Functional ecology of advance regeneration in relation to light in boreal forests[1]

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Abstract: This paper reviews aspects of the functional ecology of naturally established tree seedlings in the boreal forests of North America with an emphasis on the relationship between light availability and the growth and survival of shade tolerant conifers up to pole size. Shade tolerant conifer species such as firs and spruces tend to have a lower specific leaf mass, photosynthetic rate at saturation, live crown ratio, STAR (shoot silhouette area to total needle surface area ratio), and root to shoot ratio than the shade intolerant pines. The inability of intolerant species such as the pines and aspen to survive in shade appears to be mainly the result of characteristics at the shoot, crown, and whole-tree levels and not at the leaf level. Although firs and spruces frequently coexist in shaded understories, they do not have identical growth patterns and crown architectures. We propose a simple framework based on the maximum height that different tree species can sustain in shade, which may help managers determine the timing of partial or complete harvests. Consideration of these functional aspects of regeneration is important to the understanding of boreal forest dynamics and can be useful to forest managers seeking to develop or assess novel silvicultural systems.

Résumé : Cet article passe en revue les aspects de l'écologie fonctionnelle des semis établis naturellement dans les forêts boréales de l'Amérique du Nord, avec une emphase sur la relation entre la disponibilité de la lumière et la survie et la croissance de conifères tolérants à l'ombre jusqu'au stade perchis. Les conifères tolérants à l'ombre comme les sapins et les épinettes tendent à avoir une masse foliaire spécifique, un taux de photosynthèse au point de saturation, des rapports de cime vivante, des indices STAR (rapport de la surface de la silhouette de la pousse par rapport à la surface foliaire totale) et des rapports racines/pousse inférieurs en comparaison avec les pins intolérants à l'ombre. L'incapacité à survivre à l'ombre des espèces intolérantes comme les pins et le peuplier faux-tremble semble résulter principalement des caractéristiques au niveau de la pousse, de la cime et de l'arbre entier et non pas au niveau foliaire. Même si les sapins et les épinettes coexistent fréquemment dans des sous-bois ombragés, leurs patrons de croissance et leurs architectures de cime diffèrent. Les auteurs proposent un cadre conceptuel basé sur la hauteur maximale que les différentes espèces peuvent atteindre à l'ombre et qui pourrait aider les aménagistes à décider du moment où procéder à une récolte partielle ou totale. La prise en compte de ces aspects fonctionnels de la régénération est importante pour la compréhension de la dynamique des forêts boréales et peut être utile aux aménagistes forestiers cherchant à développer ou évaluer des systèmes sylvicoles innovateurs.

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Introduction

Growth and mortality are the most critical processes determining the fate of juvenile trees during natural regeneration (Harcombe 1987). Many trees die without reaching maturity (Harcombe 1987; King 1990*a*). In the boreal forests of North America, seedlings and saplings of shade tolerant conifers often survive and grow slowly for a long time in the shaded understory. This creates advance regeneration that can give shade tolerant species a potential advantage in reestablishing canopy dominance after a windstorm or outbreak of defoliating insects (Groot 1984; Doucet 1988; McCaughey and Ferguson 1988; Ruel 1989, 1991; Béland and Bergeron 1993; Tesch and Korpela 1993). This is in

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contrast to the advantage of shade intolerant species that prosper after colonising areas opened up by wildfires, which destroy any advance regeneration. Although seedlings of intolerant species such as jack pine (*Pinus banksiana* Lamb.) (Béland and Bergeron 1993), trembling aspen (*Populus tremuloides* Michx.) (Kelly et al. 1999), and paper birch (*Betula papyrifera* Marsh.) (Perala and Alm 1989, 1990) may be found under a closed to fairly closed canopy, they usually do not survive long enough to make a significant contribution to regeneration following gap formation. Paper birch (Perala and Alm 1989, 1990) and trembling aspen (Kelly et al. 1999) seedlings, for example, can survive for no more than a few years at 10% of full sunlight and saplings are found only in fairly large canopy gaps with higher insolation. As a consequence, the more shade tolerant spruce and fir species dominate advance regeneration in the unmanaged forests of boreal regions where fire is not frequent (Rowe 1977).

If we are to evaluate new silvicultural approaches to manage advance regeneration in boreal forests more effectively, it is important to understand the basis for interspecific differences in growth and survival from seedling to pole-size trees (here defined as saplings up to 7 m tall). We especially need to understand the ecology of advance regeneration growing in the shaded understory. While light regime is the defining characteristic of shaded understory and a critical factor affecting tree growth (Lieffers et al. 1999), trees in these situations also are exposed to a correlated set of environmental conditions, including contrasting air movement, temperature, CO_2, moisture and nutrient regimes, as well as potential competition with other vegetation for moisture and nutrients. The success or failure of silvicultural systems for shade tolerant conifers hinges on the functional responses of the target species and their competitors to these contrasting conditions. Shelterwood systems, for example, that minimise suppression in the advance regeneration of shade tolerant conifers run the risk of also favouring shade intolerant competitors. Similarly, the natural distribution and abundance of boreal trees across sites and successional stages depends on interspecific differences in functional response to different environmental conditions. By better understanding the ecology of natural regeneration in boreal trees, we can more effectively reach a balance in our silvicultural systems that favours yield in target species without sacrificing the tree diversity or functional integrity of boreal forest ecosystems.

