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MORPHOLOGICAL INDICATORS OF RESPONSE TO OVERSTORY REMOVAL FOR BOREAL CONIFER TREES

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Abstract

Regeneration of forest stands through the preservation of existing advance growth has recently gained considerable interest in various regions of North America. The effectiveness of this approach relies however on the capacity of regeneration to respond positively to overstory removal. Responses of advance growth to release is dependent on tree characteristics and site conditions interacting with the degree of physiological shock caused by the sudden change in environmental conditions. This paper presents a review of the litterature describing the relationships between morphological indicators and the advance growth response to canopy removal. No clear relationship between age, height at release and response to release could be demonstrated. Pre-release height growth has been found to be a good indicator of post-release response for many species. Live crown ratio appears to be a good indicator of vigour for tolerant species. The value of height/diameter ratio would seem of little value in predicting response to release since it varies with site and it is difficult to draw general trends for this ratio based on species tolerance (this contradict some of the text! We need to be more clear here). The ratio of leader length to length of the longest lateral at the last whorl could also serve to describe the degree of suppression before harvest for shade tolerant species. Number of nodal and internodal branches or buds has been found to be related with vigour for many species. Logging damage has been shown to be an important determinant of seedling response to overstory removal. This paper also suggests the use of combined indicators and suggests critical threshold values for these indicators.

RÉSUMÉ

La protection de la régénération préétablie a fait l'objet d'un intérêt croissant au cours des dernières décennies en Amérique du Nord. L'efficacité de cette approche repose toutefois sur la capacité de cette régénération à réagir positivement à la coupe. La réaction de la régénération préétablie dépend de ses caractéristiques au moment de la coupe et de leur interaction avec les conditions de station et le choc causé par l'enlèvement du couvert principal. Cet article passe en revue les relations entre différents indicateurs morphologiques et la réaction de la régénération préétablie après coupe. Aucun lien clair n'a pu être établi entre la réaction après coupe et l'âge ou la hauteur de la régénération au moment de la coupe. La croissance avant coupe a été reliée à la capacité de réaction de la régénération préétablie pour plusieurs espèces. Le rapport de cime vivante serait un bon indicateur pour les essences tolérantes. Le rapport hauteur/diamètre serait peu efficace à prédire la réaction de la régénération après coupe puisque les relations varient selon la station et qu'il est difficile d'en généraliser l'effet sur la base de la tolérance des espèces à l'ombre. Le rapport de la longueur de la pousse terminale à la plus grande branche latérale du verticille supérieur pourrait servir à décrire le niveau de suppression avant coupe pour les espèces tolérantes. Le nombre de branches ou de bourgeons nodaux et internodaux est indicateur de la vigueur pour de nombreuses espèces. Les dommages occasionnés par la récolte ont un effet majeur sur la réaction de la régénération après la coupe. Cet article propose aussi l'utilisation combinée des indicateurs; il suggère aussi des seuils pour certains indicateurs.

INTRODUCTION

Establishing a sufficient amount of regeneration is an essential first step in forest renewal. This can be achieved using natural regeneration or artificial regeneration, after harvesting, or through the preservation of advanced regeneration which is present underneath the stand prior to harvest. Regeneration of forest stands through the preservation of existing advance growth has recently gained considerable interest in various regions of North America (Doucet and Weetman 1990 ; McCaughey and Ferguson 1988). For instance, the preservation of advance growth has become the main mode of regeneration for boreal forests in Quebec, being applied on more than 100 000 ha of public forest (Parent 1996). Advance growth provides immediate growing stock, shade for subsequent seedlings, aesthetics, hiding cover for wildlife, and some soil protection (McCaughey and Ferguson 1988). The preservation of advance growth is a low cost alternative for securing adequate regeneration that is well suited to the site. It can be likened to a natural or one-cut shelterwood system (Smith et al. 1997). Differences remain however between preserving naturally established advance growth and a classical shelterwood system, since seedlings do not usually have to withstand heavy shade for extended periods in the latter and seedling acclimation is generally more critical after clearcutting than it is after shelterwood cutting(Tucker and Emmingham 1977).

The effectiveness of preserving advance growth relies on the capacity of regeneration to respond positively to overstory removal (Ferguson 1984). After canopy removal, seedlings have to adjust to a whole new set of environmental conditions before a growth response can take place (Tesch and Korpela 1993). High mortality has been observed when seedlings have to acclimate to the new environmental conditions. Most of this mortality has been found to occur during the first three years for balsam fir (<u>Abies balsamea</u> (L.) Mill.), black spruce (Picea mariana (Mill.) B.S.P.) and Douglas-fir (<u>Pseudotsuga menziesii</u> (Mirb.) Franco) (Ruel and Doucet 1998 ; Tesch et al. 1993).

Advance regeneration has typically developed under moderate to heavy shade. Trees acclimated to extreme shade often have short umbrella-shaped crowns that maximize light absorption, thin leaves, little conducting tissue, and greatly reduced root growth (Tucker <u>et al.</u> 1987; Waring 1987). Seedlings growing under heavy shade have developed shade foliage with a lower photosynthetic capacity in comparison with light-adapted foliage. Trees with different shade tolerances also show different degrees of morphological and physiological plasticity (Messier et al. 1999a). For instance, Williams et al (1999) have found that Douglas-fir maintained a limited number of healthy branches and developed a horizontal form in shade whereas many morphological measurements were poorly correlated with light availability for lodgepole pine (Pinus contorta Dougl. Ex. Loud.).

