

Patterns of above- and below-ground response of understory conifer release 6 years after partial cutting

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Abstract: An increased pressure to use silvicultural techniques not based on clear-cutting followed by planting has led to an interest in systems that take advantage of existing understory seedlings (advance regeneration). Earlier studies have suggested that following harvesting, understory seedlings may experience growth reductions before responding with growth increases. We hypothesize that this “growth shock” following release results because seedlings are ill adjusted to the new growing conditions and that this can be investigated through a comparison of growth in different parts of the tree over a 6-year period. This study compares the growth response of three size classes of lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings to a partial overstory removal in relatively dry conifer forests of central British Columbia. Growth was evaluated in four parts of the studied trees: radial increment in roots, in the base of the stem, and in branches, as well as leader height growth extension. Our findings show that following release from the overstory, early growth increases were largest in the roots and stems irrespective of the species or the size class. Differences between the species were observed in greater absolute height growth for pine, whereas Douglas-fir invested in greater stem growth, especially in the larger individuals. Important differences also occurred temporally. Both species (and all size classes) responded with an immediate increase in root growth followed, after a 1-year delay, by an increase in stem growth. Branch radial increment (for pine) and leader height growth (both species), however, experienced 2 to 3 year growth reductions before responding. It is therefore suggested that individuals restore the root–shoot balance by greater initial investments to root growth to offset the increased transpiration losses associated with the greater light and higher temperature conditions and the relative changes in the photosynthetic versus nutrient uptake capacity following the canopy opening. Foresters may therefore be able to manipulate tree growth responses by using an appropriate degree of overstory removal or opening size.

Résumé : Les pressions grandissantes pour abandonner l'utilisation des techniques sylvicoles basées sur la coupe à blanc suivie par la plantation ont avivé l'intérêt des systèmes qui tirent profit des semis préexistants en sous-étage (régénération préétablie). Des études antérieures ont indiqué que, suite à la récolte, les semis du sous-étage peuvent subir des réductions de croissance avant de répondre par une augmentation de leur croissance. Nous avons fait l'hypothèse que ce “choc de croissance” qui suit un dégagement est causé par le fait que les semis sont mal adaptés à leurs nouvelles conditions de croissance et que ce phénomène peut être analysé par une comparaison de la croissance dans les différentes parties de l'arbre pendant une période de 6 ans. La présente étude compare la réponse de croissance de trois classes de taille de semis de pin tordu (*Pinus contorta* Dougl. ex Loud.) et de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) à la suppression partielle du couvert de forêts relativement sèches du centre de la Colombie-Britannique. La croissance a été évaluée dans quatre parties des arbres étudiés : l'accroissement radial des racines, de la base de la tige et des branches ainsi que la croissance en hauteur de la pousse terminale. Nos mesures montrent qu'après un dégagement du couvert, les augmentations de croissance sont les plus fortes dans les racines et la tige, indépendamment de l'espèce ou de la classe de taille considérées. Des différences entre les espèces ont été observées. Le pin avait une plus forte croissance en hauteur et le douglas de Menzies avait une plus forte croissance de la tige, surtout chez les plus grands individus. Des différences importantes sont aussi apparues avec le temps. Les deux espèces (et toutes les classes de taille) ont répondu avec une augmentation immédiate de la croissance racinaire, puis, après un délai d'une année, par une augmentation de la croissance de la tige. L'accroissement radial des branches chez le pin et la croissance en hauteur chez les deux espèces ont cependant montré des réductions de croissance pendant 2 ou 3 ans.

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avant de répondre. Il semble par conséquent que les individus rétablissent l'équilibre entre les racines et la tige par un investissement initial plus important dans la croissance racinaire pour compenser les pertes additionnelles par transpiration causées par les conditions de lumière et de température plus élevées et les changements relatifs dans la capacité photosynthétique versus l'assimilation des nutriments suite à l'ouverture du couvert. Les forestiers peuvent donc manipuler les réponses de croissance des arbres en utilisant un degré approprié de dégagement ou d'ouverture du couvert.

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Introduction

Advance regeneration is made up of seedlings in the understory that have naturally established prior to harvesting. Successful integration of advance regeneration in second-growth forests has been well documented in various forest types. In eastern Canada, harvesting systems based on the protection of advance regeneration are now applied to a greater land area than clear-cutting followed by planting. Partial-cutting systems that rely on advance regeneration to restock forests have been adopted in parts of the British Columbia interior dry belt, primarily because shade-tolerant Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) has proven difficult to regenerate in clearcuts, because of high summer temperatures and associated moisture stress (Newsome et al. 1990) and susceptibility to damage from frosts during the growing season (Steen et al. 1990). Furthermore, Douglas-fir is considered to have acceptable release potential for use with partial-cutting systems (Hopwood 1990; Weetman and Vyse 1990). However, a companion species, lodgepole pine (*Pinus contorta* Dougl. ex Loud.), which also occurs widely in this ecosystem, is generally believed to respond poorly to release.

There are many benefits to partial-harvesting systems, such as providing an immediate growing stock, shading and sheltering to seedlings, providing cover to wildlife, and decreasing the risk of soil erosion. However, short-term growth reductions or even mortality may still be caused by immediate reductions in cover and subsequent exposure of advance regeneration to sudden changes in temperature, light, and moisture availability (Ferguson and Adams 1980; Tucker et al. 1987). There is, however, a lack of information on the period of growth delay, the patterns of allocation, and the degree to which Douglas-fir and lodgepole pine advance regeneration respond to release. Periods of growth delay in other species, following release, have been noted in silvicultural trials as seedlings take time to acclimate to the new growing conditions (Sundkvist 1994; Gordon 1973). Similarly, the growth response of advance regeneration following harvesting has been found to vary among individuals of different sizes, between suppressed and non-suppressed stems, and among species (Doucet and Boily 1995; Ruel and Doucet 1998; Ruel et al. 2000).

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

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

A number of hypotheses may be suggested to explain differential growth responses and possible growth delays of advance regeneration to release. Firstly, there is an unfavourable ratio between producing and consuming organs. Canopy release will influence photosynthetic and respiration rates. However, partial canopy removal normally influences light more than temperature levels (Larcher 1995), which should lead to an increase in the seedling carbon balance. However, if acclimation to shade prevents the seedling from fully responding to increased light (e.g., low light saturation, insufficient water uptake and transport capacity, pigment injury) and if the respiration rates are simultaneously increased (increased repair demand, higher temperatures), seedlings may experience or approach a negative carbon balance as suggested by Staebler (1954). If this were true, larger individuals with greater non-photosynthetic biomass would be expected to respond more slowly to openings than would smaller individuals. Second, the vascular transport system in the stem may not be sufficiently developed (cross-sectional area) to support immediate crown extension and development. The flow rate through the vascular system is proportional to the hydraulic conductivity of the system and the water tension gradient from soil to leaves. If the hydraulic conductivity of the seedlings is acclimated to low water flow rates, it will effectively prevent stomatal opening in more water-demanding environments, thus preventing the seedling from responding positively to increased radiation. On the other hand, if the seedling fails to close the stomata, it will risk permanent loss of conducting capacity as a result of embolism. The total pathway conductivity is directly proportional to conducting area and inversely proportional to the transport distance (Zimmermann 1983). If we assume that seedlings are working close to the maximum water tension they can withstand (Tyree and Sperry 1989), the only means of increasing the sap flow, and thus the potential transpiration rate, is by increasing the conducting area (and wood permeability). Assuming that all seedlings have similar wood permeability, the larger the seedling, the greater will be its need to increase its cross-sectional area to maintain an equivalent increase in sap flow and transpiration. Thus, we would expect to see a large increase in the cross-sectional area of wood after release, and it should be relatively bigger in large seedlings. Third, after release from the overstory, trees of both species may allocate a large proportion of their carbon to

