Effects of Lodgepole Pine Dwarf Mistletoe, *Arceuthobium americanum*, on Jack Pine, *Pinus banksiana*, Growth in Manitoba

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The Lodgepole Pine Dwarf Mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.) is an important pathogen of Jack Pine (*Pinus banksiana* Lamb.). Dwarf Mistletoe alters tree form, suppresses growth, and reduces volume and overall wood quality of its host. Stem analysis and a 3-parameter logistic regression model were used to compare the growth of heavily and lightly to non infected Jack Pine trees. At the time of sampling, no significant reduction in diameter at breast height and basal area were observed in heavily infected trees. However, a significant reduction in height and volume and an increase in taper were observed in heavily infected trees. Growth models predicted a 21.1% lower basal area, 23.4% lower height and 42.1% lower volume by age 60 for the high infection group.

Key Words: Lodgepole Pine Dwarf Mistletoe, *Arceuthobium americanum*, Jack Pine, *Pinus banksiana*, stem analysis, logistic regression, basal area, height, volume, tree growth, productivity, Manitoba.

Le Faux–gui du pin (*Arceuthobium americanum* Nutt. ex Engelm.) est un important agent pathogène du Pin gris (*Pinus banksiana* Lamb.). Le faux–gui modifie le défilement des arbres hôtes, réduit leur croissance et leur volume marchand ainsi que la qualité du bois. L'analyse de tige et la régression logistique à trois-paramètres ont été utilisés afin de comparer l'accroissement entre les Pins Gris sévèrement atteints et faiblement atteints. Au moment de l'échantillonnage, aucune réduction significative du diamètre à hauteur de poitrine ou de la surface terrière ne fut observée chez le groupe sévèrement atteint. Toutefois, les arbres atteints ont enregistré une baisse significative de la hauteur et du volume ainsi que du coefficient de défilement. Les modèles de régression ont prédit une perte de 21,1% en surface terrière, de 23,4% en hauteur et de 42,1% en volume pour les pins gris fortement atteints par le faux–gui à un âge de 60 ans.

Mots clés: Le Faux–gui du pin, *Arceuthobium americanum*, Pin gris, *Pinus banksiana* Lamb., analyse de tige, régression logistique, surface terrière, hauteur, volume, croisssance, productivité, Manitoba.

Jack Pine (*Pinus banksiana* Lamb.) is an important commercial tree species because of its pole-like growth form, and as a pioneer species, it is relatively easy to regenerate following harvest (Rudolph and Laidly 1990; Sims et al. 1990). An important pathogen of Jack Pine is Lodgepole Pine Dwarf Mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.). There are five species of Dwarf Mistletoe known in Canada, of which *A. americanum* is the most widely distributed, extending from British Columbia to southeastern Manitoba (Hawksworth and Wiens 1996). Individual species of Dwarf Mistletoe are generally host-specific, able to infect only a few tree species. In the case of *A. americanum*, other susceptible hosts include Lodgepole Pine (*Pinus contorta* Dougl. ex Loud.) and Ponderosa Pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.).

As of 1996, there were 670 000 ha of forest with severe *A. americanum* infections in Alberta, Saskatchewan and Manitoba (Brandt et al. 1998). In Manitoba, approximately 8.7% of mature Jack Pine stands in important growing regions were infected by Dwarf Mistletoe (Baker et al. 1992). This has resulted in a loss of up to 7.9% of the total pine volume in these regions (525 224 m^3 out of 6 648 405 m^3) and a loss of up to 70.3% within the infected stands. Aside from the substantial volume losses, there is also a reduction in wood quality, making wood less merchantable. Wood of Lodgepole Pine infected by *A. americanum* exhibited greater longitudinal shrinkage and was weaker in strength when compared to uninfected trees because of the production of tree-rings having a lower percentage of latewood, shorter tracheid length, and higher resin content (Piirto et al. 1974). Generally, Dwarf Mistletoe deprives its host of water and nutrients, thus reducing height and diameter growth as well as seed production, and weakening the tree (Franc and Baker 2000). Dwarf Mistletoe alters tree form by disrupting apical dominance (Tinnin and Knutson 1980) through formation of witches' brooms. Because Dwarf Mistletoe derives all of its nutrients from host tissue and fixes little or no carbon dioxide for its own use, witches' brooms act as sinks for metabolites produced in other parts of the host (Hull and Leonard 1964a, 1964b). Douglas-fir and Western Larch infected by *A. douglasii* and *A. laricis*, respectively, exhibited a significant increase in leaf to sapwood ratios in heavily infected trees, altering resource allocation processes and reducing the overall water-use efficiencies (Sala et al. 2001).

