Relationships between root form and growth, stability, and mortality in planted versus naturally regenerated lodgepole pine in north-central British Columbia

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Abstract: The roots of container-grown and manually planted lodgepole pine, *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm., are often deformed, potentially impacting their health relative to that of naturally regenerated trees. We evaluated 12 root characteristics to elucidate the type and severity of root deformities in planted pine aged 3–10 years, as well as to determine the impact of root form on their growth and stability. Results showed that root deformity is widespread: 95.0% of planted trees versus 50.9% of naturally regenerated trees had either moderate or severe root deformities. A logistic regression using the 12 root characteristics strongly distinguished between planted and naturally regenerated trees. Aboveground growth form was affected in that planted trees had a lower height-to-diameter ratio than naturally regenerated trees. In young planted trees with low or moderate root deformities, but not in trees with severely deformed roots (65.0% of all planted trees in our study), both height- and diameter-growth rates were higher than in naturally regenerated trees. Growth differences may be attributed to differential resource allocation resulting from translocation inhibition caused by root deformation. In spite of very different root systems, there was no difference in the horizontal stability of planted versus naturally regenerated trees. However, planted trees have a significantly lower root cross-sectional area and may therefore be at a higher risk of mortality, primarily from attack by the Warren root collar weevil, *Hylobius warreni* Wood.

Résumé : Les racines des pin tordu latifolié, *Pinus contorta* Dougl. ex Loud. cultivés en récipients et plantés à la main sont souvent déformées, ce qui pourrait affecter la santé de ces arbres comparativement à ceux qui sont issus de la régénération naturelle. Nous avons évalué 12 caractéristiques des racines pour connaître le type et la sévérité des déformations racinaires chez des pins âgés de trois à 10 ans qui ont été plantés et pour déterminer l'impact de la forme des racines sur leur croissance et leur stabilité. Les résultats montrent que les déformations racinaires sont très fréquentes : 95 % des arbres plantés comparativement à 50,9 % des arbres issus de la régénération naturelle avaient des déformations racinaires modérées ou sévères. Une régression logistique avec les 12 caractéristiques des racines distingue nettement les arbres plantés de ceux qui sont issus de la régénération naturelle. La forme de la croissance aérienne était affectée par le fait que les arbres plantés avaient un rapport hauteur:diamètre plus faible que les arbres issus de la régénération naturelle. Chez les jeunes arbres plantés qui avaient des déformations racinaires légères à modérées, les taux de croissance en hauteur et en diamètre étaient plus élevés que chez les arbres issus de la régénération naturelle mais ce n'était pas le cas des arbres dont les racines étaient sévèrement déformées, soit 65 % de tous les arbres plantés dans notre étude. Les différences de croissance peuvent être attribuées à une allocation différente des ressources provoquée par une inhibition de la translocation causée par la déformation des racines. Malgré un système racinaire très différent, il n'y avait pas de différence dans la stabilité horizontale entre les arbres plantés et les arbres issus de la régénération naturelle. Cependant, la surface transversale des racines est significativement plus faible chez les arbres plantés qui ont par conséquent plus de chances de mourir, surtout à la suite d'une attaque du charançon de Warren (*Hylobius warreni* Wood).

[Traduit par la Rédaction]

Introduction

Lodgepole pine, *Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm., is an important, widely planted commercial species in the interior of British Columbia. The number of planted lodgepole pine seedlings in British Columbia was 25 million in 1981–1982, peaked at 107 million in 1995–1996 (http://www.for.gov.bc.ca/hfp/publications/00001/2-1-3i-silv-plant-species.htm), and was 83 million in 2003–2004 (http://www.for.gov.bc.ca/hfd/pubs/docs/mr/annual/ar_2003–04/tables/t2_4.pdf). Over 42 million lodgepole pine seedlings (51% of all lodgepole pine planted in British Columbia) were planted

Received 26 October 2005. Accepted 31 May 2006. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 2 November 2006.

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Can. J. For. Res. **36**: 2642–2653 (2006) doi:10.1139/X06-146

in the Northern Interior Forest Region of British Columbia in the 2003–2004 season alone (http://www.for.gov.bc.ca/hfd/pubs/docs/mr/annual/ar_2003–04/tables/t2_4.pdf).

An outbreak of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, affecting 8.7 million ha of forest in 2005 (Westfall 2006) has led to accelerated rates of harvesting (Niemann 2005), and as a result a substantial increase in the need for reforestation is anticipated. The British Columbia Government has allocated $86 million to a special "Forests for Tomorrow" program targeting reforestation and management of areas impacted by fire and mountain pine beetle (British Columbia Ministry of Forests 2005). Consequently, pine regeneration issues remain extremely important in British Columbia as the resulting clearcuts are regenerated. This is particularly true in the Prince George Forest District, where some of the highest levels of mountain pine beetle-caused mortality have occurred (Canadian Forest Service 2005).

The root form of artificially regenerated (hereinafter "planted") lodgepole pine trees has been shown to be different from that of naturally regenerated (hereinafter "natural") trees (Halter and Chanway 1993; Halter et al. 1993; Krasowski 2003). The root form of a planted tree is a function of nursery practices used to produce the seedling as well as the method of planting used (Harrington and Howell 1998). It has long been thought that dramatic differences in the root form of planted trees affect their development. Hay and Woods (1974) suggested that increased carbohydrate and plant hormone accumulation above root deformities could stimulate stem and foliage growth. Roots spiraling around the circumference of the tree, or bent into a "J" or "L" shape, have also been shown to act as physical barriers to translocation into the root system, which can affect plant growth and development (Grene 1978; Hay and Woods 1978). Coutts (1987) reported that the process of root formation is a result of chemical signaling between the shoot and root, and that root signaling is affected by root form. He suggested that root activity could be reduced by root injury or bending and this, in combination with signals from the shoot, can affect the number of roots formed and the location of root primordia.