Past discussions of the establishment and early growth of juvenile trees have tended to concentrate solely on the ability to grow in shade, and in particular on the concept of shade tolerance. Shade tolerance has often been defined simply as the ability of trees to survive and maximise carbon gain in the understory environment (Spurr and Barnes 1980). Other definitions emphasise tree characteristics that have more to do with the basis for shade tolerance differences among species. Daniels et al. (1979) defines it as “the relative genetic and physiological capacity of the plant to develop in a given environment, with the capacity to withstand low irradiance generally being the most important characteristic.” Givnish (1988) considered shade tolerance to be a function of the degree of morphological and physiological plasticity in the face of environmental change. In this review, we adopt a comparative and functional approach that emphasises the morphological and physiological characteristics that may confer greater or lesser capacity to grow in the shaded understory. We present a summary of our current understanding of the functional basis for variation in the shade tolerance of the major boreal trees. This includes a consideration of how shade tolerance is linked to the ability to respond effectively to small canopy openings. We focus on the commercially most important shade tolerant conifers in the boreal forests of North America: balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Mill.) BSP), and white spruce (*Picea glauca* (Moench) Voss). To better understand the functional basis of shade tolerance and competition among boreal trees, we compare these species to their most important, shade intolerant counterparts: jack pine, lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), trembling aspen, and paper birch. We emphasise the functional basis for growth and survival of established seedlings and saplings up to pole size; the seedling establishment phase of regeneration is covered in a companion paper (Greene et al. 1999).

Functional traits that favour growth and survival in shade

Many factors influence the abundance of advance regeneration in the shaded understory of boreal forests, but the ability of seedlings to reach pole size is dependent on the interplay between environmental factors (see review by Lieffers et al. (1999) for the light environment in particular) and the functional ecology of boreal tree species. The ability of understory trees to grow and survive in the shade of partial or complete overstory canopies is the outcome of complex interactions between leaf- and plant-level responses to light, nutrient, and water availability (Givnish 1988, 1995). Most investigators have ignored changes in relationships among these factors as growth proceeds and environmental conditions evolve (cf. Clark and Clark 1992, 1993). Discussion usually has focused on the establishment and early growth phases of understory tree species in relation to gaps; few studies have addressed the part of the regeneration cycle from established seedling up to pole size (Lang and Knight 1983). Since above- and below-ground resource availability changes continuously as the stand develops (Runkle and Yetter 1987; Rich et al. 1993; Brais et al. 1995; Messier et al. 1998), understory trees experience a wide range of environmental conditions during their life-span. All species therefore have evolved some degree of acclimation potential and developmental plasticity (Bazzaz 1990), but this flexibility cannot ensure that a species will survive and compete effectively in all environments. Fundamental differences among species in their functional organisation may still exist. The overall growth strategy of saplings may not be optimal under early growth conditions, but it may be optimal in the long run (Lei and Lechowicz 1990). Being able to grow faster in shade may indicate lower potential for survival under persistent shade (Kitajima 1994; Walters et al. 1993*b*). Hiura et al. (1996) found a negative relationship between height growth rate and mortality rate and longevity in the forest understory for saplings of *Abies sachalinensis* (Fr. Schm.), *Picea jezoensis* (Sieb. et Zucc.), *Picea glehnii* (Fr. Schm.), and *Betula ermanii* Cham. in Japan. This also appears to be the case for shade tolerant and intolerant conifer and deciduous species of northwestern B.C. (Kobe and Coates 1997; Wright et al. 1998). Wright et al. (1998) found, however, that the relationships between growth and light, for a certain species, vary among climatic regions. Such complexity becomes especially relevant in forests where natural or anthropogenic disturbances generate frequent changes in the light regime in both space and time. Consideration of longer time spans during regeneration is essential in assessing the efficiency of silvicultural systems such as single tree or group selection cutting in regenerating the targeted species.

Following formation of canopy gaps, questions of short- and long-term interaction and adaptiveness become crucial. Rapid growth in a sufficiently large gap will allow a shade intolerant, pioneer species that has colonised the gap to reach the canopy. However, large gaps also increase plant competition and may attract defoliators and browsers. In contrast, rapid canopy closure in small gaps may result in maladapted canopy architecture of shade intolerant species that increases their risk of mortality during the subsequent suppression period. There is a poor mechanistic understanding of the factors contributing to such differential mortality across species and canopy openings of different sizes and duration. Determining the best means to encourage one species survival over another requires understanding of the functional relationships among: (*i*) the size of the canopy opening, (*ii*) the nature of the above- and below-ground environment thus created, and (*iii*) the functional responses of seedlings and saplings of each species to changing biotic and abiotic factors in the understory as the overstory canopy develops. We focus on this last point, emphasising the functional responses that optimise carbon acquisition at the leaf and crown levels and those that optimise carbon allocation between above- and below-ground parts.