The sudden removal of the canopy exposes advanced regeneration to sudden increases in light levels and evapotranspiration, and exposes protected seedlings to potential for radiation frost injury. When placed in full sunlight, shade needles may experience difficulty in controlling transpirational losses (Ferguson and Adams 1980). In the first few years following harvesting, seedlings start to produce new, sun-adapted foliage (Tucker and Emmingham 1977). The low foliar biomass of some seedlings (Comeau et al. 1993) and the small number and size of buds limit the rapid production of new foliage, thus restricting the capacity of the advance regeneration to take complete advantage of full sunlight (Harrington and Tappeiner 1991). High light levels could adversely affect shade foliage as could a combination of low root:shoot ratio and damage to the shallow root system during harvesting of canopy trees (Tucker and Emmingham 1977 ; Tucker et al.1987 ; Waring 1987). To be able to benefit from overstory removal, conducting tissues and fine-root capacity have to increase to meet the needs of the existing and newly produced foliage.

Although a response in root growth and diameter growth after a sudden release can be almost immediate, many studies have shown that height growth does not respond immediately or can even be reduced to levels below those observed before release (Gordon 1973 ; Johnstone 1978 ; McCaughey and Schmidt 1982 ; Seidel 1980; Nikinmaa 1993 ; Williams 1996). Part of this delayed response could be attributed to the fact that height growth is often predetermined in the previous growing season (Aussenac 1977 ; Kneeshaw et al. 1998) but this would not be sufficient to explain the delays exceeding one year found in many studies. On the other hand, height growth response can also be immediate, especially for the smaller regeneration (Seidel 1989 ; Boily and Doucet 1991, 1993; Paquin and Doucet 1992b). Messier et al (1999a) suggest that the light requirements of seedlings increase with size. Thus, smaller trees and more shade tolerant conifers might be less stressed at a given light level than taller and less shade tolerant ones, and so could adjust to the altered growing environment more readily. There might in fact be a threshold of vigour in advance regeneration in relation to its capacity to respond to release and that this threshold may vary among species and in relation to size.

Responses of advance growth to release is dependent on tree characteristics and site conditions interacting with the degree of physiological shock caused by the sudden change in environmental conditions (Ferguson and Adams 1980). Several studies (e.g. McCaughey and Ferguson 1988; Tesch and Korpela 1993; Tesch et al. 1993; Doucet et al. 1995;Ruel et al. 1995) have examined morphological traits that favour growth and survival of advance regeneration after release. However, results from these studies are often contradictory. In their review of the research dealing with the response of advance growth, McCaughey and Ferguson (1988) list 30 papers describing the response of 11 species of conifers. However, only three of those papers dealt with balsam fir, six addressed the response of white spruce (Picea glauca (Moench) Voss) and five covered black spruce.More recent work mostly deals with species typical of the western region of North America (Murphy et al. 1999; Tesch et al. 1993; Tesch and Korpela 1993; Carlson and Schmidt 1989).Several studies have examined the response of black spruce regenerated by layering, which comprise the majority of black spruce advance growth, but this work consists largely of retrospective studies (Doucet and Boily 1986; Doucet 1988; Doucet and Boily 1988; Paquin and Doucet 1992a; Paquin and Doucet 1992b; Doucet and Boily 1993; Lussier et al. 1992). Retrospective studies, although very informative, do not include identification of the tree condition at time of release and are biased in favor of survivors. Also, many studies on the response of advance growth to release focus on undamaged stems (Tesch et al. 1993).

Numerous variables have been tested to explain advance growth response to overstory removal. However, the inclusion of vigour standards in regeneration surveys varies both between regions and through time. In Québec, the definition of an acceptable seedling or layer has evolved during the last ten years. In 1988, a seedling had to be between 5 cm and 300 cm tall and be sound and of overall good quality (Québec 1988). In British Columbia, general free-growing guidelines recommend accepting subalpine fir (Abies lasiocarpa (Hook.) Nutt) and amabilis fir (Abies amabilis Dougl. Ex. Forbes) advanced regeneration when its height is less than 1.5 m at release, and its live crown ratio is less than 0.6 (Ministry of Forests 1995). For spruce, the same free-growing acceptability criteria are used for planted and naturally regenerated seedlings (trees must be free from damage or infection from insects, disease, mammals or abiotic, and must meet minimum height and height:vegetation ratios within a prescribed timeframe). Other provinces also require that a seedling be vigorous and healthy, without any very specific criteria (Chaudry 1981; Manitoba 1989; Alberta 1992). This kind of definition is broad and can lead to much subjective judgement. Since 1989, Quebec's rules require that the seedling must be between 1 cm and 300 cm tall and be free from harvesting wounds (Québec 1989). These restrictions about logging damage are a common feature of many other operational reforestation surveys (Manitoba 1989; Alberta 1992; Tesch et al. 1993). Today, a restriction on acceptable live crown ratio is also added for black spruce layers in Québec (Québec 1993). Elsewhere, layers are often not even considered acceptable (Manitoba 1989; Alberta 1992). However, the response of this regeneration, as well as that of seedlings not meeting these standards, remains to be tested.

