Morphological indicators of growth response of coniferous advance regeneration to overstorey removal in the boreal forest

by Jean-Claude Ruel[1], Christian Messier[2], René Doucet[3], Yves Claveau[2] and Phil Comeau[4]

Regeneration of forest stands through the preservation of existing advance regeneration has gained considerable interest in various regions of North America. The effectiveness of this approach relies on the capacity of regeneration to respond positively to overstory removal. Responses of advance regeneration 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 literature describing the relationships between morphological indicators and the advance regeneration response to canopy removal. It focuses primarily on the following species: jack pine (*Pinus banksiana* Lamb.), lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.), black spruce (*Picea mariana* (Mill.) B.S.P.), interior spruce (*Picea glauca* x *engelmannii*), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt). Pre-release height growth has been found to be a good indicator of post-release response for many species. Live-crown ratio also appears to be a good indicator of vigour for shade-tolerant species. The ratio of leader length to length of the longest lateral at the last whorl could 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. In contrast, height/diameter ratio has limited value for predicting response to release since it varies with site, species and other factors. No clear relationship between age, height at release and response to release could be demonstrated. This paper also suggests the use of combined indicators and critical threshold values for these indicators.

Key words: advance regeneration, careful logging, vigour, clearcutting

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 le prélèvement du couvert principal. Cet article passe en revue les relations entre différents indicateurs morphologiques et la réaction de la régénération préétablie après coupe. Les espèces visées sont : le pin gris (*Pinus banksiana* Lamb.), le pin de Murray (*Pinus contorta* Dougl. var. *latifolia* Engelm.), l'épinette noire (*Picea mariana* (Mill.) B.S.P.), l'épinette blanche (*Picea glauca* (Moench) Voss), le sapin baumier (*Abies balsamea* (L.) Mill.) et le sapin subalpin (*Abies lasiocarpa* (Hook.) Nutt). La croissance en hauteur avant coupe a été reliée à la capacité de réaction de la régénération préétablie pour plusieurs espèces. Le rapport de cime vivante serait aussi un bon indicateur pour les essences tolérantes. 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. De même, le nombre de branches ou de bourgeons nodaux et internodaux est un indicateur de la vigueur pour de nombreuses espèces. Les dommages occasionnés par la récolte ont aussi un effet majeur sur la réaction de la régénération après la coupe. Au contraire, le rapport hauteur/diamètre serait peu efficace à prédire la réaction de la régénération après coupe puisque les relations varient selon la station, les espèces et d'autres facteurs. 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. Cet article propose aussi l'utilisation combinée des indicateurs et suggère des seuils pour certains indicateurs.

Mots-clés : régénération préétablie, protection de la régénération, vigueur, coupe à blane

Introduction

Establishing a sufficient amount of regeneration is an essential first step in forest renewal. This can be achieved using natural or artificial regeneration after harvesting, or through the preservation of advanced regeneration that is present underneath the stand prior to harvest. Regeneration of forest stands through the preservation of existing advance regeneration has gained considerable interest in various regions of North America (McCaughey and Ferguson 1988, Doucet and Weetman 1990). For instance, the preservation of advance regeneration has become the main mode of regeneration in boreal forests of Quebec, being applied on more than 100 000 ha of public forest (Parent 1996). Advance regeneration 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 regeneration 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). There are differences, however, between preserving naturally established advance regeneration 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).

[1]Faculté de foresterie et de géomatique, Université Laval, Sainte-Foy, Québec G1K 7P4. E-mail: Jean-Claude.Ruel@sbf.ulaval.ca
[2]GREF interuniversitaire, Dép. des sciences biologiques, UQAM, C.P. 8888, Succ. Centre-Ville, Montréal, Québec H3C 3P8
[3]Ministère des ressources naturelles, Direction de la recherche, 2700 rue Einstein, Sainte-Foy, Québec G1P 3W8
[4]Dept. of Renewable Resources, 4-42 Earth Sciences Building, University of Alberta, Edmonton, Alberta, Canada T6G 2E3

The effectiveness of preserving advance regeneration relies on the capacity of regeneration to respond positively to overstory removal (Ferguson 1984). 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 *et al.* 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-tolerance also show different degree of morphological and physiological plasticity (Messier *et al.* 1999a).