belowground tissues, especially on drier sites, so that growth response would occur first in the roots and then in the aboveground tissues. The opening of the site will drastically change the relative efficiencies of the carbon uptake per unit biomass versus those of water and nutrient uptake. Assuming that a tree strives to maintain a functional homeostasis among its parts as suggested by Brouwer (1962), then it could be expected that immediately following the opening, there would be a stronger growth response below ground. The height growth response should then be directly related to the growth allocation to the roots following a certain time lag after which the seedling has had time to restore functional homeostasis. Conversely, if the overall water and nutrient availability of the site is increased because of reduced transpiration and nutrient uptake from a smaller number of overstory trees, then relative height and branch growth would be expected to exceed increases in roots and stems. An investigation of the radial increment response in the roots, branches, and the stem of the two species will permit us to determine which of these hypotheses are valid. It will also enable us to understand differences in response among individuals of different sizes in the two species.

The objectives of the study are thus to answer the following questions: (i) are there differences in the release response of the two study species, (ii) are there differences among different-sized individuals following an opening in the forest canopy, and (iii) does the release response of the tree result in greater allocation to the above- or belowground parts of the trees? We want to evaluate whether seedling growth after opening of the canopy restores the functional balance among tree parts. Immediately after the opening of the canopy, growth conditions become less light limited, and thus we suggest that trees will accordingly alter the relative sizes of their biomass compartments. We hypothesize that directly after overstory opening, the effects of increased light conditions should be observed as an immediate increase in root growth with concurrent stable or decreasing aboveground growth, which is eventually followed by a gradual increase in the aboveground growth.

Study site

The study site was located in forest stands 25 km south of Williams Lake, British Columbia (B.C.), in the dry cool Interior Douglas-fir biogeoclimatic subzone (Meidinger and Pojar 1991). The mean annual precipitation averages from 360 to 560 mm, and the mean annual temperature is 4.1°C (Environment Canada 1994). The study site had abundant naturally established Douglas-fir and lodgepole pine, both of which are major species of the interior montane forests of B.C. (Meidinger and Pojar 1991). The stand experienced a partial cut in July 1987, which reduced the preharvest density from 900 trees/ha (diameter at breast height (DBH) > 20 cm) to 300 trees/ha, with abundant seedlings and small trees of all sizes remaining in the understory. Data were collected in the summer of 1994. The remaining leaf trees were predominantly Douglas-fir but the naturally established regeneration was an equal mixture of Douglas-fir and lodgepole pine. The study area was located on a moderately dry and nitrogen-medium site (Steen and Coupé 1989) with fairly sparse understory vegetation, the most common plants being

pinegrass (*Calamagrostis rubescens* Buckl.) and red-stemmed feathermoss (*Pleurozium schreberii* (Brid.) Mitt., J. Linn.). The soils in this area have developed on deep deposits of medium-textured morainal material (glacial till) and have Orthic Gray Luvisolic soils (Annas and Coupé 1979; Steen and Coupé 1989).

Methods

Selection of study trees

One hundred and twenty-eight saplings from both species were randomly selected from 900 candidate specimens ranging in height from 30 to 450 cm and located under varying degrees of canopy coverage provided by the leaf trees. Individuals that were badly damaged or surrounded and overtopped by neighbouring individuals were not sampled. Saplings from both species were divided into three height classes for analysis: small, 30–100 cm; medium, 101–200 cm; and tall, 201–450 cm. Increment growth from 1994 was not considered, as saplings were harvested throughout the 1994 growing season. Because of problems in transportation and sample preparation in the laboratory, sample size varies for the different parts of the tree.

Growth measurements

Terminal leader growth measurements were made to the nearest millimetre, and the number of living branches for each whorl were counted. The relative height increment (RHI) for each year was calculated according to the following equation:

$$\text{RHI} = \frac{L_t}{L_t + L_{t-1}}$$

where L_t is leader length in year t , and L_{t-1} is leader length in the preceding year (Kneeshaw et al. 1998). Since earlier studies have shown the effect of initial size on height increment response following openings (Hatcher 1964; Ghent 1958), the traditional technique of using the ratio of leader growth to seedling height would lead to biased comparison. Instead we used Kneeshaw et al.'s (1998) modification of the method proposed by Brand (1986) to permit comparisons in height growth among individuals of different initial sizes. (This method is a more robust formulation that avoids the potential problem of a zero value in the denominator, as is sometimes observed in extremely shade-tolerant species that may experience years with no growth. In this formulation, constant growth is represented by a ratio of 0.5 instead of 1.0.) Formulating the RHI in this manner enables it to be more sensitive to changes in relative height than ratios based on leader length to total seedling height would allow. Comparisons of absolute height growth (or leader extension) are also conducted to provide foresters with data that is more easily digestible, and which will be useful in planning release in field settings.

Basal disks were removed for annual growth ring and diameter measurements. Disks were taken 3 cm above the soil surface to avoid swelling at the base of the trunk. Annual basal diameter growth was measured for the years 1980 to 1993 with a diameter increment microscope. The width of each growth ring was measured and averaged from two to

three different radii on the basal disk. Relative diameter growth was calculated using the same equation as for relative height growth. Disks were also taken from the three largest branches of sample trees at 2 cm from the stem to avoid sampling in the swollen area where the branch joins the main trunk.

Two disks were also removed for analysis from the root systems of sample trees. The disks were removed from lateral root(s) >3 mm in diameter from each sapling, and from 3 to 10 cm below the ground surface. The largest lateral roots were generally within 5 cm of the soil surface. In cases where no lateral roots greater than 3 mm in diameter were found, a disk was taken from the largest roots located 3 to 4 cm below the root collar. The roots were typically slightly elliptical, so measurements were taken from two to three different radii and then averaged.

Statistical analyses

The data were all analysed using SAS 6.12 (SAS Institute Inc. 1998). Both absolute and relative growth rates were used to compare growth differences for the different tree components measured, i.e., roots, stem, branches, and leader height increment. When comparing differences among different parts of the tree, data were calculated as percent change in growth of each post-harvest year compared with pre-harvest growth. This ensures that growth data will all be on the same scale and facilitates visualisation of the results, as percent change is more intuitively meaningful than relative growth rates.

To evaluate the treatment effect of the harvest, growth changes were analysed to see if there were differences in pre-harvest mean growth (1981–1987, except for height increment for which we had only 2 years of pre-harvest measurement) versus post-harvest mean growth (1987–1994). We also tested whether or not mean pre-harvest growth was a good predictor of post-harvest growth using linear regressions of relative growth rate data.