The long incubation period characterized by the life cycle of *A. americanum* (Hawksworth and Wiens 1996) poses a problem in the early detection of initial infections. In forest management situations, the current most effective methods of treatment are removal of heavily infected trees and isolation of infected stands by planting buffer zones of incompatible host species (Franc and Baker 2000). Even-aged silvicultural systems are often effective in controlling Dwarf Mistletoe, as the entire overstory may be removed.

No one has quantified volume losses on individual Jack Pine trees due to infection by Dwarf Mistletoe. One study examined the effect of *A. americanum* on the growth of Lodgepole Pine (Baranyay and Safranyik 1970). Within Manitoba, Baker et al. (1992) studied the impact of Dwarf Mistletoe on Jack Pine trees at the stand scale, focusing on loss of wood volume in the forest stands. The objective of this study was to compare the growth of heavily infected Jack Pine trees to that of non-infected or lightly infected Jack Pine trees based on differences in diameter at breast height (dbh), basal area, height, volume, and stem form. We hypothesized that there was a significant reduction in total cumulative dbh, basal area, height, and volume growth rate in trees infected with Dwarf Mistletoe.

Methods

The sampling area is located about 97 km northeast of Winnipeg, Manitoba (Figure 1) within Belair Provincial Forest (50°38'N, 96°29'W, 250 meters above sea level). The underlying bedrock consists of Archean granites and gneisses (Manitoba Geological Survey 2002*). The closest meteorological station is located at Pine Falls about 21 km from the sampling area. The climate is continental (Burton et al. 1998). The mean annual temperature for Pine Falls is 2.1°C, and the total annual precipitation is 538.5 mm (Environment Canada 2002*). In winters, the average minimum temperature reaches –23.5°C in January, and in summers, the average maximum temperature reaches 25.3°C in July.

The sampling site consists of a small, open, fire-originated Jack Pine stand, and is bound by Provincial Highway 11 to the south and a recent cutover to the north. The sample site is located near the south-eastern limit of the lodgepole pine dwarf mistletoe geographical distribution in Manitoba (Baker et al. 1992). Physically, the site is characterized by level, homogeneous terrain. The site is also homogeneous with regards to stand origin, slope variation and understory vegetation. Due to the small size of the infected stand, and the localized nature of the mistletoe infections, the number of trees for sampling was limited. There are epicentres of Dwarf Mistletoe infections scattered throughout the area. Within the sampling site, there is a relatively even scattering of heavily infected trees intermixed with lightly and non-infected trees (Figure 1).

Three transects were established approximately 50 m apart, oriented in a north-south direction, extending north from Provincial Hwy. 11. Ten sampling points were randomly established along the three transects, and the surrounding area was divided into four quadrants. One of the four quadrants was randomly selected in which the two nearest trees to the point were selected; one heavily infected tree and the nearest lightly or non-infected tree between 40 and 60 years of age. Trees with noticeable fire scars, fungal infections, or injuries were avoided to minimize the effects of other disturbances on tree growth. Trees that exhibited excessive branching or forking on the main stem were also avoided to simplify stem analysis. Trees were selected up to 50 m from plot centre, as long as they remained within the stand boundaries. If no trees matching our criteria were found within the selected quadrant, sampling was done in the next quadrant in numerical order. This method helped to eliminate bias by selecting the closest trees to the sampling points. Once candidate trees were selected, they were numbered, marked with a north-orientation line, marked at 0.5 m and 1.3 m, and locations were recorded with a GPS unit (Figure 1). Sampling took place in late July – early August 2002.