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). The sudden removal of the canopy exposes advanced regeneration to large increases in light levels and evapotranspiration, and to potential 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 can adversely affect shade foliage as can 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. This drastic change in growing conditions can lead to high mortality. Most of this mortality has been found to occur during the first three years for balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Mill.) B.S.P.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Ruel and Doucet 1998, Tesch *et al.* 1993).

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, Seidel 1980, McCaughey and Schmidt 1982, 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 growth reductions or 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 might be less stressed at a given light level than taller ones, and so could adjust to the altered growing environment more readily. Shade-tolerant species could also adjust more readily than less tolerant seedlings of the same size. There might be a threshold of vigour in advance regeneration in relation to its capacity to respond to release and this threshold may vary among species and in relation to size.

Responses of advance regeneration 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 *et al.* 1993, Tesch and Korpela 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 regeneration, 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 deals mostly with species typical of the western region of North America (Carlson and Schmidt 1989, Tesch *et al.* 1993, Tesch and Korpela 1993, Murphy *et al.* 1999). Several studies have examined the response of black spruce regenerated by layering, which comprises the majority of black spruce advance regeneration, but this work consists largely of retrospective studies (Doucet and Boily 1986, 1988, 1993; Doucet 1988; Lussier *et al.* 1992; Paquin and Doucet 1992a, 1992b). Retrospective studies, although very informative, do not include identification of the tree condition at time of release and are biased in favour of survivors. Also, many studies on the response of advance regeneration to release focus on undamaged stems (Tesch *et al.* 1993).

Numerous variables have been tested to explain advance regeneration response to overstory removal. However, the inclusion of vigour standards in regeneration surveys varies both between regions and through time. In British Columbia, general free-growing guidelines recommend accepting subalpine fir (*Abies lasiocarpa* (Hook.) Nutt) and amabilis fir (*Abies amabilis* Dougl. ex. Loud.) advance regeneration when its height is less than 1.5 m at release and its live crown ratio is greater than 0.6 (British Columbia 1995). For spruce species, 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 time frame). 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. 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). Since 1989, it 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, black spruce layers also need to have a minimum live crown ratio of 50% in Québec (Québec 1993). Elsewhere, black spruce layers are often not even considered acceptable (Manitoba 1989, Alberta 1992). It can easily be seen that standards vary a lot for different species or between regions. This can often be attributed to the fact that these standards have not been thoroughly tested in the field. Hence, a better understanding is needed.