To explore the temporal changes in growth data, multivariate repeated measures analyses were performed with differences between individual years tested by polynomial orthogonal contrasts. These were conducted on relative growth rates for each individual part of the tree to determine if important temporal differences occurred in growth across size and species classes. We also used time-lag correlations to test if early growth responses in roots and stems were correlated with subsequent responses in branch radial growth and in height increment growth. These analyses were conducted to test the hypothesis that carbon allocation to root growth was a necessary precursor to branch and height growth.

Height data were transformed using a logarithmic transformation, whereas percent data were arcsine square-root transformed.

Results

Relative versus absolute pre- and post-harvest mean growth

A comparison of pre- and post-harvest relative growth rates shows that individuals responded significantly to the harvesting treatment in roots, stems, branches, and leaders

(Table 1A). In general, there were no differences among species or individuals of different sizes in terms of relative growth increment. When using absolute growth increments, larger individuals had, as expected, greater stem, branch, and height growth than did individuals in the two smaller size classes. No differences in absolute root increment were observed among individuals of different sizes for either species (Table 1B, Fig. 1). In terms of stem radial increment, larger individuals had a greater absolute growth response than smaller individuals ($p = 0.0007$ for the size \times period interaction). Changes in stem growth of all individuals from pre- to post-cut periods averaged more than 350% for Douglas-fir and over 500% (1.15 mm) for lodgepole pine.

No differences were observed between the growth rates of Douglas-fir and lodgepole pine for any of the tree parts that were measured. The only exception being in terms of stem growth, where larger Douglas-fir outgrew lodgepole pine (Table 1, size \times species interaction; Fig. 1). In general, pre-harvest growth rates, although statistically significant, were poor predictors of post-harvest growth rates. Pre-harvest root growth, for example, accounted for only 10% of the variation in post-harvest root growth (Fig. 2). Only slightly better relationships were found for stem radial increment and branch increment. On the other hand, pre-harvest height growth was a relatively good predictor of post-harvest height growth, explaining more than 50% of the variation.

As with radial branch growth, the number of branches produced per whorl also responded to the higher light environment following timber harvesting, although this response was not immediate. The mean number of branches for Douglas-fir remained fairly constant for the 1987–1991 period (1.96 branches), but increased to 2.64 in 1992 and to 2.85 branches per whorl in 1993. A similar, but smaller pattern was observed for lodgepole pine with a relatively constant number of branches (1.04) being produced in the first few years, followed by an increase to 2.1 branches per whorl in 1993.

Growth changes over time

To more fully understand growth allocation response in saplings, it is also necessary to investigate growth responses over time. A comparison of growth rates demonstrates that significant growth differences occurred over time for all parts of the tree that were measured (Table 2).

Although stem growth appears to increase immediately following harvesting and to respond similarly to root growth (Fig. 3), stem growth does not significantly increase until 2 years after the treatment (polynomial orthogonal contrast: $p = 0.2935$ in the first period and $p < 0.05$ in the second period). Relative root growth did, however, increase in all post-harvest periods ($p < 0.05$). Height growth, on the other hand, decreased after harvesting, followed by a growth increase 2 years later. Height growth shock was greater in the larger seedlings than in the smaller seedlings in the first 2 years following harvest (Fig. 4, $p < 0.05$). After this initial period, height growth was the same among size classes ($p > 0.10$).

Since we hypothesized that root growth was required before an increase in aboveground growth, we also tested with a time-lag correlation whether or not there was a direct but delayed correlation between growth in roots and stem increment and subsequent growth in height or branch increment.

Table 1. Analysis of variance of mean pre- and post-harvest relative growth rate differences (A) and absolute growth rate differences (B) for different-sized individuals of Douglas-fir and lodgepole pine in different parts of the tree.

(A) Relative growth rate differences.												
	Roots			Stem			Branches			Height		
	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>
Model	11	6.9	0.0001	11	36.9	0.0001	11	1.88	0.0457	11	2.00	0.0313
Error	102			214			72			170		
Total	113			225			83			181		
SP	1	0.1	0.7515	1	6.8	0.0097	1	0.1	0.7777	1	0.5	0.4690
S	2	0.45	0.6408	2	0.5	0.6329	2	0.2	0.8031	2	1.5	0.2355
P	1	69.1	0.0001	1	383.7	0.0001	1	9.8	0.0025	1	7.1	0.0086
SP × S	2	1.0	0.3879	2	3.8	0.0244	2	1.4	0.2637	2	1.3	0.2811
SP × P	1	0.1	0.7777	1	0.1	0.8041	1	0.8	0.3897	1	3.6	0.0595
S × P	2	0.7	0.5229	2	0.1	0.8833	2	3.4	0.0375	2	1.2	0.2994
SP × S × P	2	0.7	0.5081	2	3.1	0.0416	2	0.03	0.9684	2	1.4	0.2407
(B) Absolute growth rate differences.												
Model	11	6.9	0.0001	11	35.7	0.0001	11	3.11	0.0019	11	4.53	0.0003
Error	102			214			72			170		
Total	113			225			83			181		
SP	1	0.3	0.5815	1	0.2	0.6390	1	1.7	0.1954	1	2.14	0.1420
S	2	2.7	0.0700	2	39.4	0.0001	2	7.6	0.0010	2	18.9	0.0001
P	1	67.9	0.0001	1	158.1	0.0001	1	10.8	0.0016	1	6.61	0.0110
SP × S	2	0.06	0.9437	2	4.9	0.0080	2	0.1	0.9420	2	0.44	0.6422
SP × P	1	0.03	0.9667	1	3.12	0.0799	1	3.9	0.0599	1	0.6	0.8021
S × P	2	0.85	0.9478	2	7.49	0.0007	2	0.4	0.6691	2	0.8	0.4499
SP × S × P	2	0.12	0.7616	2	1.5	0.2165	2	0.8	0.4551	2	0.27	0.7614

Note: SP, species; S, size; P, period.

A significant correlation that showed a delay, for example that height growth was correlated to root growth 2 years earlier, would demonstrate the existence of a time-dependent lag in growth. The results suggest a possible 1-year time lag between stem growth and height growth at least for a 2-year period. The stem growth increment in 1990 was positively correlated with the 1991 height growth ($R = 0.23$), and the 1991 stem growth was correlated with the 1992 height growth ($R = 0.21$). No such pattern was found between root growth and height growth. Furthermore, despite similarities in the patterns of root and stem growth, no correlation was found between these two variables. Stem growth and branch growth were found to be correlated in current years, suggesting that growth in these two parts of the tree respond to similar stimuli (Pearson correlations for stem and branch growth for 1989, 1990, 1991, and 1993 are 0.33, 0.34, 0.29, and 0.34 respectively; no significant correlation was observed in 1992, $p > 0.10$).

