruce stand at age 35 years, diameter increment was maximized with the heaviest thinning intensity, however, the treatment in this study was thinning from below (Stiell 1970).
   4. Frank (1973) also showed that 70-year old white spruce basal increment increased with the amount of thinning, which supports our findings.
   5. These responses may be indepednet of age:
      1. Two studies in 70-year old even-aged white spruce stands showed that thinning elicited a significant and immediate basal area increment increase in residual trees that persisted for at least 5-10 after treatment (Frank 1973, Cleve and Zasada 1976).
      2. Yang (1991) found that white spruce responded to aspen overstorey removal across a range of site conditions, stand ages and tree sizes. This implies that forest managers have flexibility to plan silvicultural treatments where the objective is to release residual white spruce trees.
   6. These studies concur with our findings. Competition for light is a key factor that limits white spruce growth, and it seems that opening up the stand to allow for increased light penetration especially enhances white spruce growth responses (Liefers). High basal area removal may also increase stand air and soil temperatures, which might favour spruce growth responses instead of fir (Lacjcerowicz et al. 2004).
2. When comparing spruce growth rates to fir, our results seem to contradict findings in thinned or released Picea-Abies stands in other jurisdictions.
   1. Subalpine fir is considered more shade tolerant than spruce, and can persist as seedlings for over a century under low light conditions (Antos et al. 2000).
   2. Studies in eastern Canada show that after thinning, balsam fir growth rates exceed red spruce (Couet and Boily 1995) for a period of up to ten years (Dumais and Prevost 2007).
   3. After a thinning release, balsam fir (Abies balsamifera) had higher growth rates than red spruce (Picea rubens) for at least 10 years in eastern Canada (Dumais and Prevost 2007). Doucet and Boily (1995) found that firs release faster than spruce after changes in the canopy, however, spruce may have a more sustained release (Doucet and Boily 1995).
   4. In natural-origin stands in central BC, subalpine fir had faster growth rates than co-occurring spruce until age 80 (Eis and Craigdallie 1983). Because spruce tends to live longer than subalpine fir, higher growth rates at later ages may allow this species to become larger than fir.
   5. These studies support the understanding that subalpine fir is better adapted to tolerate lower light conditions than spruce, and can persist for prolonged (up to a century, Antos) in the understory. Further, this species has the ability to change its crown morphology to respond to gradual increases in light (and presumably temperature) associated with canopy gaps created when the stand is in an old-growth stage. The species seems to respond best to gradual changes in overstory structure, and rapid changes resulting from complete overstory removal may exceed the capacity of these trees to acclimate.
3. True firs generally release faster following light changes than co-occurring species such as spruce (Doucet and Boily 1995); in some studies, however, species such as spruce have been shown to exhibit more sustained release (McCaughey and Schmidt 1982; Boily and Doucet 1993).
   1. Balsam fir mayu have morphological plasticity that allows it to respond better to partial canopy openings. Fir may outcompete spruce in some cases and increase its composition and crown class at the expense of spruce. This has important implications for species composition, and may be a primary reason for the assumption among foresters that partial cutting in Abies-Picea stands tends to convert the stand to Abies-leading. Results from our study suggest that under heavy removal, spruce may in fact be favoured, and may increase its composition.
   2. Response differences between spruce and fir in the HRTU may reflect important physiological differences. Both species share some similarities, in that they are considered late-seral and climax species in the Sub-Boreal Spruce biogeoclimatic zone and have been shown to respond to release from stand-level disturbances such as insect attack and partial harvesting (Crossley 1976).
4. Fir growth responses to thinning was not as substantial as spruce.
   1. Fir is considered more shade tolerant than spruce, and can persist for extended periods under low light. Under these conditions, fir seedling crown structure
   2. Growth response of fir to various levels of thinnings
   3. In naturally regenerated stands, immature fir may grow faster than spruce, up to an age of 80 years, after which spruce productivity may exceed that of fir (Eis and Craigdallie 1983).
   4. Under closed-canopy conditions, subalpine fir height and diameter growth exceeded spruce until the trees reach approximately 80 years, after which spruce growth exceeds that of fir (Eis and Craigdallie 1983).
      1. Sustained growth and lower adult mortality rates allows spruce trees to achieve a larger size than fir over a longer period (Eis and Craigdallie 1983).
   5. Subalpine fir is considered more shade tolerant than spruce, and can persist as seedlings for over a century under low light conditions (Antos et al. 2000).
5. Our study also found growth differences among tree size. Larger trees had higher absolute growth responses, whereas smaller trees had higher relative growth increases.
   1. This has been found in other studies of white spruce (Smith et al. 2016, Yang 1991).
   2. Larger trees may respond with larger growth rates because they simply have more photosynthetic area and cambial surface area, and thus can produce more new tissue.
   3. Smaller trees may respond with higher proportional growth rates because the degree of environmental change from canopy removal is higher than for larger trees. This might elicit a stronger physiological response and changes in aboveground and belowground biomass.
   4. If these responses are sustained, this will translate to most of the stand volume and basal area being concentrated in larger trees, whereas the smaller trees will increase their size proportionally and recruit into higher crown classes.
6. Stand-level differences between treatment units
   1. Quadratic mean diameter