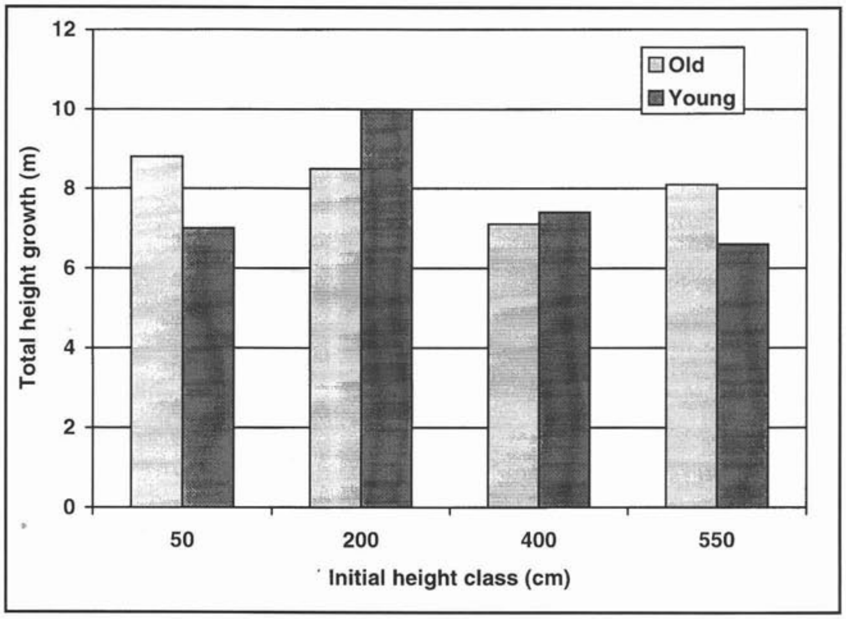

Fig. 1. Effect of age on total height growth in relation to initial height class of black spruce advance regeneration, 59 years after harvesting. The age difference between young and old seedlings is 30–40 years.
Source: Paquin and Doucet (1992b)

This paper presents a review of the literature on the relationships between morphological indicators and the response of advance regeneration to canopy removal. It attempts to assess the effectiveness of different indicators for the main conifer species present as advance regeneration in the boreal forest of Canada. Recommendations are presented for selecting threshold values for these indicators. The target species are jack pine (*Pinus banksiana* Lamb.), lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.), black spruce, interior spruce (*Picea glauca* x *engelmannii*), white spruce, balsam fir and subalpine fir. Other species of the same genera or for which unique studies were available (e.g., Douglas-fir) were also used to broaden the knowledge base when necessary.

Morphological Indicators and Response to Canopy Removal

Age

Some authors have found that younger trees are able to adjust quickly to overstory removal, although older trees 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 of comparable height, the age difference between both categories being 30 to 40 years (Fig. 1). Oliver (1985) 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 regeneration. 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, the volume of living cells in conducting sapwood and associated tissues increases disproportionately to the increase in foliage (Waring 1987, Givnish 1988). Since these non-photosynthetic tissues require energy to respire, the tree has less photosynthate available for other functions. On this basis, tall advance regeneration would be expected to react 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 Norway 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 understory for both species. They suggested that the poor root system of small seedlings left them vulnerable to water stresses caused by complete overstory removal. Their overall low total carbohydrates reserves, due to a poorly developed root system, could also be a factor. Another possibility is that the smaller seedlings are more likely to be found in low light environments than the taller ones. This effect could, however, be only a short term one. In fact, second and third year survival was negatively correlated with height for balsam fir and not correlated for black spruce and, seven years after release, the effect of height on survival was significant for black spruce but not for balsam fir (Ruel and Doucet 1998). Moreover, it was only significant when seedlings shorter than 30 cm were included. This suggests 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 height growth of taller advance regeneration 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 regeneration is slower, it can add significantly to the yield of second growth stands (Pothier *et al.* 1995, Riopel 1999).

Tall advance regeneration could also develop higher amounts of decay. The lower branches of residual trees increase in diameter until canopy closure occurs and natural pruning starts again. The death of these large branches leaves large stubs that can serve as entry points for decay. However, 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).

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 (Ferguson and Adams 1980, Seidel 1980, Helms and Standiford 1985, Oliver 1985, McCaughey and Ferguson 1988, 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). Height 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 this might be seen as an acclimation to survive in shady conditions (Beaudet and Messier 1998, Messier *et al.* 1999a). 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 shade-tolerant balsam fir but Murphy *et al.* (1999) found that it could even be useful for the shade-intolerant lodgepole pine.

Live crown ratio

The amount of foliage on a tree decreases with increasing degree of suppression. The high ratio of non-photosynthetic/photosynthetic tissues associated with seedlings and saplings with low amounts of foliage relative to their size involves 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, defined as the length of the live crown over total height, 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 *Abies sachalinensis* (Masters) has a better capability to reduce its crown length in shade than does *Picea glehnii* (Masters). However, 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 due to natural pruning, whereas many spruce and pine species tend to maintain a long live crown without expanding laterally. Williams (1996) observed that lodgepole pine maintained very sparse foliage throughout the crown in shade, whereas Douglas-fir maintained 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.* 2000), 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 conifer species. Since shade-tolerant species are the most likely to be regenerated by preserving the advance regeneration, 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, Tesch *et al.* 1993, Ruel and Doucet 1998). Survival is poor for trees with less than 33% live crown but is high for trees with more than 66% live crown (Fig. 2).