Prior to felling, the infestation index of the trees was estimated using the Hawksworth 6-class system (Hawksworth 1977). Infection was most easily determined from the ground by the presence of witches' brooms. Trees with an infestation index of 0 to 3 were classified as lightly infected, whereas trees with an index of 4 to 6 were classified as moderately to heavily infected. In order to take into account the competition of other trees, the dbh and distance of the nearest tree in each cardinal direction were measured.

Following felling of the trees, tree height was recorded and stems were sectioned at 0 m, 0.5 m, 1.3 m, and then 1-m intervals until stem diameter was less than 1 cm. Sections at points of the stem where branches emerged were avoided, and the adjusted height was recorded. For each cross-section, diameter inside-bark and outside-bark were measured along two diameters perpendicular to each other. At the laboratory, age of each cross-section was measured, and the pointer-year method of cross-dating was used to validate ages (Yamaguchi 1991). Following dating, stem analysis was performed on each tree to determine annual increments. Ring width measurements were done using the WinDENDRO™ v. 2002a program (Régent Instruments Inc. 2002*), and annual increments were calculated using XLSTEM™ 1.3a (Régent Instruments Inc. 1999*). Each cross-section was scanned with a high-resolution scanner and saved as a digital image. An image resolution of 800 dpi was used, except for cross-sections exhibiting high levels of suppression, where a resolution of 1600 dpi was used. For one tree, suppression was too great for ring detection by the WinDENDRO™

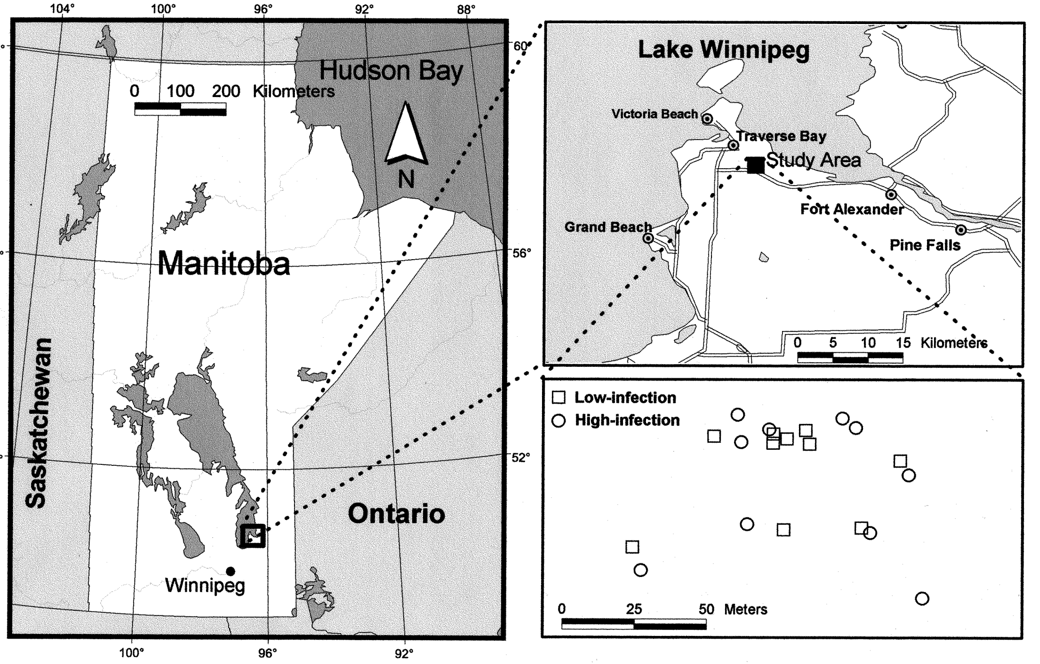

FIGURE 1: Location of the study area and distribution of the sampled trees. The lower right panel illustrates the relative position of the sampled trees and their infection level in the jack pine stand. Empty circles correspond to heavily infected trees, and empty squares correspond to lightly or non-infected trees.

program, so measurements were performed manually at a magnification of 50× using a Velmex measuring stage to a precision of 0.001 mm. Ring widths were measured, starting at the pith, along four radial paths in the north, east, south and west directions.