This paper presents a review of the litterature describing the relationships between morphological indicators and the advance growth response to canopy removal. It attempts to assess the effectiveness of the different indicators for the main conifer species found in the boreal forest of Canada. It also suggests critical threshold values for these indicators.

EFFECTIVENESS OF THE DIFFERENT INDICATORS

Age

Some authors have found that younger trees were able to adjust quickly to overstory removal, even though older trees did also respond (Ferguson and Adams 1980). In contrast, others have found no relationship between age and seedling response when height is taken into account (Crossley 1976 ; Johnstone 1978; Boily and Doucet 1993). For instance, Paquin and Doucet (1992b) have found no difference in long term height growth between old and young black spruce seedlings for a comparable height, the age difference between both categories being 30 to 40 years. (Figure 1). Oliver (1986) found a correlation between growth response of red fir (Abies magnifica (A. Murr.)) and age. However, age was also correlated with percent live crown and pre-release height growth, so that a causal relationship cannot be inferred. Helms and Standiford (1985) found relationships between growth response and age only for trees shorter than 4.5 m but not when taller trees were also included. It is likely that age was also confounded with live crown ratio in this specific case.

McCaughey and Schmidt (1982) postulated that advance regeneration is already physiologically old and thus more vulnerable to insects and diseases. Decay could then become a problem in second-growth stands originating from old advance growth. However, studies in black spruce and balsam fir found no relationships between decay and tree age (Horton and Groot 1987; Paquin and Doucet 1992a; Riopel 1999), so that we do not have any strong evidence that the age of advance regeneration is a key factor in the amount of decay in second-growth stands. However, this has become an issue for second-growth subalpine fir in Central British Columbia where a high proportion of rotten stems led to intensive salvage cuts.

Height

As trees grow larger, their maintenance and construction costs increase (Waring 1987; Givnish 1988). Since non-photosynthetic tissues require energy to respire, the tree has less photosynthate available for other functions. On this basis, tall advance growth would be expected to do poorly in comparison with small seedlings when both have developed in low light environments. However, many authors have found that small regeneration (less than 25 to 75 cm) can suffer high mortality during the first few years after harvesting (Gordon 1973; Seidel 1977, 1983; Tesch *et al.* 1993). In Sweden, first year mortality of spruce (Picea abies (L.) Karst.) after the final shelterwood cut often exceeds 50 % for seedlings smaller than 10 cm, while it is much less for 25 to 30 cm seedlings (Westerberg 1995). Ruel et al. (1995), studying several populations of balsam fir and black spruce in Québec, also found that survival during the first three years was positively correlated with height in the understorey for both species. They suggested that the poor root system of small seedlings left them vulnerable to water stresses caused by complete overstorey removal. Their overall low total carbohydrates reserves, due to a poorly developped root system, could also be a factor. Another possibility is that the smaller seedlings are more likely to be found in low light environment that the taller ones. However, second and third year survival was negatively correlated with height for balsam fir and not correlated for black spruce. Seven years after release, the effect of height at release was not evident (Ruel and Doucet 1998) suggesting that the effect of height is more on the timing of death than on the number of surviving seedlings. This stresses the importance of studies of sufficient duration to capture the full pattern of response to overstory removal.

Initial growth response after release was also positively correlated with height at the time of release for white fir [Abies concolor (Gord. and Glend.) Lindl.] (Tesch and Korpela 1993). Others have found that taller advance growth responded more slowly to release (McCaughey and Schmidt 1982 ; Paquin and Doucet 1992b ; Riopel 1999). These contradictory results may depend on the range of height that is considered in a particular study, the growing conditions before canopy removal, and/or on the species involved. In the case of black spruce, response to release was positively correlated with height for advance regeneration smaller than 2 m, but negatively correlated for the taller trees (Lussier et al. 1992). Small advance regeneration is usually much more abundant than the taller regeneration, so that its response to release might be more affected by crowding (Hatcher 1960). When only small advance regeneration is present, a relatively small number of individuals rapidly increase in height to become dominant while the others gradually fall behind (Doucet and Boily 1988; Boily and Doucet 1991), due presumably to competition. So height in itself is not a good indicator of early growth and survival (Carlson and Schmidt 1989) and no consistent trend seems to be apparent among species. However, even when the response of the taller advance growth is slower, it can add significantly to the yield of second growth stands (Riopel 1999; Pothier et al. 1995).

Tall advance growth, could also develop higher amounts of decay. Even though the occurrence and volume of decay in second growth balsam fir stands was higher after 47 years for stems that were initially taller than 5 m, the losses were not considered critical at that age (Riopel 1999). At the time of canopy removal, these residuals were left with little competition around them. They were then able to develop large branches. When natural pruning occured, the large branch stubs that were formed could have served as as entry points for decay. These tall stems did not seem more affected by the last spruce budworm outbreak.