Stem height/diameter ratio

Some conifer species have been found to change their stem height/diameter ratio (hdr) in response to changes in the understory environment (Lieffers and Stadt 1994, Wang *et al.* 1994). Gavrikov and Sekretenko (1996) found Scots 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. Height growth of true fir species was found to be much more sensitive to overstory canopy shade than diameter growth (Kohyama 1980, Duchesneau *et al.* 2000). For a certain height, hdr is higher for shade-intolerant than tolerant species and for deciduous than coniferous saplings (Hara *et al.* 1991, King 1991, Williams *et al.*

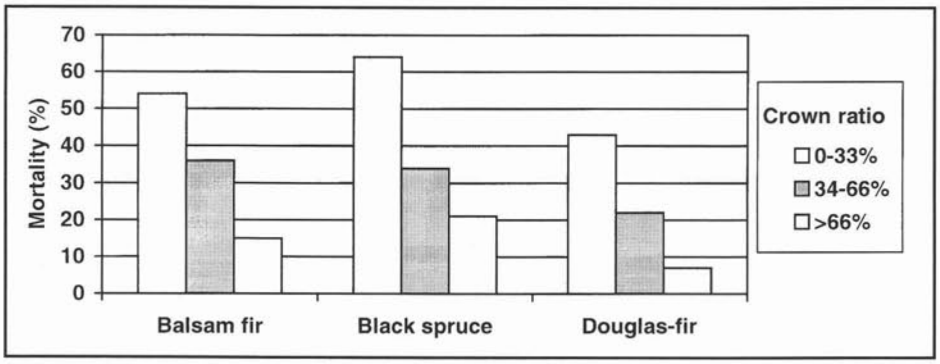

Fig. 2. Effect of live crown ratio on advance regeneration survival after six years for Douglas-fir or seven years for balsam fir and black spruce.
Source: Balsam fir and black spruce: Ruel and Doucet (1998)
Douglas-fir: Tesch *et al.* (1993)

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 species. 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.* 2000).

The magnitude of the change in hdr between light environments varies between sites. For example, in a study by Brunner (1993), regressions between hdr and light intensity for shade-tolerant hardwood and conifer species were significant on the limestone site but non-significant on the flysch site. When light is not the limiting resource, height or diameter growth can be favoured in different ways. Height growth may be constrained on droughty or nutrient-poor sites, resulting in the shrubby appearance which is typical for trees found under these conditions (Mustard and Harper 1998). Other factors, such as climate, tree age and genotype, may also influence hdr (Mustard and Harper 1998). More research on the functional aspects of this ratio is required before it is used widely as an indicator of vigour under natural conditions (Brunner 1993, Mustard and Harper 1998).

The hdr could also 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 increases with increasing pre-release hdr (Navratil 1995). Newton and Comeau (1990) suggest that long-term growth of Douglas-fir is jeopardised when hdr exceeds 60. While suitable hdr appears to vary as a function of tree size and climate, a critical value of 60 is commonly used for white spruce and Engelmann spruce (*Picea engelmannii* 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 1994). Several authors have discussed the adaptive significance of apical dominance in plant shoots (Brown *et al.* 1967, Little 1970, Cline 1991, Aarssen 1994). It appears that leader growth controls top whorl development (Wilson 1992, Oliver and Larson 1996). 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 advance regeneration vigour 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 (S. Parent, unpublished report). An estimation of the ratio of leader growth over lateral growth can then be made and it becomes easy to check whether this ratio is greater than 1.