Because of the probable link between root form and planted tree growth, there have been several studies on the effect of root form on survival and aboveground growth, which have yielded varying results. It has been suggested that initial root habit is a determining factor in the survival and development of an individual tree (Toumey 1929, cited in Preston 1942). Rudolph (1939) reported a decrease in growth of trees with cramped root systems. Conversely, Hay and Woods (1974) showed that loblolly pine, *Pinus taeda* L., saplings with severe root deformation had larger aboveground dry mass than trees with better root form. A later paper by Woods (1980) showed that 7-year-old loblolly pines with bent, balled, or slanted roots did not exhibit reduced aboveground growth or survival. However, Burdett (1979) showed that early survival of planted lodgepole pine was dependent on root growth capacity, and Harrington and Howell (1998) found a 58% decrease in yield index in loblolly pines with deformed or pruned taproots 3 years after planting relative to that of trees with straight roots. Halter et al. (1993) found that 12-year-old natural lodgepole pine trees were significantly taller and showed significantly higher growth rates than planted trees.

Root form may also affect the stability of planted conifers. Coutts and Lewis (1983) suggested that major structural roots in Sitka spruce, *Picea sitchensis* (Bong.) Carr., are established during the first 8 years of tree development. Burdett et al. (1986) further emphasized the importance of lateral-root growth to prevent toppling of planted pine. Krasowski et al. (1996) evaluated the effect of stock type, tree density, and slope position on stability of lodgepole pine seedlings in the central interior of British Columbia. They suggested that horizontal tree stability is likely a function of tree density, tree size, and distribution of lateral and sinker roots. Lindström and Rune (1999) found that natural Scots pine, *Pinus sylvestris* L., were more stable than planted container-grown trees. Thus, in planted trees, root form appears to affect normal development processes, but the association of particular root characteristics with growth parameters has not been established.

This study was designed to determine the extent and severity of root deformation in planted relative to natural lodgepole pine in the Prince George area of British Columbia. The objectives were to identify the differences in root form between planted and natural trees using 12 different characteristics, and to associate the effect of particular root forms with growth parameters, stability, and mortality in planted versus natural lodgepole pine.

Materials and methods

Site selection

Potentially suitable lodgepole pine stands 3–10 years old were identified from a Canadian Forest Products Ltd. inventory database. Trees older than 10 years were deemed too difficult to excavate for root examination. The distances between sites ranged from 1.5 to 231 km, with an average distance of 95 km. All of the sampled stands were located within 300 km of the city of Prince George. Each stand was visited to ensure that some planted trees and some natural trees were present. Each sample tree was categorized as planted or natural based on the presence or absence of plug material (i.e., mica, vermiculite, or perlite remnants attached to the root system).

A total of 16 stands were sampled. The first set of eight stands was artificially regenerated ("planted"), with some ingress of natural regeneration. Six of these stands were sampled between 15 July and 31 August 2002. The remaining two were sampled between 1 May and 15 May 2003. These eight stands were located north of Prince George (UTM Zone 10, N 6010315–6077135, E 456592–492898), and all were in the sub-boreal spruce biogeoclimatic zone (Meidinger et al. 1991) in the moist cool subzone (mk1; DeLong et al. 1993). After sampling we found that the natural-ingress trees were often smaller and younger than the planted trees. Therefore, a second set of stands (fill-planted stands) was identified for study where the natural trees would be the same size or larger than the planted trees. Fill-planted stands are predominantly naturally regenerated, but are supplemented with planted trees to meet stocking requirements. All of the fill-planted stands sampled were located southwest of Prince George (UTM Zone 10, N 5846071–5947380, E 461656–509303) in the dry warm subzone (dw 2/3; DeLong et al. 1993) of the sub-boreal spruce biogeoclimatic zone (Meidinger et al. 1991). All eight fill-planted stands were sampled between 1 June and 31 August 2003. The fill-planted stands could not be chosen from the same ecosystem as the planted stands because fill-planting is rarely conducted around Prince George, so few sites were available for study.

Sampling design

Data were collected in circular 3.99 m radius (50 m^2) plots along north–south transects. Each transect originated from a randomly chosen point. Plots were systematically chosen along the transect lines for detailed data collection. Sample plots were located at least 150 m apart along each transect. A minimum of 4 and a maximum of 20 detailed plots were completed for each site, for a total of 104 plots in the first set of eight stands and 123 in the second set of eight stands.

One planted and one natural tree were randomly chosen within each 50 m^2 plot for data collection to rule out any effects of competition and stand history. The randomly chosen sample trees were measured for aboveground growth parameters, tree stability, and root development. Any dead trees (defined as having no new growth in the current year) in the plot were excavated, classified by cause of death (if possible), and analyzed for root form and distribution.

Aboveground measurements

Sample trees were measured for diameter at stump height (30 cm above the root collar), height, and current year's and previous year's leader growth. Diameter at stump height was used to ensure that any swelling present at the root collar due to poor root form did not skew tree growth data. The height-to-diameter ratio was calculated to correct for effects of the relatively large differences in tree size found over the age classes sampled.

Tree-stability assessment

Before excavation, sample trees were tested for stability using a hanging scale to measure the horizontal force (kg) required to displace the main stem 10° from vertical (Burdett 1978). For this study we used a hanging scale measuring up to 25 kg. The force was applied at stump height (30 cm above the root collar). The 10° angle of displacement was determined using a hinged measuring stick. The force was consistently applied by pulling the tree to the west. After a tree is displaced once, its stability is reduced, therefore each tree was pulled once in only one direction.

Root-morphology assessment

Coarse-root structure and root development were assessed after excavation of the woody root system. Sample trees were cut ca. 5 cm above the root collar and approximate age was determined from the growth rings counted on the cut surface.

Roots were cleaned and each root mass was photographed from two angles 90° apart, as well as from the top. The top-view pictures were divided into six radial sections and the lateral roots (hereinafter "laterals") were counted in each section (Van Eerden 1978). If a lateral curved into more than one section, it was included in the section where it intersected a hypothetical 10 cm diameter sphere centered at the root axis just below the root collar. This count was used to determine the total number of laterals ("total laterals") and the number of sections with at least one lateral ("sections with laterals").

The diameter of all laterals >3 mm was also measured where they intersected a hypothetical 10 cm diameter sphere centered just below the root collar (the axis of the root system). These diameters were then used to calculate a cross-sectional area for each lateral. The areas were summed to give a measure of total root cross-sectional area, which is proportional to root size (Lindgren and Örlander 1978).

Finally, all root deformities were classified. Nine categories of characteristics (Table 1) were assessed on a scale from 0 to 3 (0 = no deformity; 1 = low deformity; 2 = moderate deformity; 3 = high deformity). Each root system received a rating for each root characteristic. An overall root-form classification was also assigned to each root system (good root form, i.e., no deformity (G); low deformity (L); moderate deformity (M); severe deformity (S)). The overall classification was determined by the root-characteristic rating that occurred most often. For example, if a root system had a high number of moderate deformities (2), then the overall rating was moderate (M). Roots were only classified as having no deformity when scores for all characteristics were zero.