Height growth

Pre-release height growth rate has been reported to be positively correlated with survival (Tesch et al. 1993; Ruel et al 1995) and post-release growth rates (Seidel 1980; Helms and Standiford 1985; Oliver 1985; McCaughey and Ferguson 1988 ; Ferguson and Adams 1980; Tesch and Korpela 1993; Murphy et al. 1999) for several conifer species. Because there is usually a direct link between stress and growth reduction, many authors are inclined to use growth rate as a measure of stress (Coley et al. 1985). Growth rate is also an important function because ultimately those trees that survive in the long-term are those that can reach dominant status. However, shade tolerant species might be better able to reduce their height growth in shade than shade intolerant species, and as such this might be seen as an acclimation to survive in shady conditions (Messier et al 1999a; Beaudet and Messier 1998). The usefulness of height growth as an indicator of vigour is then likely to vary with species tolerance to shade. Parent and Messier (1995) suggest that absolute height growth could constitute a good indicator of vigour for balsam fir because it tends to be very sensitive to any changes in environmental conditions. However, Murphy et al. (1999) also found that pre-release height growth was strongly related to post release height growth for the shade intolerant lodgepole pine.

Live crown ratio

The amount of foliage on a tree varies with the degree of suppression. Seedlings and saplings with low amounts of foliage relative to their size have high respiratory needs coupled with a low photosynthetic capacity. This leaves them vulnerable to the additional stress caused by sudden exposure or wounding.

Live crown ratio has often been identified as one of the best indicators of vigour for shade tolerant conifers (Seidel 1980; Helms and Standiford 1985; Tesch et al. 1993; Ruel et al. 1995). The amount of live crown retained in shaded conifer species probably varies between genera as reported by Takahashi (1996) and Larivière (1998) for fir and spruce. Takahashi (1996) found that fir species have a better capability to shed lower branches and to produce more new branches than spruce species in shade. Also, a lower live crown ratio does not necessarily mean less foliage since fir species tend to expand their crowns laterally in shade and drop their lower branches, whereas spruce and pine species tend to grow less laterally and maintain their lower branches. Williams (1996) observed that lodgepole pine maintained a very sparse foliage throughout the crown in shade, whereas Douglas-fir maintained a much denser foliage in the upper part of the crown only. Moreover, strong relationships have been reported between percent live crown and light for Douglas-fir (Williams 1996) and balsam fir (Duchesneau et al. 1999), but these relationships are very weak for lodgepole pine (Williams 1996) and eastern white pine (Pinus strobus L.) (Messier et al. 1999b). Live crown ratio appears to be a better indicator of growth stress for shade-tolerant conifer species than for shade intolerant ones. Since shade tolerant species are the most likely to be regenerated by preserving the advance growth, this variable could be useful as an indicator of potential growth response.

Live crown ratio has been found to be positively related with post-release survival or growth for black spruce, balsam fir, Douglas-fir, white and red fir (Helms and Standiford 1985 ; Ruel and Doucet 1998 ; Tesch et al. 1993). Survival is poor for trees with less than 33% live crown but is high for trees with more than 66% live crown (Figure 2).

Stem height/diameter ratio

Some conifer species have been found to change their stem height/diameter ratio in relation to changes in the understorey environment (Lieffers and Stadt 1994; Wang et al. 1994). Gavrikov and Sekretenko (1996) found Scotch pine's (Pinus sylvestris L.) diameter growth to be much more sensitive to environmental change than height growth. They also showed that pines that have been suppressed for a long time could not respond well to sudden canopy opening. This is exactly the reverse for fir species where height growth was found to be much more sensitive to shade than diameter growth (Kohyama 1980; Duchesneau et al. 1999). For a certain height, the ratio is higher for shade intolerant than tolerant species and for deciduous than coniferous saplings (Hara et al. 1991; King 1991; Williams et al 1999). Hara et al. (1991) suggested that shade tolerant species maintain their diameter growth in shade because they tend to maintain a much larger foliage biomass than shade intolerant ones. Therefore, one should expect intolerant and mid-tolerant species like pines (Williams et al. 1999; Messier et al. 1999b), spruces (Lieffers and Stadt 1994) and birches (Messier and

Puttonen 1995) to show stronger height:diameter ratio responses that tolerant species such as true firs (Kohyama 1980; Duchesneau et al. 1999).

These trends, however, differ when comparing different sites. For exemple, Chen (1997) and Chen and Klinka (1998) found respectively found significant and non significant relationships with light for shade intolerant western larch (Larix occidentalis (Nutt.)) and Ponderosa pine (Pinus ponderosa (Dougl. ex. Lawson & Lawson var. ponderosa)). Brunner (1993) also found the same pattern for shade tolerant hardwood and conifer species. This author concludes that stem height/diameter ratio is of limited value outside controlled conditions like the ones met in nurseries.

Notwhitstanding the above limitations, the height/diameter ratio could influence the mechanical resistance of trees after canopy removal. For most intolerant and mid-tolerant species, susceptibility to snow damage, wind breakage, and withdthrow following release inceases with increasing pre-release height:diameter ratio (Navratil 1995). Newton and Comeau (1990) suggest that long-term growth of Douglas-fir is jeapordized when heigh:diameter ratio exceeds 60. While suitable height :diameter ratios appear to vary as a function of size and climate, a critical value of 60 is commonly used for white spruce (Picea glauca (Moench) V0ss) and Engelmann spruce (Picea engelmanii Parry ex. Engelm.).