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 (S. Parent, unpublished report). In the case of lodgepole pine and jack pine, this ratio is not influenced significantly by light intensity (Williams *et al.* 1999, Claveau *et al.* unpublished). Results from an 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.) (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 Scots 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. The response potential to canopy removal being related to the level of pre-harvest suppression, these values could serve as indicators of response potential.

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 also reported a strong relationship between the number of lateral buds and the overall vigour of a tree (Fraser 1962, Remphrey and Powell 1984). This could be explained by the fact that the number of nodal and internodal buds and branches generally increase with light intensity and with the length of the growth segment (Parent and Messier 1995, Williams *et al.* 1999, Claveau *et al.* unpublished). Results from an unpublished study (Comeau *et al.* unpublished) suggest that when there are less than three top nodal branches on five-year-old seedlings, it indicates stress for Engelmann

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/year)	Apical dominance 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	5–10[10,14]	**	60–70[4,13]	**	**
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.* (unpublished))
**not enough information available
1. Kayahara *et al.* (1996), 2. Wright *et al.* (1998), 3. Claveau *et al.* (unpublished), 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.* (2000), 13. Art Groot, pers. comm., 14. Paquin and Doucet (1992b).

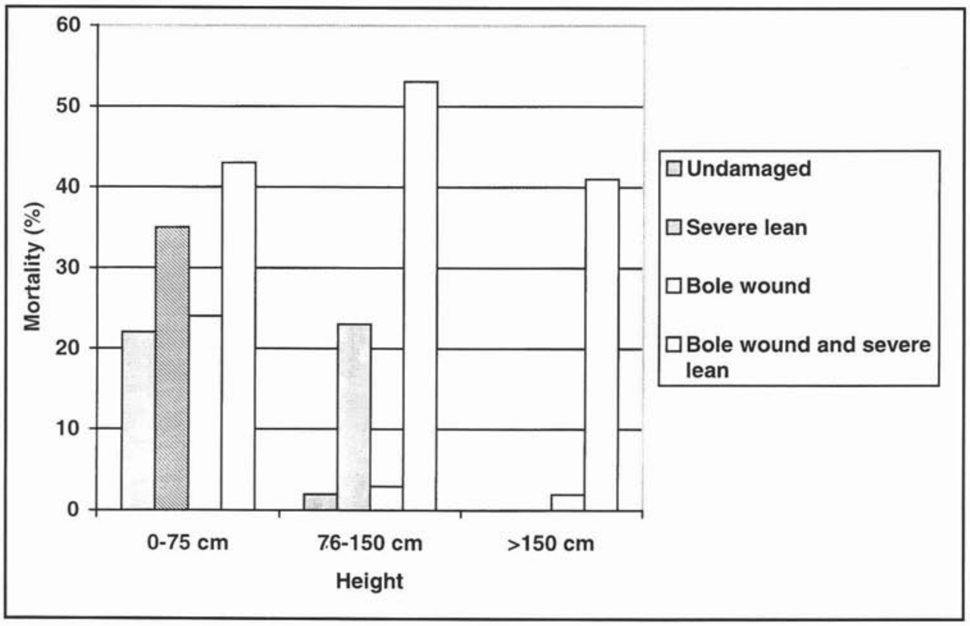

Fig. 3. Effect of damage on the mortality of Douglas-fir advance regeneration, six years after harvesting. Source: Tesch *et al.* (1993)

spruce, Douglas-fir, lodgepole pine, and western white pine. Based on the results reported above, we suggest various thresholds in the number of nodal and internodal branches as vigour indicator for the various conifer species of the boreal forest (Table 1).

Logging damage

At least part of the advance regeneration can be damaged during logging operations, possibly impairing its ability to survive and respond to release (Ferguson and Adams 1980). However, advance regeneration in some species has shown a remarkable capacity to overcome damage and this may not constitute the main cause of mortality (Gordon 1973, Tesch *et al.* 1993, Ruel *et al.* 1995). 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 (Fig. 3). Bole wounds combined with leaning were far more serious than broken terminals or stems but the importance of bole wounds, measured by the percentage of circumference 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). 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. Percentage of circumference girdled was useful in predicting survival for balsam fir and black spruce (Fig. 4) 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. Tesch *et al.* (1993) have shown a strong recovery of leaning Douglas-fir stems. They found that all trees with an initial minor lean were upright after six years. Most of the modestly and severely leaning trees had also recovered.