Data analyses

All data analyses were performed using SYSTAT® version 9.0 (SPSS Inc., Chicago) except for the Spearman's rank correlations, which were performed using STATISTICA® version 5.0 (StatSoft Inc., Tulsa, Oklahoma). Three major questions were addressed in the statistical analysis:

(1) What is the prevalence of root deformity and root-form differences between planted and natural lodgepole pine? The percentage of trees in each deformation class was calculated for planted and natural trees over all of the sampled stands to assess the prevalence of root deformities. Comparison of overall root class between planted and natural trees was done using Pearson's χ^2 test to determine whether the numbers of planted versus natural trees differed from the expected values at each level of overall root class.

A direct binary logistic regression was used to identify root characteristics (Table 1) that significantly predicted differences between planted and natural root systems. The nine root characteristics listed in Table 1 in combination with sections with laterals, total laterals, and total root cross-sectional area were used to predict tree origin (natural versus planted). Direct logistic regression (in which all characteristics are entered into the equation at the same time) was used to evaluate each characteristic after all of the other characteristics were accounted for (Tabachnick and Fidell 2001).

Two assumptions of logistic regression (Tabachnick and Fidell 2001) were violated and therefore some variables were transformed to satisfy the assumptions. The first assumption was the linearity of the logit. The Box–Tidwell

Table 1. Categories used for scoring root morphology (modified from Chavasse 1978).

Root characteristic	Rating
Taproot	0. Taproot straight and well developed 1. Taproot stunted or kinked but definite 2. Visible root deformation but the taproot can still be made out 3. No discernible taproot
J-root	0. No J 1. Angle of J less than 45°; slight bending of the system in one general direction 2. Angle of J greater than 45° and less than 90°; visible bend in the system 3. Angle of J 90° or greater
Spiral root	0. No spiral 1. Slight spiral (horizontal wrapping of one or more roots) that the tree will likely outgrow (spiral less than 30% of the circumference of the tree) 2. Spiral present but may or may not strangle the tree (spiral 30%–60% of the circumference of the tree) 3. Spiral will likely strangle the tree (spiral greater than 60% of the circumference of the tree)
Vertical compression	0. No compression 1. Vertical compression less than 10% of original plug 2. Vertical compression less than 30% of original plug 3. Vertical compression more than 30% of original plug
Lateral spread	0. Well-distributed laterals (all segments contain roots) 1. One or two radial segments contain no laterals 2. Two segments together or three radial segments contain no laterals 3. Three segments together or four or more segments contain no laterals
Lateral compression	0. No laterals squashed down 1. One lateral squashed down 2. Two or three laterals squashed down 3. Four or more laterals squashed down
Slit plant morphology	0. Laterals show no “slit” pattern 1. Laterals oriented in opposite directions but three or more laterals fill in the sides 2. Laterals, except for one or two, oriented in opposite directions 3. All laterals clearly oriented in opposite directions
Braiding	0. No braiding 1. Some braiding or twisting of one or two laterals 2. Three or four laterals twisted or braided 3. Four or more laterals twisted or braided
Root pairs	0. No cracks 1. One crack 2. Two cracks 3. Three or more cracks

Note: A “crack” occurs when two roots are pressed together. Root pairs are different from braiding in that the roots lie flat together and do not twist around each other. This is for roots larger than 3 mm diameter, and the crack must be at least 1 cm long and within the 10 cm diameter sphere used for measuring lateral diameters.

approach for testing linearity of the logit was performed for the continuous variables used in the regression. Two variables violated this assumption: spiral root and braided root. Both variables were converted to dichotomous variables. Thus, for each variable, deformation levels 0 and 1 became 0 and deformation levels 2 and 3 became 1. The second assumption was the absence of multicollinearity. All variables were entered into a Pearson’s correlation matrix. All correlations were well below 0.7 except for sections with laterals paired with total laterals. Because sections with laterals conveys a sense of the distribution of laterals around the stem, this variable was left in the analysis and total laterals was removed from this analysis.

In addition, to determine differences among overall deformation classes, the same logistic regression was performed for trees with low and moderate deformation as one group, and for trees with severe deformation as another group. The output of these analyses served to compare the root characteristics that distinguish planted from natural trees with low and moderate root deformation in both the absence and the presence of severe root deformation.

Analysis of variance (ANOVA) and analysis of covariance were used to test differences in aboveground growth form and growth rate for planted versus natural trees.

The height-to-diameter ratio was used as a measure of tree growth form. This ratio was used primarily to pool all of the trees aged 3–10 in the data set because it allows for comparison of tree heights while accounting for diameter. It also reduces the considerable variation that results when trees of a broad range of ages are sampled.

Mean annual diameter increment and mean annual height increment were used as measures of average tree growth rate.

The data were assessed using Levene’s test for homogeneity of variance, and a z statistic for skewness and kurtosis. Where necessary, the data were transformed to satisfy the assumptions of ANOVA (Townend 2002). Consequently, height-to-diameter ratio, mean annual diameter increment, mean annual height increment, and stability were transformed as $x' = \sqrt{(x + 0.5)}$ to reduce skewness to nonsignificant levels (i.e., a z score lower than 2) (Tabachnick and Fidell 2001). ANOVAs were conducted using both the transformed and the untransformed variables. Where the results were the same (e.g., where both tests were significant) the test using the untransformed variables is reported.

(2) What are the relationships between root form and growth form, growth rate, and stability in planted and natural trees?

ANOVA and analysis of covariance were used to assess variation in height-to-diameter ratio (tree growth form), mean annual diameter increment and mean annual height increment (tree growth rate), and stability among root classes. The same independence of measurements and the transformations as in the previous section are applicable. To equalize the variances for each of the levels of overall root class, the good root form and low-deformity levels were combined into one category (still called low).

Spearman's rank correlation was used to identify root characteristics associated with changes in height-to-diameter ratio, mean annual diameter increment, and mean annual height increment for both planted and natural trees. Spearman's rank correlation was used because there are no assumptions about the shapes of distributions, and ordinal data are acceptable (Townend 2002). Most of the root characteristics are ordinal (taproot, J-root, spiral root, vertical compression, lateral spread, lateral compression, slit plant morphology, braided root, and root pairs), and the rest of the variables are non-normal (total laterals, total root cross-sectional area), except for sections with laterals and age. We used a sequential Bonferroni adjustment of P values (Rice 1989) to account for the multiple correlations conducted.