Data obtained were examined for differences between the two infection groups with regards to age, competition index, dbh, basal area, height, volume and stem form. The competition index was modified from Hegyi's distance weighted size ratio index (Avery and Burkhart 2002):

$$CI_i = \sum_{j=1}^{4} \frac{D_j / D_i}{DIST_{ij}}$$

where CI_i is the competition index for the subject tree, D_j is the dbh of the jth of four competitor trees (N, E, S, and W directions), D_i is the dbh of the subject tree, and $DIST_{ij}$ is the distance between the subject tree and the jth competitor tree. Basal area at dbh was calculated for each tree by using the formula for the area of a circle. Tree volume without bark was calculated by applying Smalian's formula for volume (Avery and Burkhart 2002) to each segment. The volume of each segment was then added to obtain tree volume. Stem form expressions were determined using the Girard form class (Avery and Burkhart 2002), with the quadratic mean diameter taken at the section nearest 5 metres. Because each group had a relatively low sample size (N=10), the non-parametric Mann-Whitney U-test was performed on each variable to determine significant differences between samples from each infection group ($\alpha = 0.05$). It should be noted that the Mann-Whitney U-test and the Wilcoxon two-samples test yield the same statistic and give the same results (Sokal and Rohlf 1997). To limit the effect of environmental variability, lightly or non-infected and heavily-infected trees were also carefully matched in pairs based on the distance separating them (Figure 1). Nine pairs were formed with a mean distance of 9.49 m (standard deviation = 4.83 m) between lightly or non-infected and heavily-infected trees. A Wilcoxon signed-rank test (Sokal and Rohlf 1997) was used to test for significant differences between infection groups. Paired-sample tests are more powerful than independent-sample tests.

The cumulative dbh, basal area, height and volume average growth curves produced for each tree were compared between infection groups. First, predicted growth curves were modelled for each growth variable and tree using non-linear regression. Best fit to actual cumulative growth curves for each variable and tree were obtained using a three-parameter logistic model of the form:

$$y = \frac{a}{1 + \left(\frac{x}{x_0}\right)^b}$$

where y is the value of the subject growth variable, x is the year of growth, a is the asymptotic level of growth, b is the growth constant, and x_0 is the inflection point. Because each of these three parameters defines the shape of the growth curves, significant differences between parameters for the two infection groups were determined using the Mann-Whitney U-test ($\alpha = 0.05$). This was repeated for each growth variable. Second, the best three-parameter logistic model was determined for each variable and infection group using the 10 trees as replicates. The resulting predicted growth curves were plotted to age 60. Because trees were not all of the same age and the number of observations decreased with time, only data covering the first 45 years of growth were used in all the regression analyses.

Results

The two infection groups showed no significant difference in age, competition index, dbh, and basal area (Table 1). There was, however, a significant difference in height and form class (Table 1). Specifically, trees in the high infection group were 20.2% shorter and had more stem taper. Both independent- and paired-sample tests yielded divergent results regarding total volume, and when partially controlling for environmental variability no significant difference in total volume was observed as indicated by the Wilcoxon signed-rank test.

The analysis of the coefficients from the logistic regressions derived from each tree in each infection group revealed that the high infection group reached a significantly lower maximum basal area, height, and volume, as predicted by the asymptotic values of the regression model (Table 2). Maximum dbh did not differ significantly between groups. The logistic regression model, projected to age 60, predicts a 21.1% lower basal area (Figure 2B), a 23.4% lower height (Figure 3A), and a 42.1% lower volume (Figure 3B) for the high infection group.