Leaf-level carbon acquisition

Many studies on the acclimation of leaf morphology and physiology to shade (e.g., Logan 1969; Boardman 1977; Björkman 1981; Kamaluddin and Grace 1992; Mitchell and Arnott 1995) have revealed adaptations that optimise light-capture in shade. For both conifer and hardwood trees, shade leaves are thinner, have fewer stomata, a thinner layer of chlorophyll-containing parenchyma, a lower specific leaf mass (mass/leaf area), and a lower leaf photosynthetic compensation point and rate at saturation ($P_{\max}$) (e.g., Tucker and Emmingham 1977; Carter and Smith 1985; Abrams and Kubiske 1990). Although few studies have been done on boreal trees, there is some indication that shade leaves of shade intolerant species are less efficient at responding to sunflecks than shade tolerant species (Paliwal et al. 1994; Küppers et al. 1996; Ögren and Sundin 1996). Niinemets and Kull (1994) found, for Estonian woody species, that specific leaf mass ($g \cdot cm^{-2}$) generally increases with light availability and species light requirement, whereas leaf area was not always related to light availability.

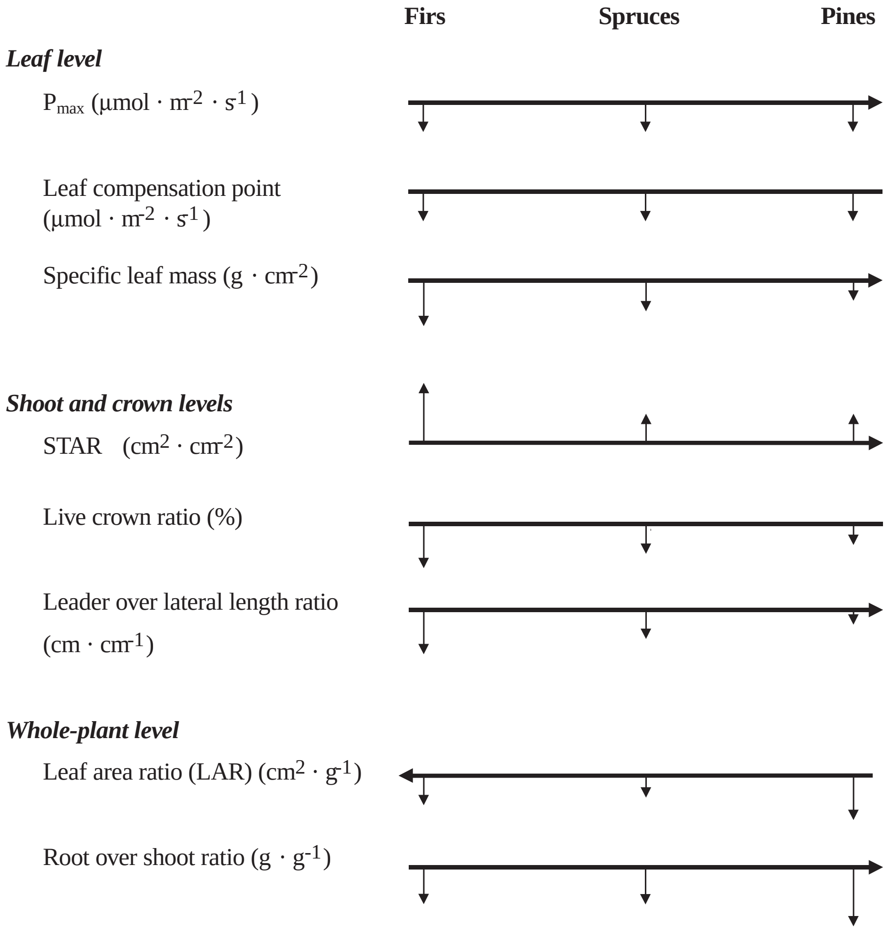
Leverenz (1996) reported that $P_{\max}$ of sun leaves increased from shade tolerant *Abies* (approximately 7.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$) to shade intolerant *Pinus* (approximately 16.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$) species. Bassow and Bazzaz (1997) also found that $P_{\max}$ decreased with increasing shade tolerance in temperate deciduous trees. Apparently the cost of maintaining high photosynthetic capacity is not justified in shade. On the other hand, a review of the literature on variation in the leaf compensation point strongly suggests that the common supposition that shade tolerant species have a lower leaf compensation point than shade intolerant species is not supported by the available data (Fig. 1). We therefore need to look at parameters other than the leaf compensation point for a functional explanation of the relative success or failure of boreal tree species grown in shade (Givnish 1988; Matthes-Sears and Larson 1990; Küppers 1994; Sipe and Bazzaz 1994; Leverenz 1995; Groninger et al. 1996).