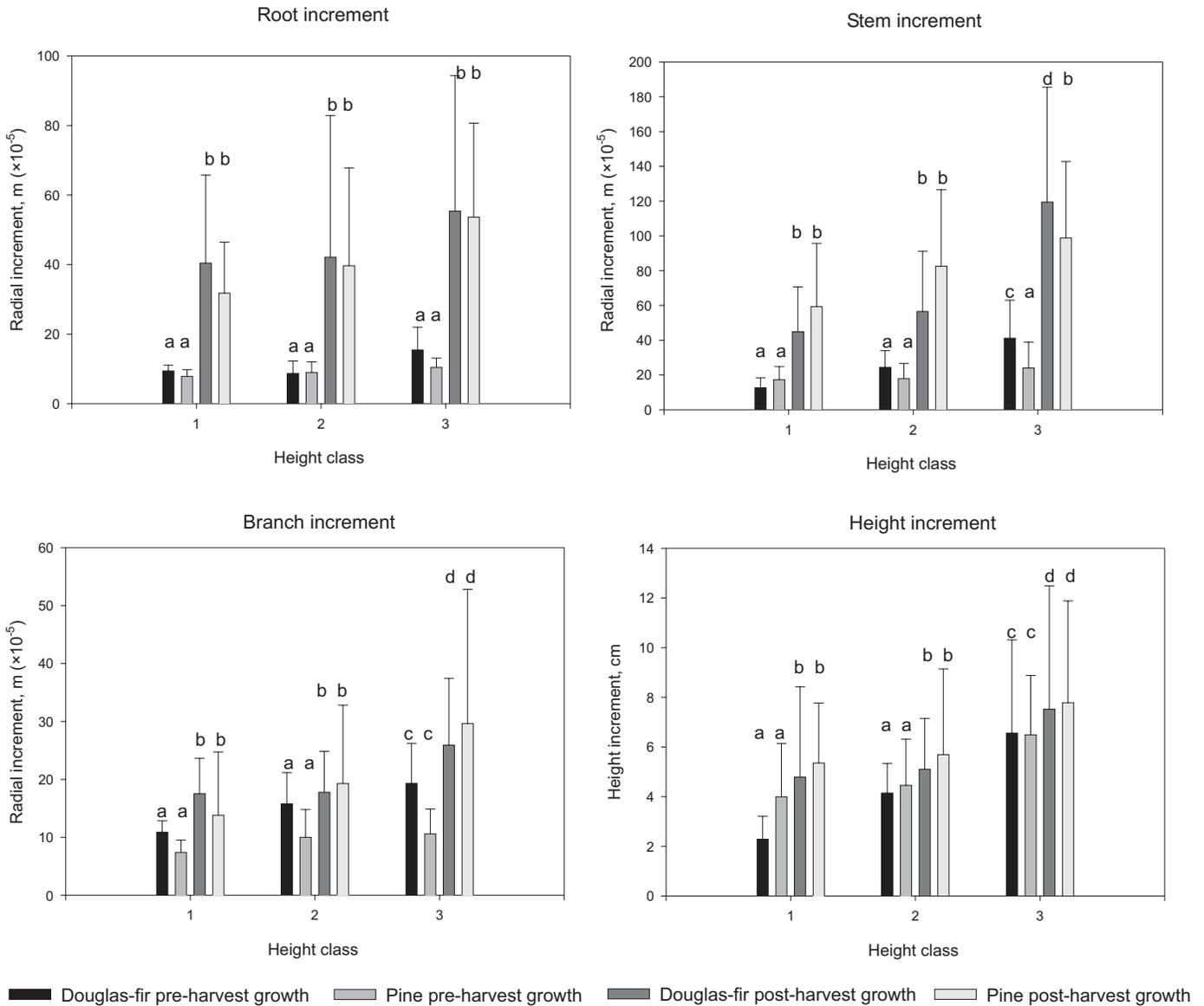
Growth differences in different parts of the tree

Roots responded immediately to overstory release with a 36% increase in growth in lodgepole pine in the first year following harvest, while stem growth and branch growth decreased. Percent stem growth follows that of root growth but to a lesser degree. The stem growth response was also generally slower in Douglas-fir than in lodgepole pine, although the medium-sized Douglas-fir responded quicker than the medium-sized pine (Table 2, year × species × size interaction; Figs. 3 and 4). Branch growth for the two species re-

sponded differently. Lodgepole pine branches grew less in the first post-harvest year than they did in the pre-harvest period, whereas Douglas-fir branches responded immediately with increased growth (Table 2, Fig. 3). Height growth, which is largely predetermined during the previous year's bud formation, remained suppressed until the third year. Overall, the greatest percent growth increase in the post-harvest period occurred in the stems, followed by the roots and then branches. Height growth was the slowest to respond to the more open conditions, but its increase was continuous, whereas growth seemed to plateau or decrease in the other parts of the tree 4 to 5 years after harvesting. Polynomial orthogonal contrasts demonstrate that growth was significantly different throughout every time period and across all positions in the tree ($p < 0.05$) except in the final time period ($p > 0.10$).

A decrease during the 1992 growing season was observed in roots and stems (Fig. 3). As this growth decrease was followed by a subsequent increase in root and stem growth, it did not seem to be associated solely with an acclimation to the new growing conditions. An investigation of climate data for the study area suggests that this growth decrease may have been due to extreme meteorological conditions occurring in 1992 (Table 3). Snow accumulation in the period from January to May was lower than in preceding years, and this was followed by below average rainfall in May, June, and July. The combination of little snow accumulation and 3 months of low rainfall would have led to dry conditions in the early part of the growing season. Temperature extremes

Fig. 1. Mean pre- and post-harvest relative growth of different parts of the tree for Douglas-fir and lodgepole pine. Columns with different letters are statistically different. Bars represent absolute height growth. Statistics are based on absolute growth.



were also experienced with frost events occurring in two of the three summer months, an anomaly not observed in any of the other study years and not recorded in the region's climatological data since 1973. Furthermore, the highest June maximum temperature in the region's 35-year weather record (1960–1995) also occurred in 1992, which may have exacerbated the drier than normal moisture conditions.