Results showed that there was a significantly higher growth rate for dbh and basal area in the high infection group (Table 2). This was also observed for volume but

TABLE 1: General characteristics of heavily infected and non-infected or lightly infected trees (n = 10 for each group) at time of sampling (Max = Maximum value, Min = Minimum value, SEM = Standard Error of the Mean). The first column of probabilities (**P**[1]) is based on the Mann-Whitney U-test (n=10 for each group). The second column of probabilities (**P**[2]) is based on the Wilcoxon signed-rank test (n=9 pairs).

	Low infection				*High infection*					
	Max	Min	Mean	SEM	Max	Min	Mean	SEM	**P**[1]	**P**[2]
Infestation index	2.0	0.0	1.2	0.29	6.0	4.0	5.2	0.20	**0.000**	**0.007**
Tree age	48.0	42.0	46.3	0.62	82.0	44.0	50.0	3.59	0.728	0.722
Competition index	3.34	0.77	1.85	0.30	1.89	0.66	1.29	0.15	0.257	0.515
Diameter at breast height (cm)	19.20	13.10	16.17	0.38	19.60	11.50	15.45	0.83	0.544	0.515
Basal area (m^2)	0.022	0.012	0.017	0.00	0.024	0.007	0.016	0.00	0.544	0.594
Height (m)	14.10	10.90	12.65	0.39	13.30	8.30	10.10	0.54	**0.004**	**0.008**
Volume (m^3)	0.16	0.09	0.12	0.01	0.17	0.04	0.08	0.01	**0.019**	0.110
Form class	0.83	0.64	0.73	0.02	0.76	0.35	0.56	0.04	**0.004**	**0.008**

TABLE 2. Values of the three parameters of the predicted logistic growth curves used to model diameter at breast height, basal area, height, and volume for heavily infected and non-infected or lightly infected Jack Pine trees (n = 10 for each group). The three parameters are the theoretic maximum (a), growth (b), and the inflection point (x_0) (Max = Maximum value, Min = Minimum value, SEM = Standard Error of the Mean). The first column of probabilities (***P***[1]) is based on the Mann-Whitney U-test (n=10 for each group). The second column of probabilities (***P***[2]) is based on the Wilcoxon signed-rank test (n=9 pairs).

		Low infection group				*High infection group*					
		Max	Min	Mean	SEM	Max	Min	Mean	SEM	***P***[1]	***P***[2]
Diameter at breast height (cm)	a	22.03	14.12	17.29	0.85	20.97	8.87	13.97	1.21	0.059	0.260
	b	-1.84	-3.30	-2.46	0.13	-2.46	-4.29	-3.26	0.19	**0.005**	**0.015**
	x_0	36.22	23.33	28.46	1.50	28.51	19.23	23.24	1.19	**0.023**	**0.028**
Basal area (m^2)	a	0.071	0.019	0.038	0.0061	0.032	0.007	0.016	0.0026	**0.002**	**0.038**
	b	-2.32	-3.51	-2.84	0.13	-3.07	-5.27	-3.84	0.20	**0.001**	**0.008**
	x_0	93.77	34.64	53.78	5.52	39.18	24.84	31.59	1.72	**0.001**	**0.011**
Height (m)	a	24.37	14.99	19.59	1.01	20.63	9.28	13.90	1.21	**0.008**	**0.015**
	b	-1.71	-2.64	-1.98	0.09	-1.44	-2.65	-2.07	0.12	0.326	0.374
	x_0	42.01	24.38	32.66	1.74	49.34	20.56	27.58	2.71	**0.034**	**0.038**
Volume (m^3)	a	3.237	0.120	0.604	0.297	0.214	0.042	0.097	0.021	**0.001**	**0.015**
	b	-2.98	-4.36	-3.60	0.13	-3.12	-6.07	-4.09	0.25	0.082	**0.028**
	x_0	111.79	40.48	60.48	6.51	48.74	30.68	36.59	1.97	**0.001**	**0.011**