Shoot- and crown-level carbon acquisition

Crown architecture, defined by how leaves are positioned along shoots and how shoots are positioned to form the tree crown, has a critical influence on how light energy is absorbed by the whole plant. Crown architecture also influences how limited resources must be distributed among leaves of different age and position to maximise whole-plant carbon gain (Field 1983). Despite the clear adaptive significance of crown architecture, the interacting effects of environmental conditions, tree architecture, and branch type are still poorly understood, especially for the architecturally more complex deciduous species. Most studies have been descriptive and have not considered architecture and its influence on light interception together. For example, tree architecture has been described by many investigators (Hallé et al. 1978; Pickett and Kempf 1980; Shukla and Ramakrishan 1986; Canham 1988; Bonser and Aarssen 1994; King 1994; O'Connell and Kelty 1994; Sipe and Bazzaz 1994) but generally without considering the significance of architectural parameters for light interception. Other studies have described how architecture and morphology change within species in various light environments (e.g., Cornelissen 1993; Hemmerlein and Smith 1994; Parent and Messier 1995; Chen et al. 1996), again without relating these changes to light interception. Morphological models, such as those used by Prusinkiwicz and Hanan (1989) or others (Fisher 1992), similarly ignore the functional significance of tree architecture. Yet other studies have described light interception and transmission through canopies (Normand and Jarvis 1974; Neufeld 1986; Messier and Bellefleur 1988; Dickmann et al. 1990; Whitehead et al. 1990; Canham et al. 1994) but without extensive analysis of the architectural attributes that determine light transmission and interception. In addition, many simulation models have been developed to predict light transmission and interception, both by forest canopies (see review by Lieffers et al. 1999) and individual trees (e.g., Kohyama 1991), but these often use highly aggregated measures of canopy structure such as average leaf area density and leaf angles. Because of their spatially explicit simulation of shoots and branches, recent modelling efforts such as that of Perttunen et al. (1996) allow a more effective evaluation of the functional significance of various crown architectures in terms of carbon gain and allocation.

In single trees, light interception is influenced by the forest light environment, crown architecture, structural characteristics of branches, and leaf morphology (Horn 1971; Carter and Smith 1985; Fisher 1986; Kuuluvainen and Pukkala 1989;

Fig. 1. Hypothetical trends in leaf, shoot, and crown morphological and whole-tree allocational changes among fir, spruce, and pine genera (horizontal arrows) and in relation to shade (vertical arrows). This figure is based on the literature and scientific evidence reviewed in the text of this paper and on other references (Aussenac 1977; Boyce 1993; Brand and Janas 1988; Brooks et al. 1991, 1994; Chen 1997; Dang et al. 1998; Ekwebelam and Reid 1984; Fry and Phillips 1977; Gilmore and Seymour 1997; Greis and Kellomäki 1981; Helms and Standiford 1985; Leverenz 1987; Logan 1966; Oliver and Dolph 1992; Smolander et al. 1994; Sprugel et al. 1996; Troeng and Linder 1982; Tucker et al. 1987; Zelawski et al. 1973). Very few supportive data were found for LAR and root to shoot ratio for these three genera, and the trend reported here is based on personal observation (for LAR) and theory (for root to shoot ratio). The horizontal arrows indicate increasing values among genera, whereas upward and downward vertical arrows indicate increasing and decreasing values, respectively, from sun to shade.



Givnish 1988; Leverenz and Hinckley 1990; King 1990*b*; Ezcurra et al. 1991; Hilbert and Messier 1996). Various architectural adaptations may be employed by trees to maintain productivity and competitive advantage under different light conditions. These include steep leaf angles that minimise photoinhibition and allow more light to be transmitted to lower leaves, horizontal leaves that shade competitors more effectively, allocations of carbon to leaves versus stem and branches that mediate the construction costs of arraying photosynthetic area, or branching patterns that serve to maximise the light-interception efficiency within the crown (Kohyama 1980; Canham 1988; Sakai 1995). At the shoot level, the light-interception efficiency of conifers has been quantified by the ratio of shoot silhouette area to total needle surface area (STAR) (Carter and Smith 1985; Leverenz and Hinckley 1990; Stenberg 1996). This ratio varies in relation to shoot geometry and orientation relative to the direction of light. Usually shade shoots have a larger STAR than sun shoots (Stenberg 1996). Shade shoots also tend to be horizontally inclined (Stenberg et al. 1993). Stenberg (1996) reviewed the STAR values for several conifers and found that STAR increases from *Pinus* (approximately 0.16) to *Abies* species (0.28) (Fig. 1). These differences in shoot and crown morphology found among the genera of boreal conifers are summarised in Figure 1.