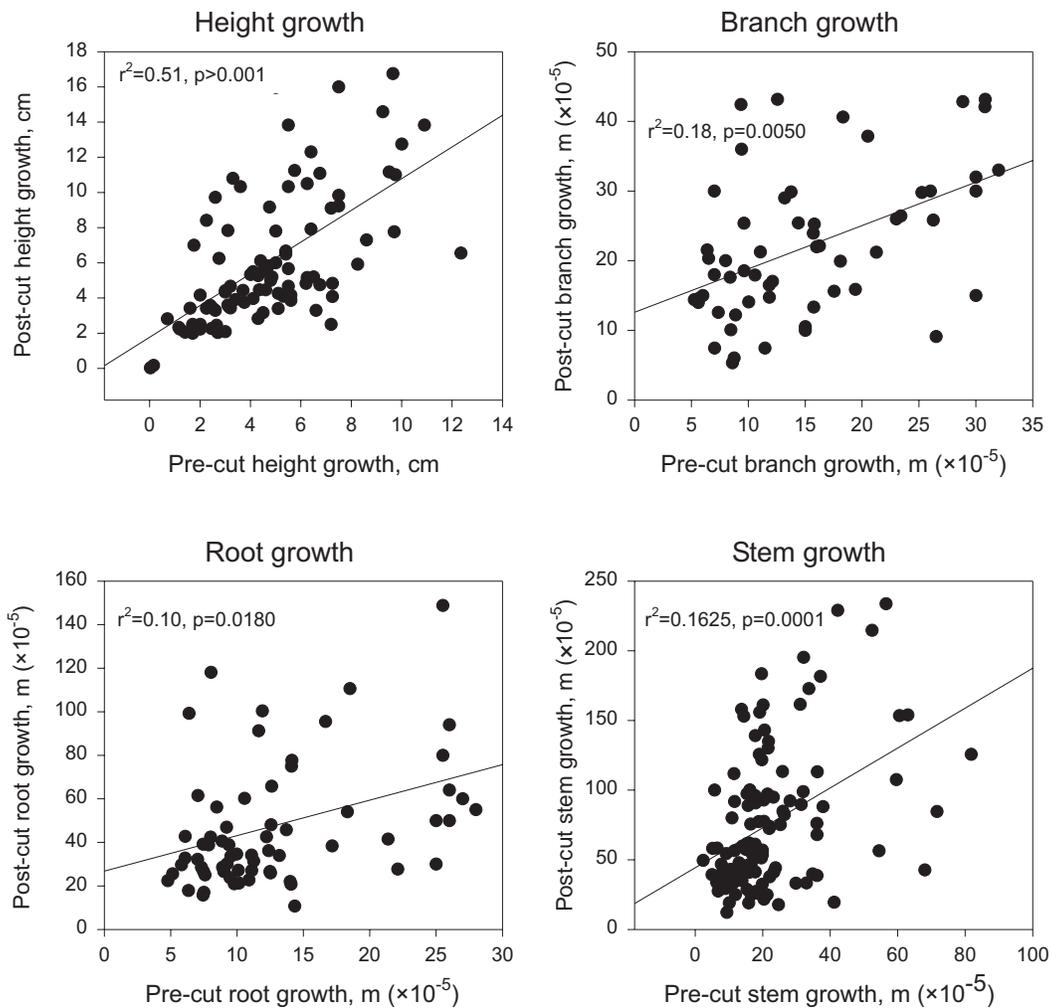
Discussion

Tree response to different treatments consisting of varying degrees of canopy removal is a well-studied phenomenon in many different forest ecosystems (Coates and Burton 1999; Kneeshaw et al. 1998; Sundkvist 1994; Stone and Wolfe 1996; Prévost 1997; Oliver and Dolph 1992). Growth reductions in height or in radial stem growth following harvesting have been noted in studies of different species in different

regions (Staebler 1954; Yang 1988; Youngblood 1991; Sundkvist 1994; Urban et al. 1994). In the present study, a 1-year reduction in stem radial growth and a delayed height reduction that lasted until the third post-harvest year were observed in both Douglas-fir and lodgepole pine. Murphy et al. (1999) also note that lodgepole pine experienced a 3-year growth lag before responding to overstorey removal, and a 2- to 4-year delay has been noted for Douglas-fir (McCaughy and Ferguson 1988).

Size-class differences

We did not measure photosynthetic rate differences before and after the release. However, if there were large differences in the photosynthetic production after cutting, these should have been reflected in response differences between the larger and smaller seedlings. Larger individuals have a greater share of their active biomass in nonproductive tissue

Fig. 2. Relationships between pre- and post-harvest growth. Nontransformed data are presented.

(Messier et al. 1999). Since it could be assumed that the respiration rate of the biomass would not decrease as a result of release, the decreasing photosynthetic rate would lead to a diminishing carbon balance and decreasing growth. Our first hypothesis, as also suggested by Staebler (1954), is that this would show up more clearly in larger than in smaller seedlings.

We, however, observed no pre- and post-harvest differences in growth between size classes in terms of relative growth. However, temporally the larger individuals experience a greater growth shock in the first post-harvest growing period than do the smaller individuals (Table 2, Fig. 4). This continues for the subsequent year in lodgepole pine, while the larger Douglas-fir saplings rejoin the growth curves of the smaller Douglas-fir saplings. Murphy et al. (1999) also report that the smaller lodgepole pine seedlings respond better to overstory removal than do the larger ones. Douglas-fir supports a greater number of branches and thus has a greater photosynthetic tissue to nonphotosynthetic tissue ratio than pine. This observation suggests that part of the growth shock may indeed be due to a greater respiration stress (McCaughey and Ferguson 1988). Earlier studies of individuals with varying degrees of live crown ratio also confirm this finding, as large individuals with small live

crowns had a lower growth response than the same-sized individuals with deeper crowns (Emmingham 1983; Ruel et al. 2000).

In various studies of understory release response, different growth variables (biomass, height growth vs. diameter growth, relative vs. absolute growth, etc.) and different periods of time following the interventions are reported. Researchers often present results using some relative form of growth to avoid interpretations that are based solely on the fact that larger trees have a greater growth potential than smaller trees (South 1995; Brand 1986). However, relative growth is often more difficult to interpret and thus has little practical value to foresters. Our study illustrates the effect of the greater growth potential of the larger individuals in terms of greater post-harvest stem growth although such differences were not observed in other parts of the trees.

Hydraulic capacity

We also hypothesized that release would need to be reflected in the hydraulic architecture of tree seedlings. Sellin (1997) observed that the total transport resistance was higher in understory Norway spruce (*Picea abies* (L.) Krast.) than in corresponding open-grown seedlings. It has been proposed that stomatal closure would occur when the transpira-

Table 2. Multivariate repeated measures analyses of relative growth rate differences for different-sized individuals of Douglas-fir and lodgepole pine conducted separately for the different parts of the tree.

	Roots			Stem			Branches			Height		
	df	F	p	df	F	p	df	F	p	df	F	p
Y	5 (47)	28.3	0.0001	5 (103)	95.0	0.0001	5 (32)	28.4	0.0001	5 (81)	42.8	0.0001
Y × SP	5 (47)	1.6	0.1760	5 (103)	1.6	0.1285	5 (32)	8.0	0.0002	10 (162)	4.7	0.0652
Y × S	10 (94)	0.8	0.6688	10 (206)	1.5	0.1535	10 (64)	4.1	0.0001	5 (81)	1.8	0.0008
Y × SP × S	10 (94)	0.6	0.8100	10 (206)	2.2	0.0196	10 (64)	1.5	0.1559	10 (162)	1.0	0.4344

Note: The df in parentheses are those for the Wilk's λ denominator. Y, year; SP, species; S, size.

Fig. 3. Percent change in radial root increment, radial increment of the base of the stem, branch radial increment, and height growth through leader elongation in Douglas-fir and lodgepole pine following harvesting.

