THE EFFECT OF DWARF MISTLETOE ON THE PRODUCTIVITY OF JACK PINE TREES IN BELAIR PROVINCIAL FOREST, MANITOBA

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Abstract

Dwarf Mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.) is an important pathogen of the important commercial tree species jack pine (*Pinus banksiana* Lamb.). Dwarf mistletoe alters the growth form, suppresses growth and reduces volume and overall wood quality of the host tree. Few studies have quantified these effects on jack pine in Manitoba. We hypothesize that there is a significant reduction in diameter at breast height, basal area, height, and volume growth between heavily infected, and lightly to non-infected jack pine trees. Statistical analysis was performed to compare the growth of 10 lightly to non-infected, and 10 heavily infected jack pine trees growing in Belair Provincial Forest in Manitoba. Stem analysis was performed on each tree to determine annual growth increments, and average cumulative growth was modeled using a 3-parameter logistic regression model. Results showed that 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 was observed. Logistic growth models predicted significant reductions in maximum basal area (57%), height (29%) and volume (84%), but no significant reduction in maximum diameter at breast height. Our results support those observed in other species, and highlights the importance of dwarf mistletoe on jack pine productivity.

Keywords: dwarf mistletoe, Manitoba, jack pine, productivity, tree growth

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Introduction

Ecology of jack pine

Jack pine (*Pinus banksiana* Lamb.) is an evergreen coniferous tree species belonging to Pinaceae that is native to central and eastern Canada, as well as the north-central and northeastern United States (Rudolph and Laidly, 1990; Sims *et al.*, 1990). It is a common tree species in the boreal forest ecosystem, growing well in a continental climate characterized by long, cold winters, and short cool to warm summers. Jack pine generally grows best on well-drained loamy sands, preferring less alkaline soils. It is also capable of growing on very dry sandy to gravely sites unsuitable to most other trees (Rudolf, 1965). The jack pine tree can range from 19 m to 30 m in height, and 12 to 38 cm in diameter, and can reach ages of 90 to 160 years (Sims *et al.*, 1990). This species is classified as being highly shade intolerant, and it is important as an early-successional species. It is particularly adapted to the fire regimes characteristic of the northern boreal forest. Jack pine has serotinous cones that require high levels of heat to open prior to seed dispersal, and seed germination is most successful on exposed mineral soil (Burns and Honkala, 1990; Sims *et al.*, 1990) making it ideal for early colonization after fires that expose the mineral soil under the duff layer. Because of these characteristics, jack pine usually occurs as even-aged, post-fire forests in pure coniferous stands, or mixedwood stands (Sims *et al.*, 1990). Some common overstory associations include black spruce (*Picea mariana* (Mill.) BSP), trembling aspen (*Populus tremuloides* Michx.) and white birch (*Betula papyrifera* Marsh.). The species is harvested extensively for a range of uses, including wood pulp for paper, poles, and as general construction timber (Farrar, 1995). The tree is desirable because of its pole-like growth form, and as a pioneer species, it is relatively easy to regenerate following a harvest.

Impact of dwarf mistletoe

An important pathogen for jack pine is the lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.). There are about five species of dwarf mistletoe that are 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, and jack pine is one of the principal hosts of *A. americanum*. Other susceptible hosts include lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.), but occasionally other species of trees such as *P. flexilis*, *P. jefferyi* and *P. albicaulis* may be infected as well (Hawksworth and Wiens, 1996). Brandt (1997) reported that as of 1996, 430,202 ha of forest with severe *A. americanum* infections had been mapped in Alberta, Saskatchewan and Manitoba. In Manitoba, Baker *et al.* (1992) found that approximately 8.7% of mature jack pine stands in important growing regions was infected by dwarf mistletoe. This has resulted in a volume loss of up to 7.9% in these regions (525,224 m^3 out of 6,648,405 m^3) and a volume loss of up to 70.3% within the infected stands. Aside from a significant loss in wood volume, there is also a general reduction in wood quality, making the wood less merchantable. Piirto *et al.* (1974) found that the wood of lodgepole pine infected by *A. americanum* exhibited greater longitudinal shrinkage, a lower percentage of latewood, and was generally weaker in strength when compared to uninfected trees.