Apical dominance

Apical dominance is "the preferential growth of a plant shoot (or root) from the apical or terminal meristem and the corresponding suppression of lateral subtending meristems and branches" (Aarssen 1995). Several authors have discussed the adaptive significance of apical dominance in plant shoots (Brown et al. 1967; Little 1970; Cline 1991; Aarssen 1995). It appears that leader growth controls top whorl development (Oliver and Larson 1996; Wilson 1992). In the Pinaceae family, a positive correlation between light availability and the ratio of terminal length over mean lateral branch length at the last whorl has been frequently observed in situ (Kohyama 1980; Klinka et al. 1992; O'Connell and Kelty 1994; Parent and Messier 1995). Little (1970) also observed that this ratio was lowered by water and nutrient stresses and by severe defoliation for eastern white pine. This ratio could be of interest in characterizing vigor in shade because (1) it is sensitive to light availability, (2) it indicates current year or recent growing conditions and (3) it can easily be evaluated in the field by simply bending the longest top whorl lateral branch over the leader (Parent et al., 1999).

Studies involving conifer species along light gradients show that the sensitivity of this ratio varies between species. Shade tolerant species present more variation in this ratio than less tolerant species (Parent et al. 1999). In the case of lodgepole pine and jack pine (Pinus banksiana Lamb.), this ratio is not influenced significantly by light intensity (Williams et al. 1999; Claveau et al. 1999). Results from one unpublished study indicate that the apical dominance ratio is strongly correlated with light levels for subalpine fir, Engelmann spruce, and Douglas-fir, but poorly correlated with light levels for lodgepole pine and western white pine (Pinus monticola Dougl. Ex. D. Dun.) (P. Comeau, unpublished). This ratio is probably most useful as an indicator of stress for tolerant and mid-tolerant conifers.

Fabijanowski et al. (1974, 1975) proposed using apical dominance ratio to classify advanced regeneration of European silver fir (Abies alba Mill.), Norway spruce and Scotch pine . In the case of European silver fir, a value below 0.25 represents a very suppressed seedling, between 0.25 and 0.5 a suppressed seedling, between 0.5 and 1 a moderately suppressed tree, between 1 and 1.20 a healthy seedling and finally a value higher than 1.2 a very healthy seedling.

Number of nodal and internodal branches or number of buds

Ghent (1958) suggested that the number of lateral branches could be used as an indicator of release potential for balsam fir. Some authors have reported a strong relationship between the number of lateral buds and the overall vigor of a tree (Ghent, 1958; Fraser 1962; Remphrey and Powell 1984,). The number of nodal and interwhorl buds and branches is known to increase with light intensity (Parent and Messier, 1995; Duchesneau et al. 1999; Williams et al. 1999) which in turn influence hormone production, nutrition (Kramer and Kozlowski 1979) and the increase in height growth leaves a greater surface for bud initiation (Cannell and Bowler 1978).

Duchesneau et al (1999), Williams et al. (1999) and Claveau et al. (2000) indicate that balsam fir, subalpine fir, white spruce, interior spruce, lodgepole pine and jack pine react significantly to varying light intensity, making the number of nodal and internodal branches a good indicator of vigour. The number of nodal branches does not vary significantly with total height for the species presented here but there is a significant effect on the number of internodal branches in gaps and open area (>25% of full light) (Claveau et al. 1999). Results from an unpublished study (Comeau, DeLong and Hutcheon unpubl.) suggest that when the number of top nodal branches is less than 3 for 5 year old seedlings, it is indicative of stress for Engelmann spruce, Douglas-fir, lodgepole pine, and western white pine. However, no clear trends in the number of upper nodal branches were evident for subalpine fir.

One interesting characteristic of this indicator is its possible quick response to treatment. Following cleaning, Tappeiner *et al.* (1987) found that, for Douglas-fir, the number of internodal buds responded in the year after treatment while height and basal area growth responses did not occur until the 2nd and 3rd years after treatment.

Logging damage

At least part of the advance growth can be damaged during logging operations, possibly impairing its ability to survive and respond to release (Ferguson and Adams 1980). However, advance regeneration has shown a remarkable capacity to overcome damage and this may not constitute the main cause of mortality (Tesch et al. 1993; Ruel et al. 1995 ; Gordon 1973). In Douglas-fir, no difference in survival was noted between damaged and undamaged advance regeneration smaller than 75 cm (Tesch et al. 1993), whereas mortality increased with number and severity of damage for larger trees (Figure 3). Bole wounds combined with leaning were far more serious than broken terminals or stems but the percentage of bole girdled did not differ between dead and surviving trees after six years. In balsam fir and black spruce, damage affected survival for both small (< 1m) and large (> 1m) trees (Ruel et al. 1991). Percentage of stem girdled was useful in predicting survival for balsam fir and black spruce (Figure 3) but lean angle was retained only for balsam fir. It is likely that the lean angle of black spruce advance regeneration is more related to its layer origin so that it does not imply a logging damage.

Murphy et al. (1999) also found that the percent circumferential damage to the bole was negatively correlated to height growth after canopy removal for lodgepole pine.

Logging wounds could also serve as entry points for decay. The rapid healing observed by Tesch et al. (1993) could minimize the severity of this problem. The long term impact of wounds should be studied in more detail.