(3) What are the root differences between live and dead trees?

Direct logistic regression was used to determine the root characteristics that were important in distinguishing between live and dead trees, regardless of origin (planted or natural). Total laterals was removed from the analysis as above because it was moderately correlated ($r^2 < 0.7$) with sections with laterals (Tabachnick and Fidell 2001).

Results

Prevalence of root deformity and root-form differences between planted and natural lodgepole pine

Of the planted trees sampled, 94% ($n = 306$) had an overall root class of moderate or severe deformation, with 65% in the severe-deformation root class. The natural trees showed a lower prevalence of root deformities: 50% ($n = 255$) of natural trees were classified as having moderate or severe deformation, with 9% in the severe-deformation root class.

Because of the higher number of planted trees with severe root deformation, the frequency distributions of trees in each root class (Fig. 1) were significantly different for planted and natural trees ($\chi^2 = 223.537$, df = 3, $P < 0.001$). The distribution of root classes for planted versus natural trees remained fairly constant across all the ages sampled; there were high numbers with low root deformity for natural trees of all ages and high numbers with severe root deformity for planted trees of all ages (data not shown).

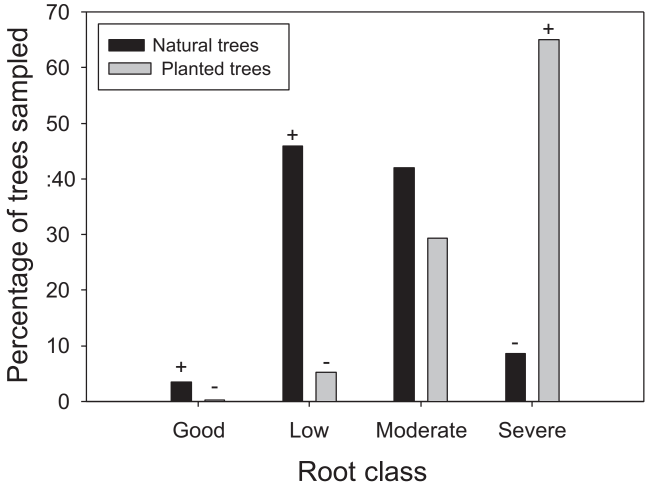


Fig. 1. Percentages of artificially regenerated (planted) and naturally regenerated (natural) trees in each root class; + indicates significantly higher numbers than expected, based on a 50:50 distribution in each category, and – indicates significantly lower numbers than expected (good root form: $\chi^2 = 6.400$, df = 1, $P = 0.011$; low deformation: $\chi^2 = 76.699$, df = 1, $P < 0.001$; moderate deformation: $\chi^2 = 1.467$, df = 1, P = ns; severe deformation: $\chi^2 = 141.760$, df = 1, $P < 0.001$; Pearson's χ^2 test; $n = 306$ and $n = 255$ for planted and natural trees, respectively).

Root characteristics allowed us to distinguish between trees of planted versus natural origin ($\chi^2 = 439.74$, df = 11, $P < 0.001$). The output of the direct logistic regression using all the root characteristics to predict tree origin (planted versus natural) revealed that the best predictors of planted trees were J-root, spiral root, lateral spread, lateral compression, braiding, root pairs, and sections with laterals (Table 2). Also, prediction accuracy was high, with 85% correct classification of planted versus natural trees in the data set. A relatively high McFadden's ρ^2 value (0.636) indicated that a significant portion of the difference between planted and natural trees is accounted for by individual root characteristics. Of the significant variables in the direct logistic regression, spiral root, lateral compression, and braided root had the largest effect (largest odds ratio; Tabachnick and Fidell 2001) on the determination of planted versus natural origin.

To determine whether the same root characteristics predicted whether trees were planted or natural trees among root classes, the same logistic regression was run for trees in the low- and moderate-deformity classes as a group and for trees in the severe-deformation class. The characteristics that significantly distinguished between planted and natural trees in the low- and moderate-deformity group were taproot, J-root, spiral root, lateral compression, braided roots, root pairs, and sections with laterals. The characteristics that significantly distinguished between planted and natural trees in the severe-deformation group were lateral spread, lateral compression, and braided roots. Therefore, lateral compression and braided roots differentiated between planted and

Table 2. Results of direct logistic regression using root characteristics to predict the origin of young lodgepole pine trees.

	Estimate						
	Mean	SE	*t* ratio	*P*	Odds ratio	Upper 95% CI	Lower 95% CI
Taproot	0.417	0.206	20.024	**0.043**	1.517	2.271	1.013
J-root	0.460	0.169	2.727	**0.006**	1.585	2.206	1.138
Spiral root (two categories)	1.051	0.440	2.386	**0.017**	2.860	6.777	1.206
Vertical compression	0.250	0.219	1.141	0.254	1.284	1.973	0.836
Lateral spread	0.422	0.189	2.228	**0.026**	1.525	2.210	1.052
Lateral compression	1.294	0.249	5.196	**<0.001**	3.648	5.943	2.239
Slit plant morphology	–0.110	0.204	–0.539	0.590	0.896	1.337	0.600
Braided roots (two categories)	1.943	0.469	4.147	**<0.001**	6.982	17.493	2.787
Root pairs	–0.602	0.224	–2.692	**0.007**	0.548	0.849	0.353
Sections with laterals	0.298	0.141	2.122	**0.034**	1.348	1.775	1.023
Total root cross-sectional area	–0.000	0.000	–0.242	0.809	1.000	1.000	1.000

Note: Planted trees are the response variable (value of 1) and naturally regenerated (natural) trees are the reference variable (value of 0). Values in boldface type are significant at $P < 0.05$.

natural trees, regardless of root class. In addition to these two characteristics, taproot, J-root, spiral root, root pairs, lateral spread, and sections with laterals were worse in planted trees when root deformation was severe (severe-deformation class).