Depending on the morphological and developmental plasticity of a species, these characters may change along light gradients (cf. vertical arrows in Fig. 1). Parent and Messier (1995) and Carter and Smith (1985) reported the following changes in shade tolerant conifers along a diminishing light gradient: lateral branch growth was favoured over height growth; the number of whorl and interwhorl branches decreased; live crown ratio decreased; and horizontal display of needles and branches increased. In contrast, shade intolerant lodgepole pine appears to display less morphological plasticity, with height growth and strong apical dominance being the rule under all types of light regimes (Chen et al. 1996; Williams et al. 1999). Firs tend to show more plasticity in their shoot and crown morphology in relation to light availability than either spruce or pine species (Kohyama 1980; O'Connell and Kelty 1994; Stenberg 1996). Much less is known about shoot and crown morphological differences among deciduous tree species, but paper birch and trembling aspen do not display much morphological plasticity in relation to light availability (Messier and Puttonen 1995; Nelson et al. 1981; C. Kelly, personal communication). Differences in insolation within crowns also can trigger plastic responses in crown architecture. For example, Schoettle and Smith (1991) found that the annual shoot length increment for *Pinus contorta* was strongly correlated with light availability as measured at shoot tips; shoot length increment decreased from top to bottom within the crown. They also showed that leaves are retained only above a critical threshold of light availability. Since the array of leaves in the tree crown strongly influences light interception and therefore potential productivity, we can assume that all of these plastic responses are in some way conditional on light-interception efficiency.

Crown architecture in trees reflects a balance in complex systems that are performing several somewhat contradictory tasks simultaneously (Farnsworth and Niklas 1995). It can be misleading or counter-productive to seek a single factor or simple, optimal design to explain crown architecture. For example, Sprugel (1989) concluded that the leaf, shoot, and crown morphology of conifer trees serves mainly to enhance photosynthesis, while Smith and Brewer (1994) suggested that adaptation for survival during winter months might be at least as important. Similarly, Sprugel (1989) suggested that the morphology of sun shoots allows light to penetrate deeper in the crown, allowing maintenance of a deep crown, while Smith and Brewer (1994) argued that very little sunlight is transmitted through the sun branches of conifers and that it is the conical form of the crown that allows light to penetrate to deeper crown layers. The analysis and interpretation of such alternative optimisations are further complicated by the size of a tree and its neighbours. Very different optimisations may be found over the life of a tree. Analysing functional responses in different traits or in contrasting environments clearly calls for caution and for a multifactorial and holistic approach that will not be confounded by coordinated optimisation of different, countervailing functions at the whole-plant level.

Plant-level carbon allocation

Tree growth and survival in the forest understory is strongly influenced by patterns of allocation to above- and below-ground organs. Several studies have shown how patterns of whole-tree carbon allocation can affect the ability of understory trees to grow and survive in shade. Gleeson and Tilman (1994) showed that late successional species have a lower relative growth rate and a higher root allocation than early successional ones, which agrees with results of Canham et al. (1996) for several temperate tree species. Walters et al. (1993*a*,1993*b*) showed that carbon allocation and respiratory costs incurred in the construction and maintenance of stems and roots are critical factors in explaining the success of temperate tree seedlings in shade. As trees grow larger, their maintenance and construction costs increase (Waring 1987; Givnish 1988). This is related to an increase in the proportion of nonphotosynthetic tissues as trees grow (Waring 1987; Gerrish 1990; Roberts et al. 1993). Since nonphotosynthetic tissues require energy to respire, the tree has less photosynthate available for other functions. Gerrish (1990) discussed what he called the "carbon starvation" caused by this declining ratio of photosynthetic to nonphotosynthetic tissue as plant size increases. Whittaker and Woodwell (1967) calculated that larger trees and shrubs have a higher ratio of stem surface area to leaf area than smaller individuals of the same species. Givnish (1988) estimated that *Liriodendron* requires 12% of full sunlight when it measures 1 m, while it requires 25% of full sunlight when it reaches 10 m tall. This increasing light requirement with increasing size could, in part, explain why dark understories often are covered with a dense carpet of small seedlings without any larger ones. Greater allocation of carbon to foliage and stem growth makes a species a better competitor for light, whereas greater allocation of carbon to fine-roots should enhance the capacity to compete for nutrients and water. Generally, theory suggests that plants that allocate more carbon to shoot growth will have a higher maximal growth rate than those that allocate less (Mooney 1972; Gleeson and Tilman 1992), and should then be able to exploit increased resources. What is at issue, however, is not simply allocation to shoot versus root, but also the degree to which the shoot grows tall as opposed to spreading laterally and becoming more leafy.