Combined indicators

Studies of advance regeneration in Douglas-fir (Tesch et al. 1993), as well as balsam fir and black spruce (Ruel and Doucet 1998), have shown that survival or development into crop trees could be predicted reasonably well by a combination of the live crown ratio and the percentage of bole wounded during harvest, the first variable being by far the most important. Pre-release height growth was also included for Douglas-fir but this variable is likely to be related with crown ratio. Recovery from logging damage is better for trees with a high live crown ratio (Tesch et al. 1993). However, mortality was still about 20 % even for good quality trees, suggesting the need for additional indicators to improve predictability. Age, pre-release height growth rate and a number of site variables were useful in predicting growth rates for the first five years after release in Douglas-fir and white fir, but the proportion of variance explained remained below 40% (Tesch and Korpela 1993). However, it seems that most regeneration that survives will ultimately respond and grow reasonably well (Tesch and Korpela 1993). These results are promising and suggest that further exploration of vigour indices that combine various individual measures will be worthwhile.

TENTATIVE THRESHOLD VALUES FOR MORPHOLOGICAL INDICATORS

The morphological indicator values presented in table 1 were deduced from two groups of studies covering British Columbia and Québec boreal tree species. For British Columbia species (subalpine fir, interior spruce, and lodgepole pine), Kobe and Coates (1997) study allowed us to select a probability of mortality as our main indicator of vigour. We considered that a 10% probability or lower over three years was acceptable and thus such seedlings were considered vigorous. We then extrapolated the radial growth associated with this 10% mortality rate, and used it to calculate the associated height growth rate (which is much easier to assess in the field) using the companion study by Wright *et al.* (1998).

In the case of Quebec's species (balsam fir, white spruce, and jack pine), we considered that shade tolerant species growing at or less than 10% light were not vigorous and that shade intolerant species growing at or less than 40% light were not vigorous. These light values correspond very well to the values obtained in Kobe and Coates (1997) and Wright et al (1998)'s study for a 10% probability of mortality.

These morphological indicator values are tentative and more than one indicator should be used to assess the vigour of a seedling. It must also be kept in mind that these indicators were not deduced from an intensive inventory and therefore, they may have to be adapted from region to region. Seedlings below 1m were not considered because their growth and morphology are found to not be very responsive to the change in understory environmental conditions (Claveau et al. 1999). For exemple, in low light conditions, they have an unusual large live crown ratio compared to taller seedlings. The same study also showed that small seedlings have a poor height growth even in high light conditions.

SUMMARY AND RECOMMENDATIONS

1) The ability of some advance regeneration to grow and survive following sudden overstorey removal varies from species to species and depends in part on the growing conditions prevailing prior to release. The more vigorous the advance regeneration is before release the better it will respond to release.
2) Height growth is often reduced to levels below those found prior to release, whereas stem diameter and structural root growth usually increase immediately following release. Increased height growth and foliage biomass occur only when the conducting tissues (by stem growth) and presumably the fine-root biomass (associated with the increase in large structural roots) is large enough to supply the increasing demands of the new environment. This is likely to vary depending on the size of the individual, species and growing conditions prior to overstorey removal.
3) Several different morphological indicators of vigour measured prior to release have been found to predict survival rate and growth after release. Although no single indicator seems

to be universally applicable to all species, reasonably good predictions can be attained when a combination of live crown ratio, bole damage during disturbance, and prerelease height growth rate is used.

4) Different growth and morphological indicators need to be used for different species and more importantly between shade tolerant and shade intolerant species because of their different priorities in carbon allocation. Shade intolerant species tend to sacrifice diameter growth over height growth in shade, whereas shade tolerant species will tend to reduce their live crown ratio more effectively in shade. Thus, indicators such as height:diameter ratio and number of buds or branches, are potentially useful indicators for mid-tolerant and intolerant species, whereas apical dominance ratio and live crown ratio are useful indicators for the more shade tolerant species.
5) This review highlights the need for further evaluation of the potential use of growth and morphological indicators. At present, only limited information is available on the usefulness of these indicators for estimating the vigour potential for release of boreal conifer species. There is also a need for a better understanding of how site and other environmental factors, and stand tending practices influence the morphology and growth of these species. This review also calls for long term monitoring since the conclusions can vary between 3 and 7 years.

ACKNOWLEDGMENTS

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Table 1. Tentative morphological indicator values of good vigour in understory conditions for seedlings over 1 meter high

species	threshold values				
				current number of	
	height growth (cm)	leader/branch ratio	live crown ratio (%)	nodal branches	internodal branches
jack pine	20-30 [3,6]	- *	75 [3]	4 [3]	3 [3]
lodgepole pine	15-30 [1,2,3,5,11]	- *	75 [3,5]	3-4 [3,5]	3 [3]
black spruce	10 [10]	1?	60?	4?	3?
interior spruce	10-15 [1,2,3]	1 [3]	60 [3]	4 [3]	3 [3]
white spruce	10 [3,9,10]	1 [3]	60 [3]	4 [3]	3 [3]
balsam fir	10-15 [3,8,10]	0.75 [3,7,12]	50 [3,4,12]	3 [3,7]	1-2 [3,7,12]
subalpine fir	10 [2,3]	0.75 [3]	50 [3]	3 [3]	1 [3]

Note:
* not applicable because this ratio varies poorly with light intensity (Chen *et al.* (1996), Claveau *et al.* (1999)
1. Kayahara *et al.* (1996), 2. Wright *et al.* (1998), 3. Claveau *et al.* (1999), 4. Ruel *et al.* (1995), 5. Williams *et al.* (1999), 6. Logan (1966), 7. Parent and Messier (1995), 8. Bakuzis *et al.* (1965), 9. Lieffers and Stadt (1994), 10. Logan (1969), 11. Chen *et al.* (1996), 12. Duchesneau *et al.* (1999).