Differences in growth form and growth rate between planted and natural trees

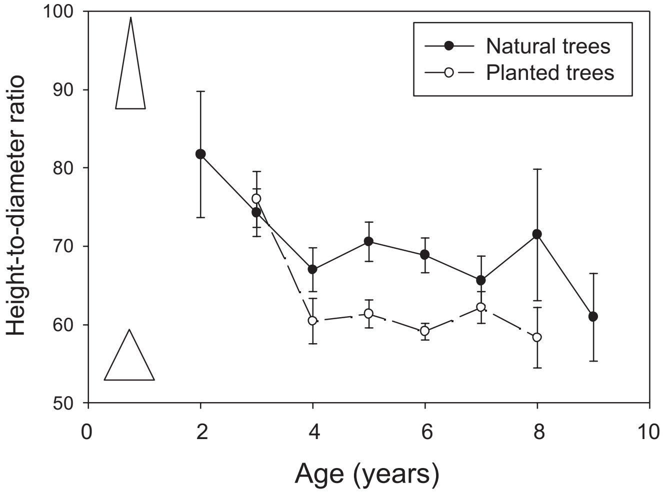
Planted trees and natural trees showed different patterns in growth form: natural trees showed a greater height-to-diameter ratio than planted trees only after age 4 (Fig. 2). Planted trees showed increased growth rate (mean annual diameter increment and mean annual height increment) relative to natural trees from age 4 to age 6. The significant interaction term for variation in mean annual diameter increment ($F_{[319,312]} = 7.315$, $P < 0.001$) and mean annual height increment ($F_{[319,312]} = 5.101$, $P < 0.001$) over the ages sampled confirms that growth-rate patterns differ significantly with age between natural and planted trees. As well, changes in growth rate were associated with root class only in planted trees, where those with low root deformity had the highest growth rate and those with severe root deformity had the lowest growth rate (Fig. 3).

Impact of root form on differences in growth form, growth rate, and stability between planted and natural trees

Differences in growth form between natural and planted trees depended on root class. Neither natural nor planted trees showed any significant difference in height-to-diameter ratio across root classes ($F_{[155,153]} = 2.038$, $P = 0.134$, and $F_{[174,172]} = 2.247$, $P = 0.109$, respectively). Natural trees, however, had a greater height-to-diameter ratio than planted trees in the low and moderate root deformity classes (Fig. 4).

Growth rate (mean annual diameter increment and mean annual height increment) was significantly greater in planted versus natural trees in the low- and moderate-deformity root classes. Planted trees showed a significant reduction in mean annual diameter growth ($F_{[171,169]} = 4.639$, $P = 0.011$) between moderate- and severe-deformation root classes. Mean annual height increment ($F_{[171,169]} = 4.235$, $P = 0.016$) was significantly lower in the severe-deformity root class than in the low-deformity root class. Natural trees, however, showed no significant difference in mean annual diameter increment across root classes ($F_{[147,145]} = 1.266$, $P = 0.285$), nor was there any significant difference in mean annual height increment across root classes ($F_{[147,145]} = 0.302$, $P = 0.740$) (Fig. 5).

Fig. 2. Height-to-diameter ratios (mean ± SE) for planted and natural trees at each age (determined at 5 cm height). The triangles beside the *y*-axis illustrate how tree shape at a given height would change with changing height-to-diameter ratio.



Finally, horizontal stability was not associated with overall root class when diameter was used as a covariate ($F_{[164,162]} = 0.240$, $P = 0.787$). However, lateral-root measurements (the number of sections with laterals, total laterals, and root cross-sectional area) did change significantly with increasing deformation of root systems, but only in planted trees. All three of these measurements decreased with increasingly severe root deformation in planted trees (sections with laterals: $F_{[157,155]} = 14.140$, $P < 0.001$; total laterals: $F_{[157,155]} = 6.665$, $P = 0.002$; total root cross-sectional area: $F_{[157,155]} = 7.241$, $P = 0.001$).

Spearman's rank correlations showed that several root characteristics were associated with height-to-diameter ratio, mean annual diameter increment, and mean annual height increment in planted trees and natural trees (Table 3). Both lateral-root measurements were negatively correlated with

Fig. 3. Annual diameter increments (A and B) and height increments (C and D) (mean ± SE) for each root class of natural (A and C) and planted (B and D) lodgepole pine trees (age was determined at 5 cm height).

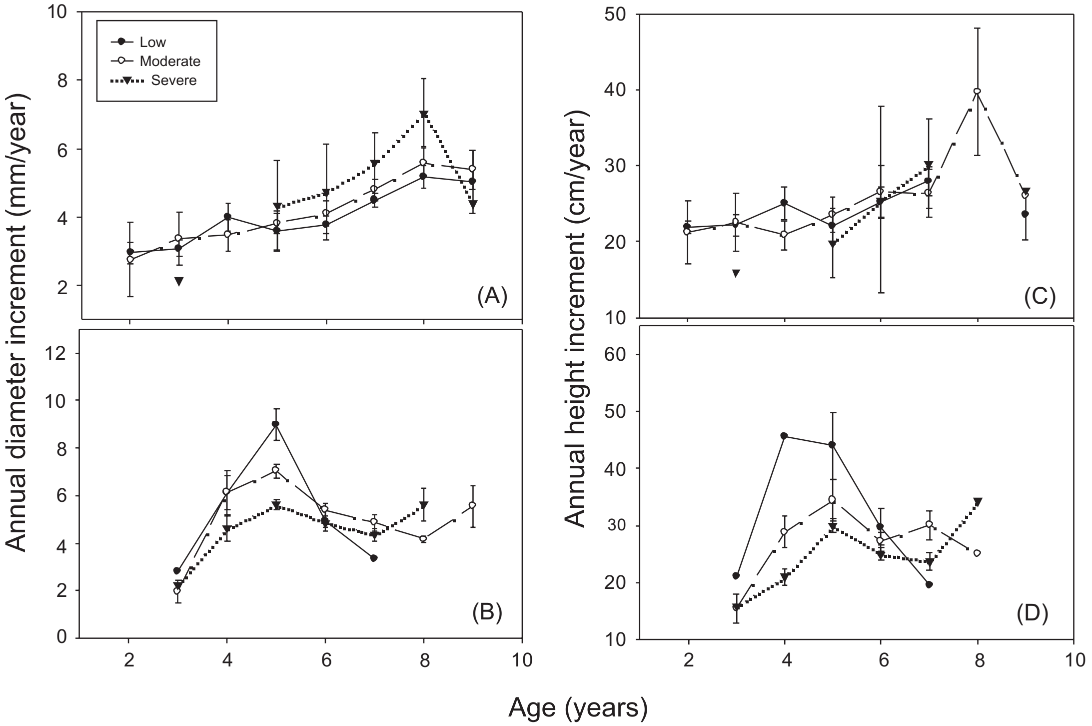
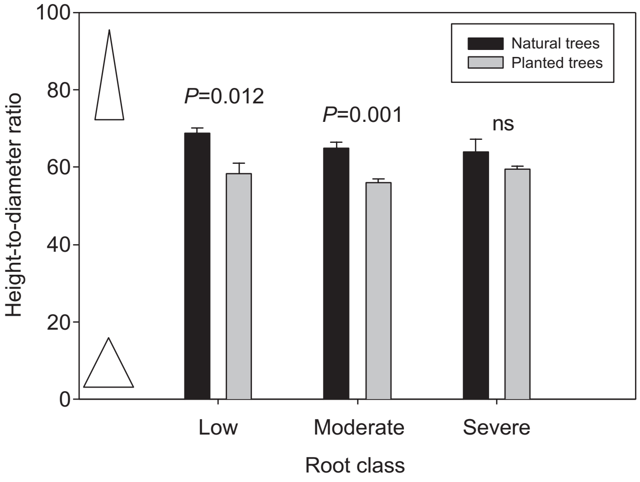