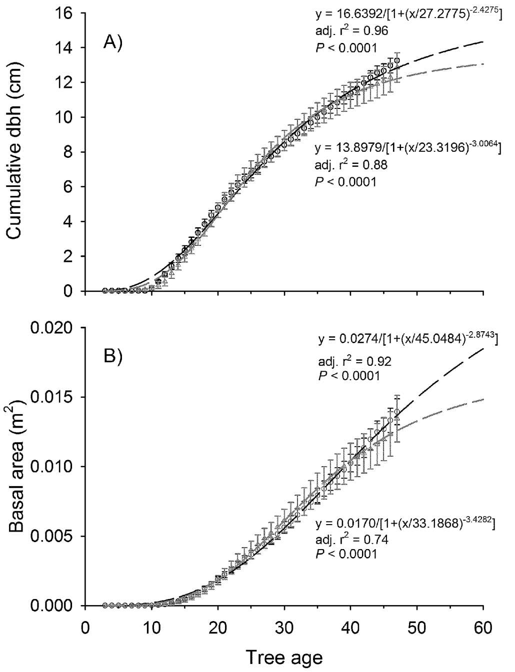

FIGURE 2: Average cumulative dbh growth (A) and average cumulative basal area growth (B) for each of the two infection groups. Dashed lines represent predicted growth up to year 60 for the infection groups, based on the 3-parameter logistic regression models depicted. Vertical bars represent standard errors of the mean. The black dashed line and empty circles indicates the low infection group, and the dark grey dashed line and empty triangles indicates the high infection group.

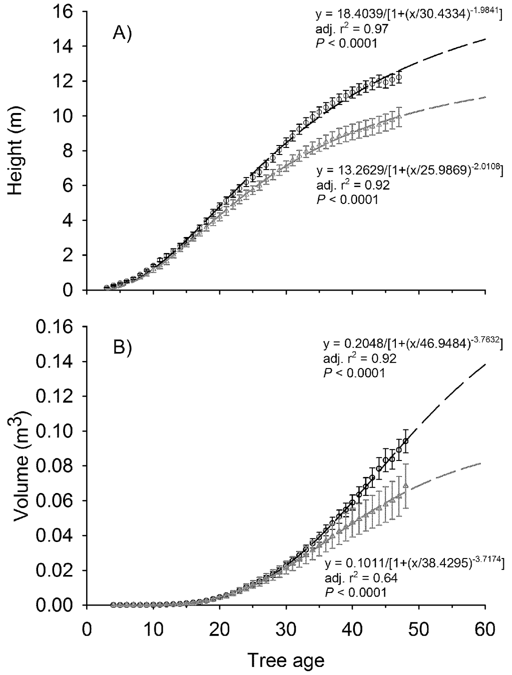

FIGURE 3: Average cumulative height growth (A) and average cumulative volume growth (B) for each of the two infection groups. Dashed lines represent predicted growth up to year 60 for the infection groups, based on the 3-parameter logistic regression models depicted. Vertical bars represent standard errors of the mean. The black dashed line and empty circles indicates the low infection group, and the dark grey dashed line and empty triangles indicates the high infection group.

only after the Wilcoxon signed-rank test. It should be noted that in a logistic regression, there is an inverse relationship between the growth constant and the actual growth rate. The significantly lower growth constant observed in the high infection group indicates a faster rate of growth. No significant difference in the growth rate for height was observed. However, all four cumulative growth variables of the high infection group reached their inflection point significantly sooner than the low infection group (Table 2), suggesting that the high infection group reached its maximum growth rate sooner. Dbh (Figure 2A) and basal area (Figure 2B) of the two infection groups were not predicted to diverge until after 45 years of age, while height growth curves began to diverge at about 20 years of age (Figure 3A), and volume growth curves began to diverge at 35 to 40 years of age (Figure 3B).