Ecology of dwarf mistletoe

Dwarf mistletoes are parasitic angiosperms belonging to Viscaceae. The plant has no photosynthetic leaves, deriving all nutrients from its host through the haustoria, via direct tracheary element connections, and indirectly, through an apoplastic continuum between parasite and host parenchyma (Calvin and Wilson, 1995). The life cycle of *A. americanum* as described by Hawksworth and Wiens (1972) (Figure 1) begins as airborne seeds with a viscous coating are intercepted by the needles of a potential host during the fall season, and then washed down to the twig tissue. The following spring, seed germination occurs. To successfully germinate, the seed usually requires contact with young (< 5 years old) host branch tissue, however *A. americanum* can infect tissues up to 60 years old (Hawksworth, 1954). Evidence also suggests that infection success is primarily dependent upon the level of seed displacement due to wind, snow, or rain (Robinson and Punter, 2001). Once the seed germinates, the penetration of the haustoria into the host tissue occurs throughout the rest of the growing season. This is followed by a four-year incubation period after which the first aerial shoots appear. Dwarf mistletoe is dioecious, and the shoots will develop into separate male and female plants. This is followed by a further two years of development, in which micro and megasporogenesis and insect pollination occurs. The female plants will then develop fruit during spring, the year after fertilization. That fall, after the fruit matures, the seeds are explosively discharged and intercepted by other potential hosts. Seeds are dispersed up to 18 m. from the host canopy through explosive discharge from the fruit (Punter and Gilbert, 1991).

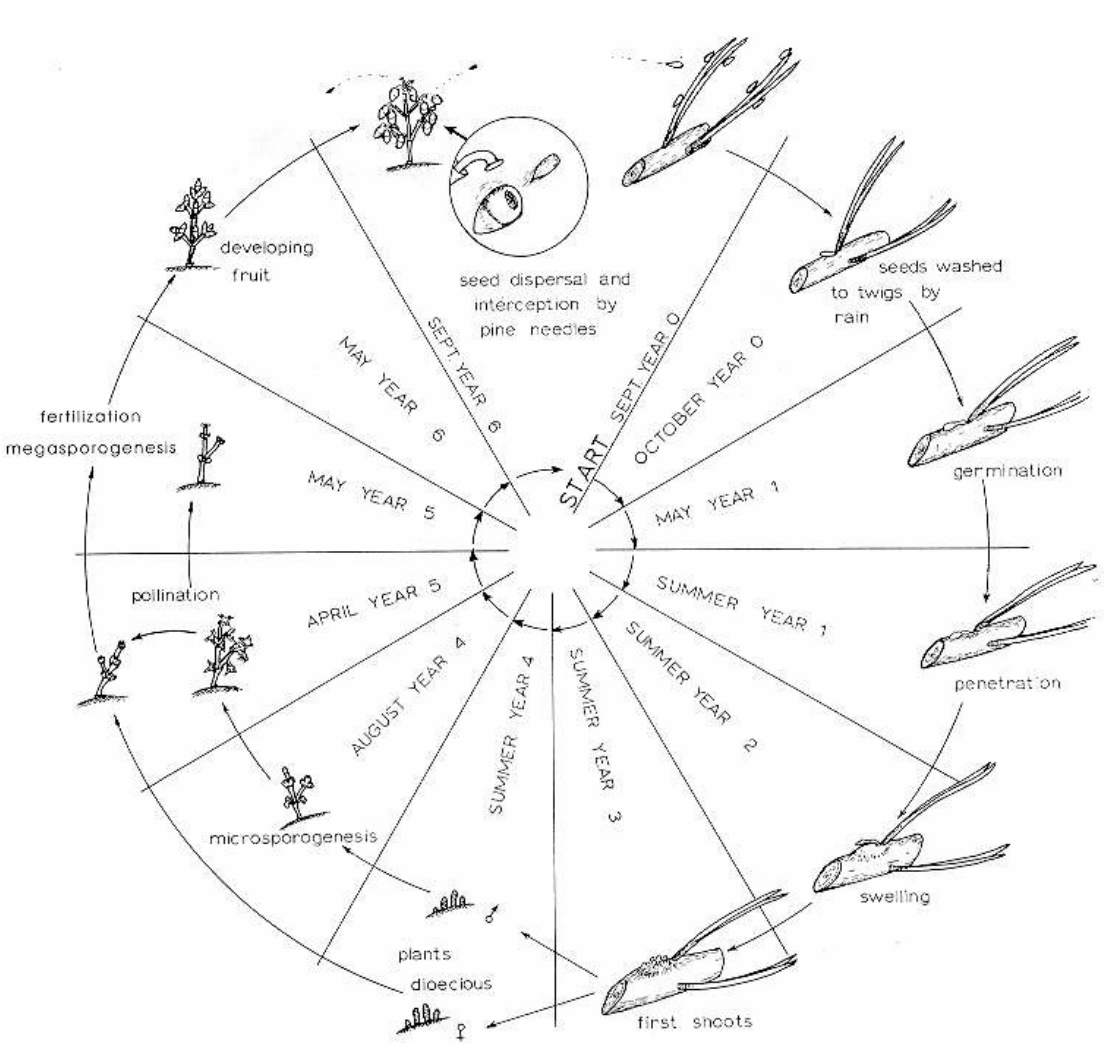

Figure 1: Life-cycle of the lodgepole pine dwarf mistletoe (*Arceuthobium americanum*). From Hawksworth and Wiens (1972).