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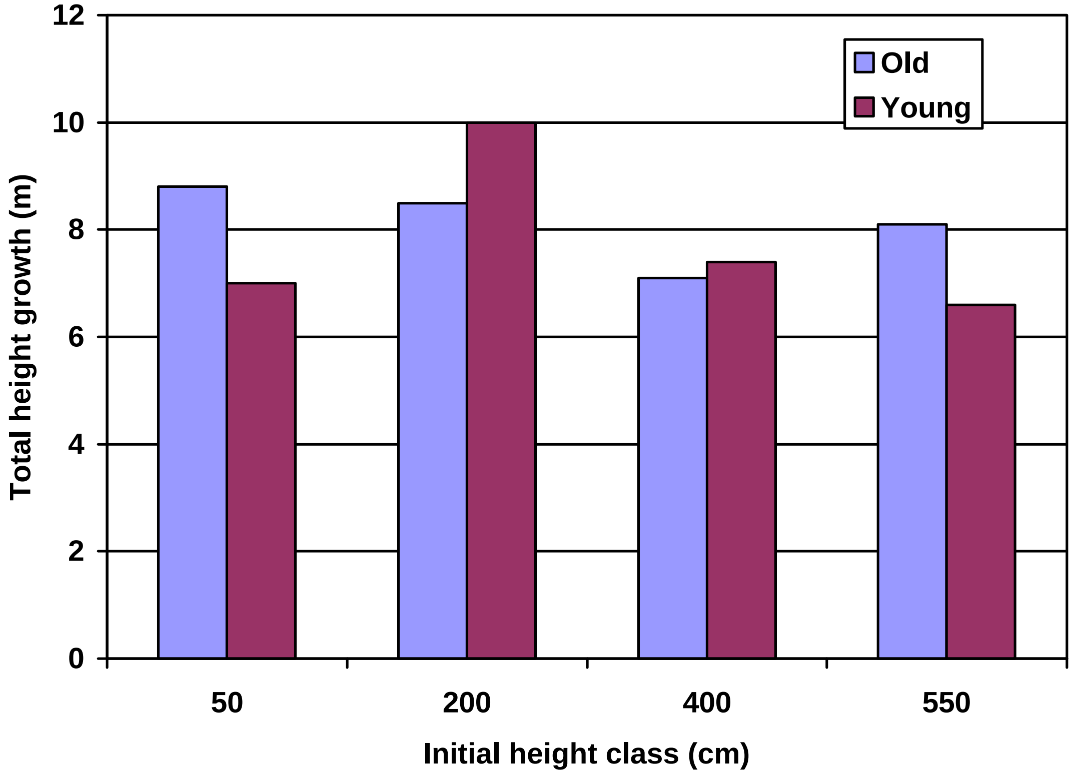
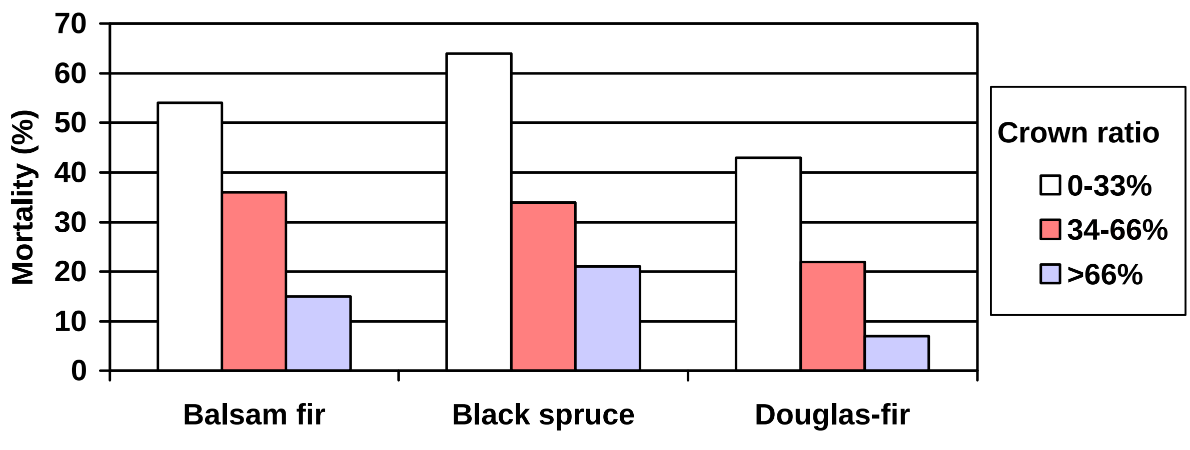
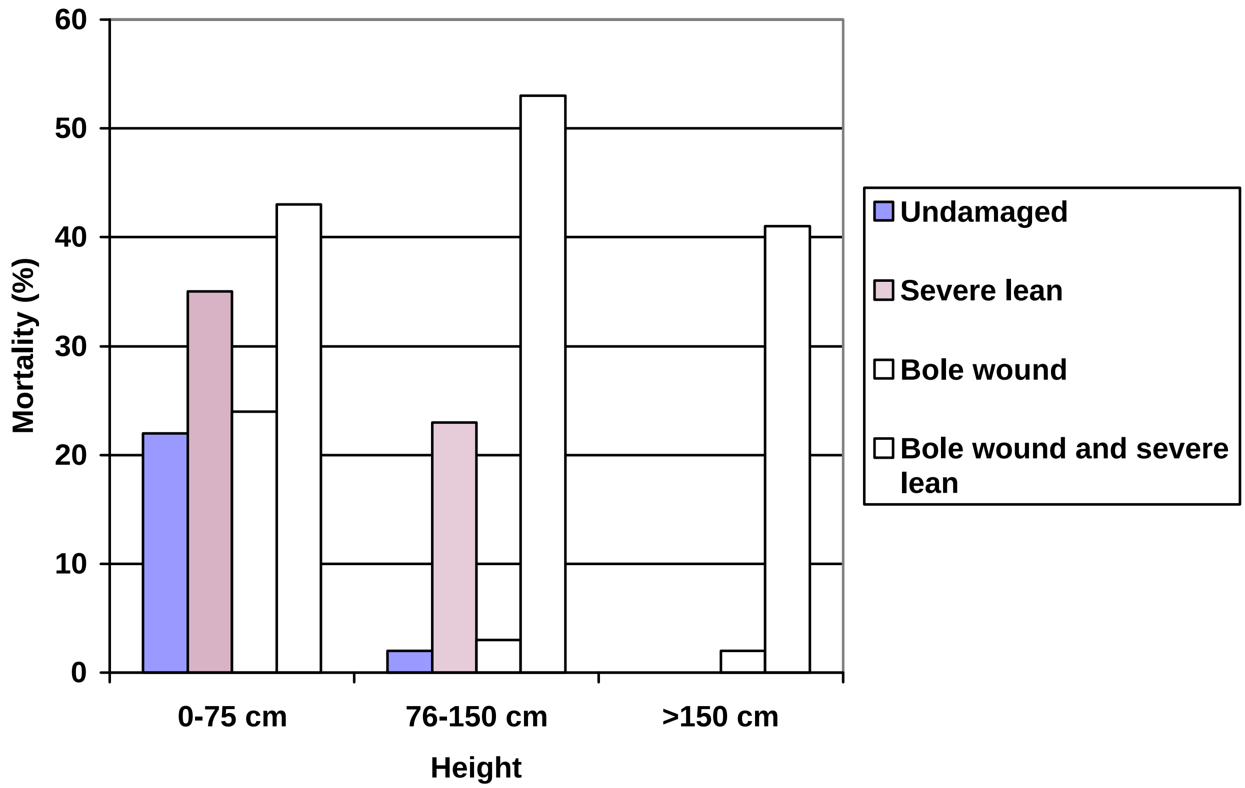