A model developed by King (1990*a*) considered the constraints and advantages related to height growth. Height is an important determinant of improved light interception in some environments, but it has associated costs. Selection for vertical growth over lateral growth is believed to be adaptive only if the overall forest structure is such that light availability increases sharply with height, as it does at more open, early successional sites. Under closed conifer stands, however, understory vegetation often is sparse (Alaback 1982; Messier et al. 1998) and any increase in height would not necessarily be rewarded by an increase in light. In such shaded environments, the whole-plant light requirement can be lowered if plants allocate a large fraction of their fixed carbon to leaf production instead of branches and stems. King (1991) suggested that differential allocation to leaf versus woody tissues can be important in determining shade tolerance. This expectation is supported by the lower ratio of total leaf area to plant dry mass (leaf area ratio, LAR) in shade intolerant compared to shade tolerant species (Popma and Bongers 1988; Kitajima 1994). Shade intolerant species often allocate a high proportion of their carbon to stem growth, which increases their light interception in competition with neighbours. Shade intolerant species with narrower crowns and thinner stems, such as lodgepole and jack pine, thus can grow faster in gaps due to a lower biomass increment required per unit height growth (Takahashi 1996; Williams et al. 1999). Sakai (1995) developed a model that supports the idea that shade intolerant species should hold to this allocational pattern even in shaded understories as any height advantage over their immediate neighbours will maximise their success if a canopy gap does open. Shade tolerant species with wider crowns and thicker stems, such as balsam fir, increase assimilative capacity and the probability of survival under a closed canopy, but thereby reduce their rate of height growth. In general, shade tolerant species are better able than shade intolerant species to modify their shoot and crown morphology to improve light interception in shaded environments while minimising respiratory cost in low light; thus firs and spruces are able to reduce or almost stop their height growth when heavily shaded and divert resources to storage. As a consequence of these differences in allocation, large infrequent gaps and small but frequent gaps should favour intolerant species with a fast height growth such as birch, aspen, and pine, whereas small and infrequent gaps should favour tolerant species such as fir and spruce with slow height growth in shade that allocate more to leaf.

A framework for evaluating growth and survival of boreal trees in shade

Another insufficiently investigated possibility is that at some height in a given environment, allocation in a shade tolerant species may be to neither shoot nor root growth, but only to storage tissues and maintenance costs. This maximum height that saplings of shade tolerant species can sustain in any particular environment appears to be determined by (*i*) the net photosynthate remaining after root and foliage requirements are met and (*ii*) by the maintenance and construction cost per unit of height growth (Givnish 1988; King 1991). Because of the increasing light requirement with increasing size, increasing height might be detrimental to the survival of a sapling. When light availability is not improved by an increase in height, such as in the dense understory of conifer forests, it may result in death. Height growth can be expected to nearly stop in situations where growing taller yields gains in light interception inadequate to meet the costs of maintaining the new tissues.

The idea of a "maximum sustainable height" in trees growing in the forest understory is supported by diverse data. In a dark, old-growth conifer forest in northern Japan, Kubota et al. (1994) observed a maximum "waiting height" of 7 m for *Abies sachalinensis* compared to 3 m for *Picea jezoensis*. This "waiting height" is presumably higher for the fir because of an intrinsic ability to maintain a positive carbon balance at lower light. Parent and Messier (1995) found balsam fir less than 30 cm at around 3% insolation; taller firs were found only at microsites in the understory that had higher insolation. Simard et al. (1998) found that light did not limit early survival of balsam fir less than 30 cm tall. Leemans (1991) reported that in mature spruce forests of Sweden, larger tree saplings are often clumped, mainly in and around gaps. Kelly et al.[3] found that the maximum height of aspen sprouts in the understory increased with light availability from 1 m at 10% to 7 m at 40% of full sunlight. Limitations on sapling height in the understory of North American forests also have been reported for some temperate deciduous tree species. Sugar maple (*Acer saccharum* Marsh.) saplings attained a maximum height of 80 cm and age of 25 years under a dense overstory where light within the first 6 m varied between 1 and 3% of full sun (C. Messier, unpublished data); maple saplings were taller in small gaps and adjacent to a recent clearcut. This supported the finding by Messier (1994) that maximum height of understory sugar maple, yellow birch (*Betula alleghaniensis* Britt.), and American beech (*Fagus grandifolia* Ehrh.) trees increased rapidly from 1 to 4% of full sun in closed mature sugar maple stands of eastern North America. Based on these results, we can summarise the apparent relationships between the maximum sustainable height for the main genera of boreal trees and the relative size of gaps in which they are growing (Fig. 2). The line for each genus represents the hypothetical height versus gap size threshold at which carbon gain more or less equals respiratory cost; understory trees in a particular light microenvironment cannot survive long above this threshold line. There exists some evidence that overall respiratory cost increases with tree size (Waring 1987; Givnish 1988; Yokota and Kagihara 1998), although this has been challenged by Ryan and Yoder (1997).

In light of what has been said above, it may not be surprising that understory tree survival has been often found to be negatively correlated with growth (Walters et al. 1993*b*; Kitajima 1994; Hiura et al. 1996). The ability of saplings of shade tolerant species to almost stop their height growth when suppressed (Kohyama 1980; Hara et al. 1991; Klinka et al. 1992; Lieffers and Stadt 1994; Parent and Messier 1995; Lesage 1997) therefore can be seen as an adaptation to not grow above their "maximum sustainable height." Williams et al. (1999) found 30- to 60-year-old saplings of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) and lodgepole pine, two conifer species considered somewhat shade intolerant, growing in as low as 5% full sun in the dry interior zone of B.C., and in both cases, height growth was only a few centimetres per year.