Results indicate a higher level of variability in the basal area and volume of the high-infection group when compared to the low-infection group, as indicated by the lower value of the adjusted r^2 for each logistic regression model. This may indicate variation in environmental conditions at early stages of growth for the trees, or variation in genetic resistance to mistletoe infection. Examination of the stem profiles also revealed that some trees in the high-infection group exhibited little or no evidence of growth reduction despite a high infection index (not presented). These trees could have been recently infected by Dwarf Mistletoe.

Discussion

No significant differences in tree age or competition levels between the two infections groups were observed indicating that Dwarf Misteltoe was was the key factor affecting Jack Pine growth. The lack of a significant difference in dbh between the heavily infected and lightly infected Jack Pine trees at the time of sampling likely reflects the young age of the subject trees and the duration of the infection period. Tinnin et al. (1999) found that there was a significant reduction in the diameter growth of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) heavily infected by *A. douglasii* (infection index = 5 and 6) when compared to non-infected trees (infection index = 0) for trees having mean ages between 78 and 84 years. In Lodgepole Pine, diameter growth was not significantly affected at stump height, but significant decreases in diameter growth were apparent at heights further up the stem because of greater stem taper (Baranyay and Safranyik 1970). Our study also showed that stem taper was significantly more pronounced in the high infection group.

At the time of sampling, basal area in the high infection group was not significantly different than that of the low infection group. Comparison of the logistic regression coefficients provided similar results to dbh, except that the high infection group was predicted to reach a significantly lower basal area compared to the low infection group as trees continue to grow after age 45. Assuming that basal area increment after the age of 45 years will continue to follow that predicted by the logistic regression model, the projected maximum basal area of the high infection group was approximately 57.9% lower than that of the low infection group. Pierce (1960) also found a 68.5% reduction in basal area for heavily infected Douglas-fir, and a 41.0% reduction in moderately infected Douglas-fir.

Of the significantly affected growth variables, height increment showed a reduction first, i.e., between the ages of 20 and 25 years. Pierce (1960) also found that differences in height were statistically significant between all infection classes, in contrast to diameter. This corresponds with the highly significant 20.2% lower tree height in heavily infected trees in this study. The greater sensitivity of this variable is likely due to the initial response of trees to Dwarf Mistletoe infections. Dwarf Mistletoe infected trees accumulate a high level of biomass in their brooms, which detracts the allocation of resources from biomass production elsewhere in the tree (Tinnin and Knutson 1980). In contrast to the other growth variables, height of the high-infection group had similar variability to the low-infection group, as indicated by similar adjusted r^2 values in the logistic regression curves. This suggests that height growth is less sensitive to temporal changes in factors such as stand density and competition (Avery and Burkhart 2002). Height growth diverged between the two infection groups at a much earlier age than volume, diameter, or basal area, further suggesting that height growth begins to show significant decreases shortly after the development of brooms and loss of apical dominance (Tinnin and Knutson 1980).

At the time of sampling, there was a 33.3% lower average total volume in the high infection group, which was mostly due to a significant reduction in tree height. However, despite early reduction in height growth, volume growth of the heavily infected trees was not significantly affected until 30 to 40 years of age. Our values very closely correspond with those reported by Baranyay and Safranyik (1970), where a group of infected Lodgepole Pine trees with an average age of 37 showed a 35.5% reduction in volume. From the logistic growth model, it was found that the predicted maximum average volume of the high infection group was 83.9% lower than the low infection group. This projected value exceeded the estimated volume reduction in infected stands made by Baker et al. (1992), which was between 53.4% and 70.3% depending on the level of potential crown closure. However, it should be noted that our findings reflected the volume loss in individual trees, and not the volume loss as averaged through an entire stand.

In conclusion, this study confirmed the significance of the impact of Dwarf Mistletoe on the growth of commercial Jack Pine forests, and the potential economic loss due to severe infection. Despite early reduction in height growth, volume growth of the heavily infected trees was not significantly affected until 30 to 40 years of age. Further study on the effects of Dwarf Mistletoe over a wider range of age classes and site indexes would be beneficial in modelling the impact of the parasite.

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