Source : Paquin and Doucet 1992b



Source : Balsam fir and Black spruce : Ruel and Doucet 1998

Douglas-fir : Tesch et al. 1993



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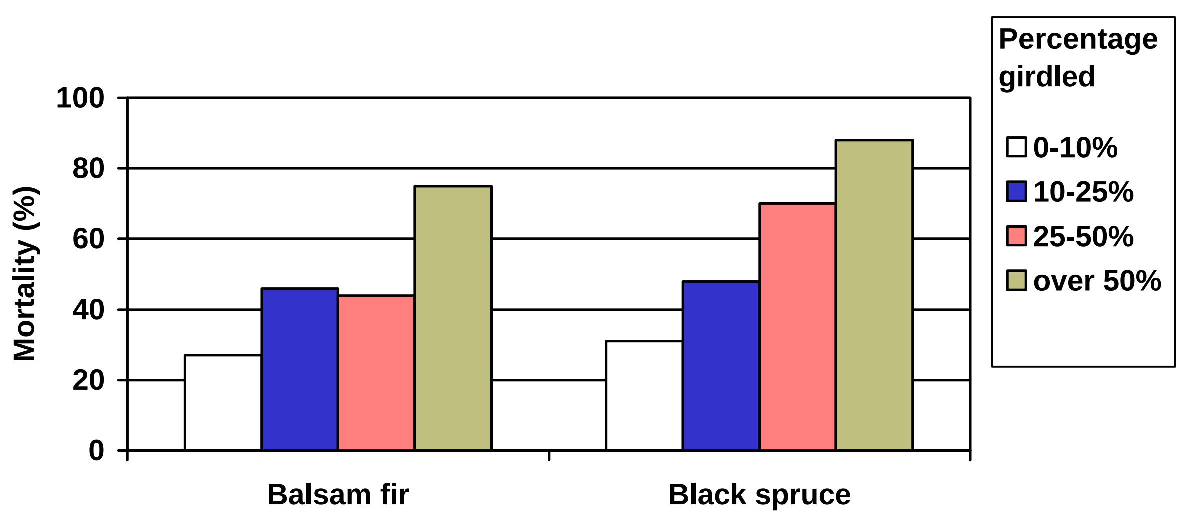

Source : Ruel and Doucet 1998