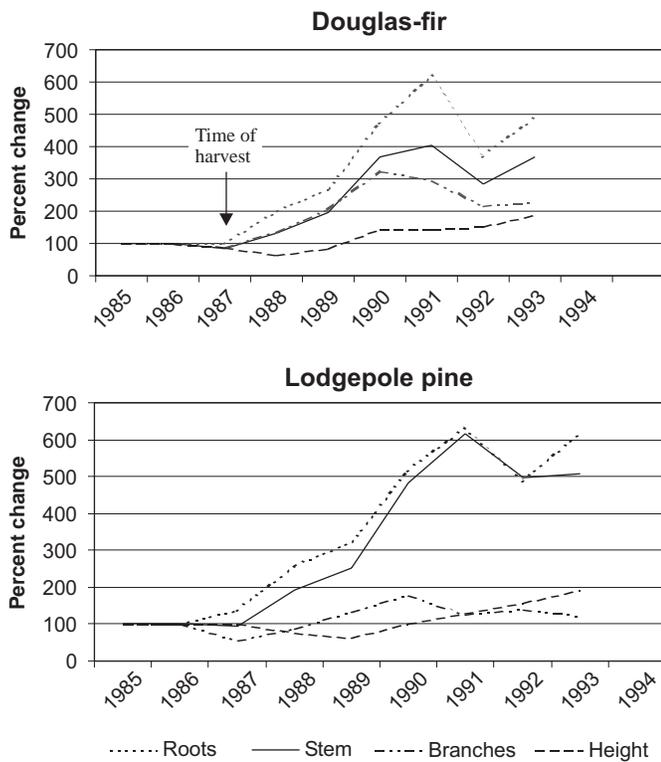
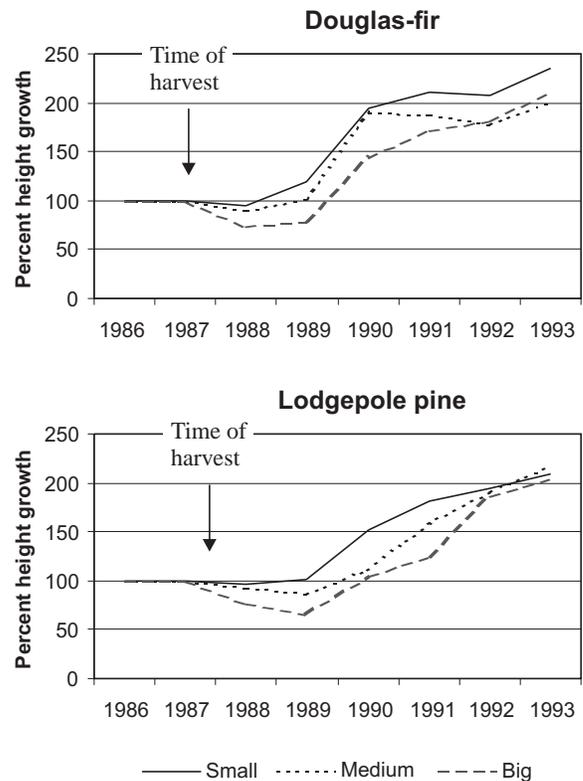


Fig. 4. Changes in the percent height growth of different-sized seedlings of Douglas-fir and lodgepole pine. Significant differences between growth occurred between the largest seedlings and the other two classes until 1989 (polynomial orthogonal contrasts: $p = 0.0025$).



tion demand exceeded the transport capacity of the seedling (Williams et al. 1996; Maherali et al. 1997). Upon release, the transpirational demand of the seedlings increases because of higher irradiance (Nobel 1999). Assuming that the sensitive stomatal closure in understory seedlings is due to insufficient transport capacity in the seedlings, then they would continue to rapidly close their stomata with increasing vapor pressure deficit, even if the soil moisture situation is temporarily better after the removal of the main canopy trees (Sellin 1997). The transport path conductivity depends on wood permeability, conducting area, and transport distance. As the understory seedlings are released, a considerable net gain in carbon could be achieved if stomata would remain open for longer periods.

We observed strong and immediate increases occurring first in root growth followed by a very clear response in stem growth. This supports the hypothesis that seedling

growth responds to the transport demand (Magnani et al. 2000). The root system has a large contribution to flow resistance (Running 1980; Sperry et al. 1998) and is most likely the biggest limitation to water transport in the relatively under-developed root system of the understory seedlings (Wang et al. 1994; Canham et al. 1996). The rapid stem thickness growth that follows also increases the total path conductivity. Height growth resumed after a balance was achieved in these two compartments. It could be that new height growth was only possible after the hydraulic conductivity of other tree parts allowed sufficient water flow without excessively high water tensions developing in the shoots.

In principle, we could expect to observe stronger growth response in roots and stem and more delayed height growth

Table 3. Climate information for the study site (data are from Environment Canada).

	Snow (cm)	Rain (mm)			
	January–May	May	June	July	August
1984	-14.6	+1.8	+24.0	-9.3	+2.2
1985	+7.7	-21.7*	+8.2	-45.5*	-19.4
1986	-32.3	+12.0	-10.7	+14.8	-19.3
1987	-49.7*	+5.1	-26.7	-4.5	-5.8
1988	-2.8	+13.2	-25.0	-15.9	+35.5
1989	-23.9	+31.6	+1.0	-7.8	+79.8
1990	-2.1	+2.8	+8.0	-9.6	-15.8
1991	-19.5	-12.7	+24.9	+5.3	-5.8
1992 ^a	-31.8*	-7.9*	-12.6*	-15.2*	+0.8
1993	-32.8*	+16.3	+2.4	+53.4	+19.5
1994	+10.2	-4.9	+38.1	-23.8	-17.6
Mean (mm)	100.7	32.9	46.8	51.1	44.5

Note: Data for each year are presented as being above (+) or below (-) the overall mean normally associated with that period to highlight years with extreme meteorological conditions. Numbers with asterisks represent extreme values. It can be noted that 1992 was a year with many extreme conditions.

^aIn 1992, two of the three growing season months experienced below zero temperatures. In this same year a 35 year high June maximum temperature was achieved. The only other presented year with a below zero growing season temperature was in 1984 for the month of June.

in large versus small seedlings, since the total seedling conductivity is inversely proportional to the transport distance, i.e., the seedling height. On the other hand, it has often been observed that wood permeability increases with increasing tree size (Mencuccini et al. 1997; Maherali et al. 1997). As mentioned above, over the entire observation period few differences among seedlings of different sizes were observed (only for height growth in the first period). So, if hydraulic capacity limited production, it would be equally strong in small and large seedlings. However, dynamically the growth reduction was stronger and lasted longer in large versus small seedlings. The small differences observed may indicate that all seedlings were still able to respond positively to the canopy opening, and that greater size differences would be required to see real variation.

Functional balance

According to the functional balance theory, an opening in the canopy would alter the resource that was limiting the growth of understory seedlings, and the seedlings would thus change their growth pattern to restore a new functional balance among different parts of the tree. The immediate reduction in height growth that we observed took place with a concurrent increase in root growth. Height growth was restored only after considerable root growth had taken place. This tends to suggest that aboveground reductions in growth rate are not caused by decreasing productivity, but are instead a result of allocational changes in seedlings. Sims et al. (1994) reported that in the shade-adapted *Alocasia macrorrhiza*, the photosynthetic capacity, on an area basis, is similar for shade-acclimated and sun-grown seedlings, and that the actual performance differences in sun and shade are connected to seedling architecture and growth pattern changes.