From Smith et al. 2016L: vigorous, small and young trees are generally assumed to have the 132 best potential for release partly because of the greater change in resource availability 133 (Bevilacqua et al. 2005; Vincent et al. 2009). However, larger conifers most often 134 exhibit the highest rates of absolute volume growth following release treatments 135 because of their superior growing surface area (Mäkinen and Isomäki 2004; Gagné et 136 al. 2012).

If there aren’t any differences between species, perhaps this reflects that these species are similar in terms of growth strategies/

From (Kneeshaw et al., 2002) Furthermore, Douglas-fir is considered to have acceptable release potential for use with partial-cutting systems (Hopwood 1990; Weetman and Vyse 1990). However, a companion species, lodgepole pine (Pinus contorta Dougl. ex Loud.), which also occurs widely in this ecosystem, is generally believed to respond poorly to release.

Strong release responses (i.e., large growth increases) have been observed in more shade-tolerant species, such as spruce and subalpine fir, following windstorm or insect disturbance (Groot 1984; Doucet 1988; McCaughey and Ferguson 1988), even after pro- longed suppression (Alexander 1984; Kneeshaw et al. 1998; Antos et al. 2000).

Understorey subalpine fir and spruce were found to release well following a spruce bark-beetle epidemic with sustained growth for over 40 years, possibly up to 100 years in some cases (Veblen et al. 1991). True firs generally release faster following light changes than co-occurring species such as spruce (Doucet and Boily 1995); in some studies, however, species such as spruce have been shown to exhibit more sustained release (McCaughey and Schmidt 1982; Boily and Doucet 1993).

Conversely, shade-intolerant species (where present in the advance-regeneration cohort) will likely exhibit relatively poorer release responses compared to shade-tolerant species following mpb attack due to their more fixed crown physiology and structure (Messier et al. 1999; Williams et al. 1999) and more lingering effects of prolonged suppression (Gavrikov and Sekretenko 1996; Wright et al. 2000; Kneeshaw et al. 2002). If man- agement targets seek to utilize shade-intolerant advance regeneration to form future tree crops on some sites, it will be critical for forest managers to assess the potential of these trees to release and achieve adequate growth

## What are some other sources of variation in tree growth that could be considered in future studies? Stem mapping, radial growth response can provide annually resolved growth responses.

Differences in the magnitude of individual-tree growth responses not ex- plained by tree age may be attributable to spatial variation in postharvest stand structures; such factors could account for a substantial fraction of the unexplained variation in the observed (Thorpe et al., 2007).

# Stand structure

How did tree density change over time, and among treatment units and species?

Were there patterns of mortality in the study?

How did the diameter class distribution change over time, by treatment unit?

3. **Stand basal area and volume**

What are the differences in basal area/volume increment over time (periodic and entire period) among treatment units?

Was there a lag effect in stand basal area/volume? Can this be explained by tree-level growth responses discussed previously?

Can we identify primary sources of basal area/volume increment from diameter classes and species? In other words, did most of the basal area increment come from trees of a certain size or species?

4. **Implications for partial harvest silviculture systems in central BC**

Can we make any future projections about stand volume, structure and composition among treatments? Will treatment units converge over time? When?

Can we infer implications to total stand volume from partial cutting?

Will partial harvest in central BC spruce-fir stands inevitably result in stand conversion to fir-leading if spruce are targeted for harvest?

How can our results inform the use of partial cutting to achieve different management objectives (e.g., timber production, shelterwood, bark beetle salvage, structural diversity)

5. **Other considerations of partial harvest silviculture systems in central BC**

Increasing interest in these types of silviculture systems to salvage bark beetle-killed trees while protecting residual live trees for mid-term timber supply, wildlife habitat, carbon, etc…

Blowdown is a key stand-level consideration in designing these systems. Very little blowdown in this study – can we relate this to elements of the system design (e.g., block configuration).

6. **Conclusions**