These results suggest the possibility that the sustainable height characteristic of a species may be useful in deciding the timing of partial or total harvests; once height growth in advance regeneration has stagnated, the productivity of the site should profit from harvests that open the canopy to some degree and allow release of the understory saplings. However, there is some evidence that a threshold exists between the size of a gap and the ability of shade tolerant species such as balsam fir to regenerate because of potential competition by less tolerant species in larger gaps. Kneeshaw and Bergeron (1998) found that balsam fir regeneration was less abundant in large natural gaps created by spruce budworm than in smaller gaps, and they related this to the ability of mountain maple (*Acer spicatum* Lamb.) to respond quickly to large gap openings, which then reduces the light level near the forest floor below the critical level for fir growth and survival. Indeed, M. Beaudet (personal communication) found that the light level at the forest floor was significantly lower a few years after partial cutting in large gaps than in uncut temperate deciduous stands. This was caused by the strong growth of understory tree and shrub species resulting from the opening of the overstory canopy. While this hypothetical framework built on the idea of sustainable height clearly requires further refinement and testing, the concept may provide a practical guideline that managers could use to decide the timing and design of

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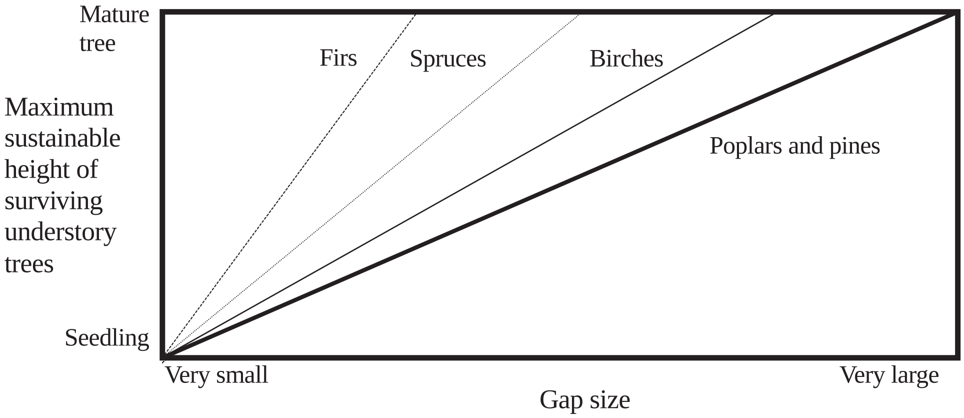
[3] Kelly, C., Messier, C., and Bergeron, Y. Mechanisms of shade intolerant deciduous tree recruitment between catastrophic disturbance in the southern boreal mixed-wood forest of Québec. Submitted to Ecology.

Fig. 2. Hypothetical relationships between the maximum relative height at which understory trees of each of the main tree genera found in the boreal forest can survive and relative gap size. The line represents the survival threshold at which carbon gain more or less equals respiratory cost at the whole-tree level. It suggests that for a certain gap size and tree genera, individuals could not be found above the threshold line. This figure is based on the literature and scientific evidence reviewed in the text. See text for further explanations and supporting data.



rotational cuts that would maximise timber yields without compromising the success of advance regeneration for commercially desirable species.

Subtleties in managing for fir versus spruce advanced growth

When species are strongly differentiated (e.g., intolerant pines or aspen versus tolerant spruces or firs), it is easy to decide on management strategies that favour one species over another. On the other hand, the management of two more or less equally shade tolerant species such as fir and spruce that are often found growing together in the boreal and subboreal forests may require a more subtle assessment and exploitation of functional differences in shade tolerance. We know that these two species differ greatly in their early establishment strategies (Greene et al. 1999), but we know much less about how some possible differences in their functional ecology, once established, may affect their growth and survival in shade.