Our data show quite convincingly for the studied site that in both species and in all size classes the reduction in aboveground growth is not repeated below ground. Instead root

growth is immediately stimulated, increasing in the first post-harvest growing season and continuing for 5 years. It has also been noted elsewhere that lodgepole pine root growth is stimulated by increased light and photosynthetic activity (Carlson 1976). An immediate increase in root growth (Fig. 3) supports our hypothesis that released individuals initially allocate growth to belowground tissues. Greater root growth will lead to a more extensive root system, which will permit greater water and nutrient uptake. This will allow higher stomatal conductivity and photosynthetic productivity. If this factor is indeed the primary cause of growth shock, it should be expected to have a greater impact in drier environments or in harvesting operations that lead to a greater change in exposure (such as clearcuts). Urban et al. (1994), working in a relatively dry region of northern Alberta, also noted a delay of 4 years in radial stem growth and higher radial growth in roots than in trunks for 9 years. The bigger difference that they noted may be due to the greater degree of exposure of the trees in their study when compared with the smaller change following the partial cuts in our study. This can be contrasted with a study in eastern Canada where small cuts in a relatively humid area did not result in immediate aboveground reductions in height growth (Kneeshaw et al. 1998). It has been suggested that releasing advance growth is best applied in ecosystems with abundant moisture (McCaughey and Ferguson 1988).

The combination of the sudden reduction in height growth lasting a few years, immediate root growth, and 1-year delay in stem growth following partial cutting suggests that on this dry site, trees are both limited in water availability (so the tree invests rapidly in belowground growth) and constrained in their ability to move water (so that the trees must invest fairly rapidly in producing more conducting tissue in the stem). Furthermore, the lack of a relationship between height growth reduction and root growth further suggests that these trees do not reduce height growth because of a lack of carbon, but rather as a result of the tree's inability to provide

enough water to the foliage. Only when the tree has produced enough new fine roots and conducting tissue, can the tree then respond by increasing height growth.

Silvicultural implications of the findings

Observed periods of reduced height growth (growth shock) in seedlings and saplings following overstorey removal appear to be linked to moisture-related stress. Our results of the post-release growth response would agree with Sellin's (1997) observation that understory seedlings are limited because of insufficient capacity to take up and transport water. Although the period of growth shock was relatively short in this study, increased root growth was observed for at least 5 years following harvesting. It is speculated that changes in growth allocation patterns from aboveground tissues to belowground tissues should vary with climate and degree of overstorey removal. Delays in aboveground growth response should be longer in drier sites and stands with greater overstorey removal than in moister sites or those harvested using partial cutting techniques. Forest managers should therefore consider the choice of silvicultural system to minimize delays in seedling response. However, the size of seedlings, when similar to those in this study, need not be of concern, as seedlings of all size classes will respond with the same proportional growth rate. There were some signs that only the largest lodgepole pine seedlings may experience some problems in responding positively to canopy openings. Care must, however, be taken in the generalization of these results as they come from only one site and, because of the laborious nature of the work, the sample size is limited.

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References

- Annas, R., and Coupé, R. 1979. Biogeoclimatic zones and sub-zones of the Cariboo Forest Region. B.C. Ministry of Forests, Victoria, B.C.
- Beaudet, M., and Messier, C. 1998. Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. *Can. J. For. Res.* **28**: 1007–1015.
- Björkman, O. 1981. Responses to different quantum flux densities. *In* Encyclopedia of plant physiology. New Ser. Vol. 12A. *Edited by* O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler. Springer Verlag, Berlin. pp. 57–197.
- Brand, D.G. 1986. A competition index for predicting the vigour of planted Douglas-fir in southwestern British Columbia. *Can. J. For. Res.* **16**: 23–29.
- Brouwer, R. 1962. Distribution of dry matter in the plant. *Neth. J. Agric. Sci.* **10**: 361–376.
- Canham, C.D., Nerkowitz, A.R., Kelly, V.R., Lovett, G.M., Ollinger, S.V., and Schurr, J. 1996. Biomass allocation and multiple resource limitation in tree seedlings. *Can. J. For. Res.* **26**: 1521–1530.
- Carlson, L.W. 1976. Root initiation of lodgepole pine and white spruce seedlings grown under varying light conditions. Northern Forest Research Centre, Environment Canada, Forestry Service. *Bi-Monthly Res. Notes* 32. pp. 21–23.
- Coates, D.K., and Burton, P.J. 1999. Growth of planted seedlings in response to ambient light levels in northwestern interior cedar-hemlock forests of British Columbia. *Can. J. For. Res.* **29**: 1374–1382.
- Doucet, R., and Boily, J. 1995. Croissance en hauteur de la régénération d'épinette noire et de sapin baumier après la coupe. Ministère des Ressources naturelles du Québec, Québec. Note Rech. 68.
- Emmingham, W. 1983. Thinning: an important timber management tool. The woodland workbook. Oregon State University, Corvallis, Ore. Pac. Northwest Ext. Publ. 184.
- Environment Canada. 1994. Canadian climate data for Williams Lake. Atmosphere and Environment Service, Environment Canada, Ottawa, Ont.
- Evans, J.R. 1987. The relationship between electron transport components and photosynthetic capacity in pea leaves grown at different irradiances. *Aust. J. Plant Physiol.* **14**: 157–170.
- Ferguson, D.E., and Adams, D.L. 1980. Response of advance grand fir regeneration to overstorey removal in northern Idaho. *For. Sci.* **26**: 537–545.
- Ghent, A.W. 1958. Studies of regeneration in forest stands devastated by the spruce budworm. II. Age, height growth and related studies of balsam fir seedlings. *For. Sci.* **4**: 135–146.
- Gordon, D. 1973. Released advance reproduction of white and red fir. USDA For. Serv. Res. Pap. PSW-95.
- Hatcher, R.J. 1964. Balsam fir advance growth after cutting in Quebec. *For. Chron.* **40**: 86–92.
- Hopwood, D. 1990. Shade tolerance of Douglas-fir in the CDF/fd-Oregon Grape Site Association: a pilot study. B.Sc. thesis, University of British Columbia, Victoria, B.C.
- Kellomäki, S., and Oker-Blom, P. 1981. Specific needle area of Scots Pine and its dependence on light conditions inside the canopy. *Silva Fenn.* **15**: 190–198.
- Kneeshaw, D.D., Bergeron, Y., and Degrandpré, L. 1998. Early seedling response of *Abies balsamea* to artificially created gaps. *J. Veg. Sci.* **9**: 543–550.
- Larcher, W. 1995. Physiological plant ecology: ecophysiology and stress physiology of functional groups. Springer-Verlag, Berlin.
- Magnani, F., Mencuccini, M., and Grace, J. 2000. Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. *Plant Cell Environ.* **23**(3): 251–264.
- Maherali, H., DeLucia, E.H., and Sipe, T.W. 1997. Hydraulic adjustment of maple saplings to canopy gap formation. *Oecologia*, **112**: 472–480.
- McCaughey, W.W., and Ferguson, D.E. 1988. Response of advance regeneration to release in the inland mountain west: a summary. *In* Future Forests of the Mountain West: A Stand Culture Symposium. *Proceedings. Edited by* W.C. Schmidt. USDA For. Serv. Gen. Tech. Rep. INT 243. pp. 255–266.
- Meidinger, D., and Pojar, J. 1991. Ecosystems of British Columbia. B.C. Ministry of Forests, Victoria, B.C. Spec. Rep. Ser. 6.
- Mencuccini, M., Grace, J., and Fiovaranti, M. 1997. Biomechanical and hydraulic determinants of tree structure in Scots pine: anatomical characteristics. *Tree Physiol.* **17**: 105–113.