Fig. 4. Height-to-diameter ratios (mean ± SE) for each root class. *P* values are shown where a significant difference in height-to-diameter ratio for planted versus natural trees occurs within a given root class ($\alpha = 0.05$); ns, nonsignificant difference. The triangles beside the *y*-axis illustrate how tree shape changes with changing height-to-diameter ratio.



height-to-diameter ratio but positively correlated with mean annual height and diameter increments.

Spiral root was also correlated with mean annual diameter increment for planted trees but not for natural trees, and, similarly, with mean annual height increment for planted trees but not for natural trees (Table 3). It is noteworthy that while the correlations were marginally insignificant for natural trees, the sign of the correlation coefficient for this root characteristic differed between planted and natural trees.

Root-form differences in live versus dead trees

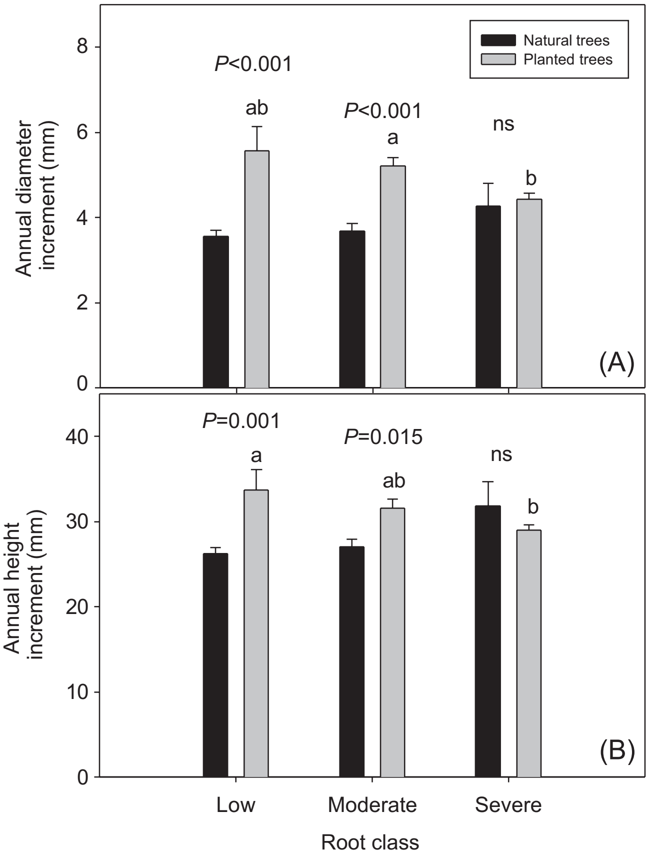
Data for planted and natural trees were pooled to produce a logistic regression that used all of the root characteristics to predict dead versus live trees. Root characteristics distinguish between live and dead trees ($\chi^2 = 75.340$, df = 12, $P < 0.001$). The analysis revealed that the best predictors of dead trees are J-root, spiral root, and total root cross-sectional area. Although the analysis produced a high overall prediction accuracy (79%), only 26% of the dead trees were identified correctly. The overall prediction accuracy was brought up significantly by a much higher number of live trees in the analysis. Of the live trees, 88% were accurately classified. The poor classification of dead trees was reflected in a relatively low McFadden's ρ^2 value (0.164). McFadden's ρ^2 value is considered "good" for values as low as 0.2–0.4 (Tabachnick and Fidell 2001).

Total root cross-sectional area was a significant predictor of live versus dead trees; live natural trees had a significantly larger root cross-sectional area ($F_{[506,504]} = 8.545$, $P = 0.004$) than live planted trees when diameter was controlled for.

Discussion

The percentage of planted trees with moderate and severe root deformation shows a high prevalence of root deformation in planted lodgepole pine trees around Prince George. Poor root form is widespread even in trees planted within the last 3–10 years in spite of efforts by licensees to improve planting techniques. Canadian Forest Products Ltd., the company responsible for reforestation of the sites used in this study, used contractors for post-harvest regeneration but conducted thorough planting checks themselves to identify

Fig. 5. Annual diameter increments (A) and annual height increments (B) (mean ± SE) associated with root class in natural and planted trees. Where ANOVA is significant between root classes (mean annual diameter increment: $F_{[171,169]} = 4.639$, $P = 0.011$; mean annual height increment: $F_{[171,169]} = 4.235$, $P = 0.016$) within tree origin, means accompanied by the same letter are not significantly different as identified by the Bonferroni post-hoc test for mean separation. P values are shown where a significant difference in growth increment for planted versus natural trees occurs within a given root class ($\alpha = 0.05$; ns, nonsignificant difference).



“planting-fault” characteristics such as J-roots. Improvement in planting techniques is evident in the insignificant amount of slit plant morphology, indicating that the lateral compression reported by Rudolph (1939) is no longer distinguishable in planted container-grown trees. The fact that J-root is still a significant predictor of planted versus natural origin of trees, however, suggests that further improvements in planting technique are still desirable.