Logging wounds serve as entry points for decay. The importance of decay will then be a function of wound size and rapidity of healing. The rapid healing observed by Tesch *et al.* (1993) for Douglas-fir could minimize the severity of this problem. This potential problem must however be studied over a longer period for each of the species depending on advance regeneration.

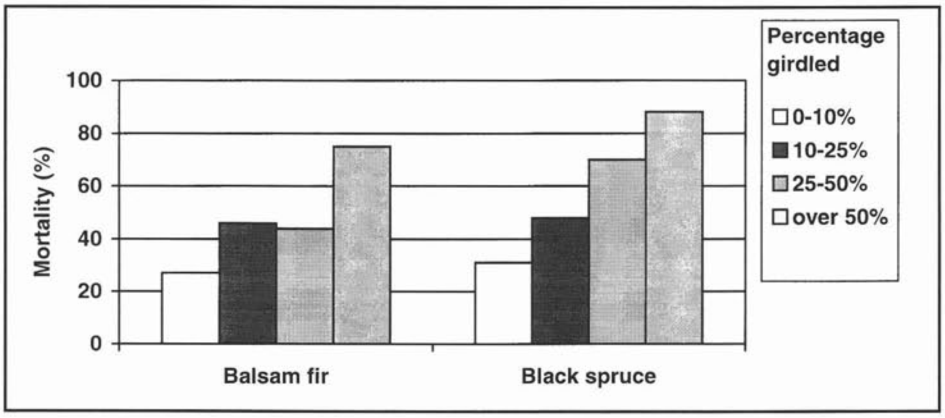

Fig. 4. Effect of different levels of bole girdling on mortality of advance regeneration of balsam fir and black spruce, seven years after harvesting. Source: Ruel and Doucet (1998)

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). Ferguson and Adams (1980) were also able to explain only 35% of the variation in annual growth for grand fir (*Abies grandis* (Dougl.) Lindl.) even though their model included variables related to both site and seedling quality. Seedling quality was characterized by age, pre-harvest height growth, height, and bole damage. McCaughey and Schmidt (1982) were able to explain between 27 to 58% of the post-harvest height growth of Engelmann spruce on different sites. The variables used differed between sites and only pre-harvest height growth was common to all sites. For subalpine fir, their regressions explained a lower proportion of the variance in post-harvest height growth (11–41%) and no variable was retained consistently across sites. Some of these results are promising but further exploration of vigour indices that combine various individual measures is required.

Tentative Threshold Values for Morphological Indicators

The morphological indicator values of vigour 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 the probability of mortality as response variable. 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 response potential 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 shorter than 1m were not considered because their growth and morphology are found not to be very responsive to the change in understory environmental conditions (Claveau *et al.* unpublished). For example, in low light conditions, they have an unusually 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. However, this does not mean that these seedlings cannot play a very significant role in a regeneration strategy based on advance regeneration. Their survival is only more difficult to predict but their usually greater number makes survival prediction less critical.

Summary and Recommendations

1) The ability of some advance regeneration to grow and survive following sudden overstory removal varies with species shade-tolerance and depends in part on the light conditions prevailing prior to release. The more vigorous the advance regeneration is before release the better it will respond to release.
2) Height growth rate is slower to react in comparison with stem diameter and structural root growth that 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 overstory removal.
3) Several morphological indicators of vigour measured

prior to release have been found to predict survival and growth rate 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 pre-release height growth rate is used.

4) Different growth and morphological indicators of response potential 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 and expand laterally 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 response potential to release for 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 of literature also suggests long-term monitoring since short-term conclusions can be misleading.

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