- Messier, C., and Puttonen, P. 1995. Growth, biomass and morphological responses of *Betula pubescens* and *B. pendula* to shade in developing Scots pine stands. *Can. J. For. Res.* **25**: 629–637.
- Messier, C., Doucet, R., Ruel, J.-C., Claveau, Y., Kelly, C., and Lechowicz, M. 1999. Functional ecology of advance regeneration growth and survival up to pole-size in coniferous boreal forests. *Can. J. For. Res.* **29**: 812–823.
- Murphy, T.E.L., Adams, D.L., and Ferguson, D.E. 1999. Response of advance lodgepole pine regeneration to overstory removal in eastern Idaho. *For. Ecol. Manage.* **120**: 235–244.
- Newsome, T., Sutherland, C., and Vyse, A. 1990. Establishing Douglas-fir plantations in the dry belt of interior B.C. B.C. Ministry of Forests Bull.
- Niinemets, Ü., and Kull, O. 1995a. Effects of light availability and tree size on the architecture of assimilative surface in the canopy of *Picea abies*: variation in needle morphology. *Tree Physiol.* **15**: 307–315.
- Niinemets, Ü., and Kull, O. 1995b. Effects of light availability and tree size on the architecture of assimilative surface in the canopy of *Picea abies*: variation in structure. *Tree Physiol.* **15**: 791–798.
- Nobel, P.S. 1999. *Physicochemical and environmental plant physiology*. 2nd ed. Academic Press, San Diego, Calif.
- Oker-Blom, P., and Smolander, H. 1988. The ratio of shoot silhouette area to total needle area in Scots Pine. *For. Sci.* **34**: 894–906.
- Oliver, W.W., and Dolph, K.L. 1992. Mixed-conifer seedling growth varies in response to overstory release. *For. Ecol. Manage.* **48**: 179–183.
- Prévost, M. 1997. Effects of scarification on seedbed coverage and natural regeneration after a group seed-tree sutting in a black spruce (*Picea mariana*) stand. *For. Ecol. Manage.* **94**: 219–231.
- Ruel, J.-C., and Doucet, R. 1998. Élaboration de classes de qualité pour les inventaires de régénération. Ministère des Ressources naturelles du Québec, Québec. Note Rech. For. 91.
- Ruel, J.-C., Messier, C., Doucet, R., Claveau, Y., and Comeau, P. 2000. Morphological indicators of response to overstory removal for boreal conifer trees. *For. Chron.* **76**: 633–642.
- Running, S.W. 1980. Field estimates of root and xylem resistances in *Pinus contorta* L. using excision. *J. Exp. Bot.* **31**: 555–569.
- SAS Institute Inc. 1998. SAS/STAT™ user's guide, version 6.12 ed. SAS Institute Inc., Cary, N.C.
- Sellin, A. 1997. Variation in shoot water status of *Picea abies* (L.) Karst. trees with different life histories. *For. Ecol. Manage.* **97**: 53–62.
- Sims, D.A., and Pearcy, R.W. 1994. Scaling sun and shade photosynthetic acclimation of *Alocasia macrorrhiza* to whole plant performance—I. Carbon balance and allocation at different daily photon flux densities. *Plant Cell Environ.* **17**: 881–887.
- Sims, D.A., Gebauer, R.L.E., and Pearcy, R.W. 1994. Scaling sun and shade photosynthetic acclimation of *Alocasia macrorrhiza* to whole plant performance—II. Simulation of carbon balance and growth at different photon flux densities. *Plant Cell Environ.* **17**: 889–900.
- South, D.B. 1995. Relative growth rates: a critique. *S. Afr. For. J.* **172**: 43–48.
- Sperry, J.S., Adler, F.R., Campbell, G.S., and Comstock, J.P. 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant Cell Environ.* **21**: 347–359.
- Staebler, G. 1954. Evidence of shock following thinning of young Douglas-fir. *J. For.* **54**(5): 339.
- Steen, O., and Coupé, R. 1989. A field guide for the identification and interpretation of ecosystems of the Cariboo Forest Region. B.C. Ministry of Forests, Victoria, B.C.
- Steen, O., Stathers, R., and Coupé, R. 1990. Identification and management of summer frost-prone sites in the Cariboo Forest Region. Canada – British-Columbia Forest Resource Development Agreement. B.C. Ministry of Forest, Victoria, B.C. FRDA Rep. 157.
- Stone, W.E., and Wolfe, M.L. 1996. Response of understory vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. *Vegetatio*, **122**: 1–12.
- Sundkvist, H. 1994. Initial growth of *Pinus sylvestris* advance reproduction following varying degrees of release. *Scand. J. For. Res.* **9**: 360–366.
- Tucker, G.F., Hinckley, T.M., Leverenz, J.W., and Jiang, S.M. 1987. Adjustments of foliar morphology in the acclimation of understory Pacific Silver fir following clearcutting. *For. Ecol. Manage.* **21**: 249–268.
- Tyree, M.T., and Sperry, J.S. 1989. Vulnerability of xylem to cavitation and embolism. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **40**: 19–38.
- Urban, S., Lieffers, V., and Macdonald, S. 1994. Release in radial growth in the trunk and structural roots of white spruce as measured by dendrochronology. *Can. J. For. Res.* **24**: 1550–1556.
- Wang, G.G., Qian, H., and Klinka, K. 1994. Growth of *Thuja plicata* seedlings along a light gradient. *Can. J. Bot.* **72**: 1749–1757.
- Weetman, G., and Vyse, A. 1990. Natural Regeneration. Chap. 10. *In Regenerating British Columbia's forests. Edited by D.P. Lavender.* UBC Press, Vancouver, B.C. pp. 188–130.
- Williams, M., Rastetter, E.B., Fernandes, D.N., Goulden, M.L., Wofsy, S.C., Shaver, G.R., Melillo, J.M., Munger, J.W., Fan, S.-M., and Nadelhoffer, K.J. 1996. Modelling the soil–plant–atmosphere continuum in a *Quercus–Acer* stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant Cell Environ.* **19**: 911–927.
- Yang, R.C. 1988. Growth response of white spruce to release from trembling aspen. *Can. For. Serv. North. For. Cent. Inf. Rep. NOR-X-302*.
- Youngblood, A.P. 1991. Radial growth after a shelterwood cut in a mature stand of white spruce. *Can. J. For. Res.* **21**: 410–413.
- Zimmermann, M.H. 1983. *Xylem structure and the ascent of sap.* Springer-Verlag, Berlin, Heidelberg.