The other root characteristics that distinguish planted trees from natural trees (poor taproot, spiral root, poor lateral spread, lateral compression, braiding, and root pairs) cannot be attributed definitively to poor planting and may be the result of container constraints. These characteristics represent the bulk of the root deformities and this is consistent with the results of other studies of the effect of containers on root form (McMinn 1978). For example, previous studies have reported the following deformities: tree root balling or knotting (Hay and Woods 1968; Hay and Woods 1974; Woods 1980), spiral rooting (Lindgren and Örlander 1978), J-rooting or L-rooting (Hay and Woods 1968; Hay and Woods 1974; Sutton 1978; Woods 1980), slit plant morphology (Rudolph 1939; Gruschow 1959; Schultz 1973), taproot deformation (Martinsson 1986), and container-shaped root forms (Halter and Chanway 1993; Halter et al. 1993). In spite of a long history of study, the major root-system deformities that have occurred in the past are still prevalent in planted trees in our study area, and in all likelihood wherever container-grown seedlings are used extensively, as evidenced by fairly recent interest in this issue (e.g., Harrington and Howell 1998; Lindström and Rune 1999; Krasowski 2003; Rune 2003).

Studies of the effects of root form on growth and development of trees often focus on one particular aspect of root form (e.g., J-root; Seiler et al. 1990), or treat different root characteristics as different treatments (e.g., Woods 1980). Our study shows that a suite of root deformities distinguish planted trees from natural trees, and that they can act singly or in combination to affect aboveground characteristics. This can make the effects of root morphology on aboveground features difficult to interpret, which may explain why many studies show little effect of planting problems alone on tree growth or survival (Schantz-Hansen 1945; Hay and Woods 1974; Owston and Seidel 1978; Woods 1980).

The results of our study also suggest that planted and natural trees exhibit different growth patterns. The greater diameter- and height-growth rates of planted trees may be influenced by greenhouse conditions in combination with root form. The greenhouse growing environment likely provides a substantial advantage (e.g., trees are better able to compete with vegetation or adverse environmental conditions) by producing high initial growth rates (Hellum 1978; Barnett 1984). Planted trees exhibit changes in growth rate associated with root class, whereas natural trees do not (Fig. 3). Our results show that severely deformed roots (distinguished by severe lateral compression, poor lateral spread, and braiding) in planted trees (i.e., the majority of the planted trees) do not show this increased initial growth rate. Although we did not measure root density directly, lateral compression, poor lateral spread, and braiding produce, by definition, more compact, dense root systems. Stevenson (1967) suggested that dense roots (those with high rooting intensity) must compete for moisture, resulting in less aboveground growth of planted seedlings. Thus, it is possible that for trees with severely deformed roots, the lack of an apparent greenhouse advantage in terms of aboveground growth rates is directly due to their compacted and twisted root systems, potentially leading to a decrease in water uptake.

The occurrence of changes in aboveground growth parameters could be due to the nature of the individual root characteristics that combine to create a low- or moderate-deformity rating in planted or natural trees. While planted trees showed a reduction in growth rate with increasingly severe root deformation, natural trees showed an increase in growth rate with an increase in the severity of taproot deformation, spiral root, or braiding. The root characteristics that distinguished between planted and natural trees for the low- and moderate-deformity classes revealed that the best predictors of planted trees are J-root, spiral root, lateral compression, braiding, and root pairs. These characteristics all

Table 3. Spearman's rank correlation coefficients (*R*) and *P* values for the association of root forms with growth (height-to-diameter ratio) and growth rate (mean annual increments) in planted and natural trees.

	Height-to-diameter ratio		Mean annual diameter increment		Mean annual height increment	
	R	*P*	*R*	*P*	*R*	*P*
Planted trees						
Sections with laterals	–0.256	**0.011**	0.613	**<0.001**	0.558	**<0.001**
Total laterals	–0.436	**<0.001**	0.760	**<0.001**	0.653	**<0.001**
Total root cross-sectional area	–0.414	**<0.001**	0.828	**<0.001**	0.745	**<0.001**
Root pairs	–0.053	1.956	0.321	**<0.001**	0.340	**<0.001**
Spiral root	0.023	1.532	–0.241	**0.018**	–0.259	**0.009**
Natural trees						
Sections with laterals	–0.308	**0.011**	0.645	**<0.001**	0.531	**<0.001**
Total laterals	–0.309	**0.012**	0.695	**<0.001**	0.581	**<0.001**
Total root cross-sectional area	–0.309	**0.013**	0.783	**<0.001**	0.657	**<0.001**
Root pairs	–0.173	0.248	0.350	**<0.001**	0.329	**<0.001**
Spiral root	–0.141	0.546	0.206	0.072	0.199	0.090

Note: The *P* value is the adjusted value using a sequential Bonferroni method. Values in boldface type are significant (α = 0.05).

arise when root twisting and overlap lead to root grafting and possible inhibition of translocation. If the deformation is severe, the tree may be unable to store resources below ground, owing to blocked translocation (Graham and Bormann 1966; Hay and Woods 1968; Hay and Woods 1978), or harness resources (because of high rooting intensity) to allocate above ground. Although these results appear contradictory, this may be because the root forms that characterize natural trees are different from those that characterize planted trees in each root class. Even in the severe-deformation root class, planted and natural trees can be distinguished by lateral spread, lateral compression, and braiding. Thus, natural trees in the severe-deformation root class may have poor taproots but they are not characterized by a highly interwoven or balled-up root system (lateral spread, lateral compression, and braiding). Therefore, allocation may be blocked only to the taproot or to the lower roots in natural trees, whereas it is blocked by a suite of deformities that create an interwoven, compressed root system at the root collar and below in planted trees. Lateral development in the upper portion of the soil may allow for an increase in nutrient uptake (Hays and Woods 1978) that would explain the positive relationship between growth rate and root deformation for natural trees. Dean (2001) shows a strong inverse relationship between allocation to the fine roots and the stem. If translocation into the root is inhibited by root deformities, the excess carbon may be used to increase diameter growth. Kozlowski (1992) states, however, that the mere presence of carbon is not sufficient for cambial growth. Water availability and hormones regulate the conversion of carbon into stem material. Hay and Woods (1974) suggest that the production of carbohydrates and geotrophic auxin is inhibited by root deformities. Thus, the lower height-to-diameter ratios (different growth form) associated with moderate and severely deformed root systems could be due to increased diameter growth in a region where both excess carbon and excess plant growth hormones accumulate above the root collar. If this is true, then the lower height-to-diameter ratio may have a negative effect, as excessive aboveground allocation occurs without a corresponding increase in root mass.