Takahashi (1996) found that in shade, fir species are better able to shed lower branches and produce more new branches than spruce species. Such trait can explain why we tend to find that spruce species maintain a higher live crown ratio in shade than fir (Takahashi 1996; Larivière 1998). Larivière (1998) and S. Parent, M.-J. Simard, and C. Messier (unpublished data) have also reported that balsam fir is better able to stop growing vertically and grow laterally when suppressed than white spruce. This ability of fir species to greatly reduce height growth while maintaining lateral growth in shade has been reported by numerous authors (Kohyama 1980; Klinka et al. 1992; Parent and Messier 1995; King 1997). Hara et al. (1991) also reported that small suppressed firs were able to almost completely stop height growth, but maintained some diameter growth. Spruce species are also able to reduce height growth and modify their height to lateral growth ratio when suppressed (Greis and Kellomäki 1981), but our limited evidence suggests that they do not do that as much as fir species. Fir species also appear to grow more quickly in height than spruce when suddenly exposed to open conditions (Doucet and Boily 1995; Hiura et al. 1996; Doucet 1999), but growth of spruce may be maintained over a longer period of time (McCaughey and Schmidt 1982; Boily and Doucet 1993; Doucet 1999). Interestingly, Takahashi (1996) found that the higher branch turnover in fir compared to spruce is accompanied by a higher needle turnover rate; he suggested that fir species are adapted to maximise height growth in less crowded conditions (i.e., more open conditions) and to enhance lateral crown development with short-lived branches in crowded conditions (i.e., shaded conditions) at the expense of construction cost of new branches. In contrast, spruce reduce growth rates in all conditions with conservation of the branches present in crowded conditions. There also appears to be a compromise between the higher growth rate of fir in open conditions and its shorter tree longevity compared with spruce (White et al. 1985; Hiura et al. 1996). This may also force fir to be more opportunistic in the understory, whereas spruce can afford to wait longer in the understory until a gap is formed. This idea is supported by the results of White et al. (1985) who found that red spruce (*Picea rubens* Sarg.) can “reach older ages before release” than Fraser fir (*Abies fraseri* (Pursh) Poir.). This is not always the case, however, and Trethewey (1991) found that advance regeneration of Engelman spruce (*Picea engelmanii* Parry ex Engelm.) survived up to 50 years under suppression in the understory, whereas subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) survived up to 100 years in a subboreal forest of B.C. Several studies (Morin and Gagnon 1991; Paquin and Doucet 1992; Groot and Horton 1994; Lussier 1997) have reported that survival of black spruce individuals in the understory for more than 100 years is common. However, Morin and Laprise (1997) suggested that balsam fir understory saplings may have up to 40 missing rings, which suggests that we may have substantially underestimated the age of balsam fir growing in the understory. Sullivan and Peterson (1994), reviewing the possible mechanisms for segregation between spruce and fir in the southern Appalachian forests, concluded that red spruce should increase in dominance when disturbance is low whereas Fraser fir should dominate where disturbance is frequent because of its rapid growth and greater ability to respond to disturbance. This concurs with Takahashi (1996) who concluded that local variation and unpredictability of gap formation and turnover within a forest enabled these two contrasting growth/architecture strategies to co-occur. All of these ideas generally are consequent with the model developed by Sakai (1995) who predicts that species maintaining a higher proportion of foliage in shade (like spruce) should be well adapted to survive when disturbance frequency is low. With the limited evidence reported here, we suggest that silvicultural systems involving longer intervals between cuts should favour spruce over fir.

Summary and recommendations

(*i*) The ability of the boreal tree genera to grow and survive in shade up to pole size depends on the functional responses of saplings to the changing biotic and abiotic factors in the understory as overstory canopy develops over time; these environmental changes during succession are a function of site conditions and the size and frequency of gaps created by disturbance at the site.

(*ii*) At the leaf level, the only consistent differences among boreal tree genera are in specific leaf mass (SLM) and maximum photosynthetic capacity ($P_{\max}$). SLM tends to increase from shade tolerant to shade intolerant species and, within species, from individuals growing in shade to those in full sunlight. Differences in leaf-level attributes alone cannot explain the successional dynamics of boreal tree species, but may explain differences in growth rate between shade tolerant and intolerant tree species in fully illuminated trees.

(*iii*) At the shoot and crown levels, clear structural differences were found among conifer tree genera. Shade tolerant conifer species such as firs and spruces tend to have a lower live crown ratio, STAR (shoot silhouette area to total needle surface area ratio), and root to shoot ratio than the shade intolerant pines.

(*iv*) Shoot and crown structural traits show most plasticity in relation to light availability for firs and least for pines. We suggest that it is more this lack of plasticity in shoot and crown morphology than plasticity in leaf-level traits, that is responsible for the shade intolerance of poplars, birches, and pines.

(*v*) At the whole-plant level, shade intolerant tree species such as pines tended to be more affected by shading than shade tolerant ones. Shade tolerant species reduce or even cease height growth when growing in shade, something that shade intolerant species cannot do very well. The overall light requirement also increases with tree size, so increasing height can be beneficial only if it is associated with an increase in light availability. More specifically, we suggest that it is the ability of understory trees to stop their height growth and modify their crown to maximise light interception that determines the ability of shade tolerant conifers to survive in shade.

(*vi*) Considering these general attributes, we propose a framework for assessing advance regeneration in sapling performance that links interspecific differences in crown structural plasticity, growth strategies, and light requirements as size increases on the one hand with the size and frequency of canopy gaps on the other. The framework rests on the idea of a characteristic “maximum sustainable height” for each species set by the combination of (*i*) increasing light requirement with tree size, (*ii*) greater shoot and crown plasticity of shade tolerant versus shade intolerant species, and (*iii*) the ability of shade tolerant tree species to reduce or cease height growth in shade, which can explain the various patterns of succession found in the boreal forest. Large and infrequent gaps or small and frequent gaps favour intolerant species such as birches, poplars, and pines, whereas small and infrequent gaps favour tolerant firs and spruces. Forest managers can use this knowledge to create disturbance patterns that promote or deter targeted tree species.

(*vii*) Management of the firs and spruces, which frequently co-occur, depends on recognising the fairly subtle differences in their crown architecture and growth patterns. Compared with spruces, firs are better able to shed lower branches, grow laterally in shade, stop their height growth when shaded, and grow quickly in height when suddenly exposed. The combinations of these functional traits should enable firs to get established and survive in darker microsites than spruces, but they should disappear more quickly in less shady microsites if no major canopy disturbance occurs.

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