Our study also shows that root deformities persist until trees are at least 8 or 9 years old, the oldest trees we could study because of the difficulty in excavating the large root systems of older trees. Although Burdett et al. (1983) suggest that chemical pruning of root systems grown in containers allows the continuation of lateral development after planting, our observations indicate that characteristics of severely deformed root systems are still very apparent in the majority of planted trees between 3 and 10 years after planting. Halter et al. (1993) excavated 12-year-old lodgepole pine trees from an area approximately 400 km west of our study site and described root characteristics similar to those we found in planted lodgepole pine. They also found that natural pine trees were significantly taller and had greater growth rates than planted pine trees in the 2 years preceding their study. Because they did not further group planted and natural trees by severity of root deformation, they could not describe how planted trees with low to moderate root deformation performed when compared with natural trees with low and moderate root deformation. However, the results of our study suggest that although the vast majority of planted trees possess severely deformed root systems, those with better root systems outperform natural trees early in development. Further research into the long-term implications of an early increase in growth of planted trees with deformed roots would be ideal. In addition, whether or not trees with severe root deformation suffer higher mortality rates than trees with good root form up to rotation age also requires further investigation.

The effect of root form on stability

We did not find differences in stability between planted and natural trees in this study. Krasowski (2003) suggests that horizontal stability is a function of the number, size, and distribution of lateral and sinker roots. We did not count the sinker roots, which may maintain stability even when there is a reduction in the number, distribution, and cross-sectional area of laterals. Planted trees may have a higher number of sinker roots because taproots are often malformed.

If poor root form, especially poor lateral-root development, is retained as the tree becomes older, then problems with stability could occur, particularly on sandy soils. Coutts (1983), in a discussion of root stiffness and force, suggested that fewer thicker roots have more stiffness and therefore are better able to resist horizontal force on the stem (e.g., wind or snow press). He also suggested that unequal loading of wind force on roots reduces tree stability and increases the probability of windthrow. If the root deformation observed in our study persists as trees grow older, planted trees may be at a higher risk of windthrow as they grow tall enough and have sufficient crown to become a significant barrier to wind. A lodgepole pine stand approximately 15–20 years old on sandy soil at the Aleza Lake Research Forest near Prince George, British Columbia, had a high incidence of trees with severe lower-stem sweep and lean. One such tree was excavated and showed evidence of spiral root and poor lateral-root development (B.S. Lindgren, personal observation), indicating that long-term stability may be a problem, at least on sandy soils.

The effect of root form on mortality

A low McFadden's ρ^2 value in the analysis shows that a significant proportion of the difference between live and dead trees remains unexplained when root characteristics are used in this model. Insect attack, the presence of pathogens, or environmental stresses in combination with the extent of root formation may more completely explain the probability of death for a given tree.

The results of our study also suggest that only trees with low total root cross-sectional area appear to have an increased chance of dying. The negative slope on the estimate indicates that with increasing cross-sectional area, the probability of tree death decreases. This is consistent with the effects of root form on growth form and growth rate. A tree with good total root cross-sectional area may establish above- and below-ground reserves that will help make it more resilient under stress. Alternatively, because most of the dead trees we sampled (77%) had been killed by the Warren root collar weevil, and Cerezke (1994) showed significant reductions in total root cross-sectional area after attack by this weevil, the reduced root cross-sectional area in dead trees may result in part from girdling by the insect.

Although limited to young trees operationally planted by one forest company, this study has a number of important implications for the regeneration of lodgepole pine in British Columbia. Root deformation in planted trees was widespread on our study sites and the differences between planted and natural root forms were pronounced. These differences in root form may alter resource allocation by planted trees and increase the initial growth rate. Any advantage in terms of initial tree growth rates in planted trees is lost, however, when the root system is severely deformed. While the adverse effects of root deformation may not be readily visible above ground or result in reduced tree stability in the young stands assessed in this study, planted trees with severe root deformation may be at increased risk of mortality in the longer term because of a significantly lower total root cross-sectional area than in planted trees with low and moderate root deformation. Given that 65% of planted trees evaluated in our study had poor root form, plantations of lodgepole pine are likely to be less productive and resilient than if all of the trees showed low to moderate root deformation. Although young natural trees do not show better aboveground growth parameters than planted trees, much better root characteristics overall suggest that in the longer term, natural lodgepole pine will have a more stable and more balanced underground root system than most planted trees. Halter et al. (1993) found similar problems with natural versus planted lodgepole pine trees at age 12, and showed that natural trees exhibited better aboveground growth. This indicates that planted trees may ultimately be less productive and resilient than natural trees over time as well. While Lindström and Rune (1999) found that spiral root, poor root distribution, and stem bending that were evident in Scots pine at age 7–9 years had largely been corrected by age 19–24 years, they pointed out that internal problems would remain, e.g., abnormal fiber orientation, compression wood, and inferior root strength due to bark inclusion from the spiral root.

Improvement in the quality of seedlings and better planting techniques would alleviate some of these problems. Rune (2003) found that slits in the walls of containers reduced root and growth problems in Scots pine. Harrington and Howell (1998) found a 58% decrease in yield index in loblolly pine trees with deformed or pruned taproots compared with straight-root planted seedlings 3 years after planting. They determined that the cost of the extra effort required for straight-root planting was too high to justify. Nevertheless, with the large increase in the number of young lodgepole pine plantations in British Columbia, and the demonstrated effects of poor root form, increased efforts to ensure good root-system development in seedlings and planted trees may be warranted.

Acknowledgments

We thank Canadian Forest Products Ltd. for financial and logistical support; Mount Begbie Consultants for financial support; H. Giroday, L. Zukewich, and T. Robert for assistance in the field and laboratory; M. Gillingham for statistical advice; and M. Krasowski, and three anonymous reviewers for valuable comments. K. Otter, A. Fredeen, and S. Simard provided valuable comments on an earlier version of the manuscript. This research was funded by a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) to BSL and a University of Northern British Columbia entrance scholarship, a NSERC post-graduate scholarship, scholarships from the Entomological Society of Canada, and a Graduate Research in Engineering and Technology (GREAT) award from the Science Council of British Columbia to JAR.

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