Interaction with host

Generally, dwarf mistletoe deprives the host of water and nutrients, thus reducing height and diameter growth as well as seed production, and generally weakens the tree (Franc and Baker, 2000). Often, the first obvious indication of a mistletoe infection is irregular branching and growth in the crown. Dwarf mistletoe alters the growth form of trees by disrupting apical dominance (Tinnin and Knutson, 1980), causing the formation of witches' brooms. Because the mistletoe derives all of its nutrients from the host tissue and fixes little or no carbon dioxide for it's own use, centres of infection (witches' brooms) act as nutrient sinks for metabolites produced in other parts of the host (Hull and Leonard, 1964a, 1964b). A study done on Douglas fir and western larch by Sala *et al.* (2001) showed a significant increase in leaf to sapwood ratios in heavily infected trees, altering resource allocation processes in trees, and reducing the overall water use efficiencies. The rapid increase in biomass in the witches' brooms acts as a sink for resources, and causes a significant decrease in wood production.

The long incubation period of the parasite poses a problem in the early detection of initial infections. There have been studies done to determine an alternate means of dwarf mistletoe detection prior to the appearance of aerial shoots or brooms. Marler *et al.* (1999) suggested a polymerase chain reaction method for detecting the presence of mistletoe DNA during the endophytic stage of infection prior to shoot appearance. This method was successful, but only positively identified up to 38% of the infected trees. In forest management situations, the current most effective methods of treatment are removal of heavily infected overstory trees, and isolation of infected stands by planting buffer zones of incompatible host species (Franc and Baker, 2000). Pruning infected branches is generally not effective due to difficulty in detecting latent infections (per.

comm., 2003). Even-aged silvicultural systems are often effective in controlling dwarf mistletoe, as the entire overstory may be removed. Hawksworth and Wiens (1996) suggested retaining only non-infected trees when using the shelterwood system, favouring non-susceptible trees for regeneration, and taking advantage of barriers such as open spaces and non-susceptible trees to hinder the spread of infections.

Purpose of study

Few studies have been done to quantify the productivity loss on individual jack pine trees due to infection by dwarf mistletoe. There have been studies on the effect of mistletoe on the growth of other tree species, such as lodgepole pine (Baranyay and Safranyik, 1970) and Douglas fir and western larch (Pierce, 1960; Tinnin *et al.*, 1999). Within Manitoba, Baker *et al.* (1992) have done studies on the effect of dwarf mistletoe on jack pine trees at the stand scale, particularly focusing on loss of wood volume in the forest stands. The objectives of this study are to investigate the growth of dwarf mistletoe-infected jack pine trees with respect to five different growth variables. These include diameter at breast height (dbh), basal area, height, volume and stem form. For each of these variables, total tree dimensions, as well as cumulative growth of infected trees was compared to the dimensions and growth of non-infected trees. I hypothesized that there was a significant reduction in total cumulative dbh, basal area, height and volume growth rate in trees infected with dwarf mistletoe. This information will be useful in conjunction with the results of studies on the impact of dwarf mistletoe at the stand scale. It may also confirm and/or improve the accuracy of estimates of volume loss and the economic impacts due to dwarf mistletoe.

Methodology

Sampling Area

The sampling area is located approximately 97 kilometres northeast of Winnipeg, Manitoba (Figure 2). More specifically the area is within Belair Provincial Forest (50°38'N, 96°29'W) located on the eastern side of Lake Winnipeg near Victoria Beach (Figure 2). The bedrock in the area consists of Archean granites and gneisses (Manitoba Geological Survey, 2002). The closest meteorological station is located approximately 21 km from the sampling site, at Pine Falls, Manitoba. The site is located in the boreal eco-climatic zone, and is continental (Burton *et al.*, 1998), with cold winters reaching an average minimum temperature of –23.5°C in January, and warm summers reaching an average maximum temperature of 25.3°C in July. The mean annual temperature recorded at Pine Falls is 2.1°C, and the mean annual precipitation is 538.5 mm (Environment Canada, 2002).

The sampling area is within a pure, fire-originated jack pine stand, and is bound by Provincial Highway 11 to the south, and a recent cutover to the north (Figure 3). Physically, the sampling site is characterized by generally level, homogeneous terrain, minimising differences in the effect of slope and other physical factors on growth between subject trees. The elevation at the site is approximately 250 m above sea level, and the area is scattered with concentrated centres of dwarf mistletoe infection.

Sampling Methods

Three transects were established approximately 25 m. apart, oriented in a north-south direction, extending north from Provincial Hwy. # 11 (Figure 3). A total of 10

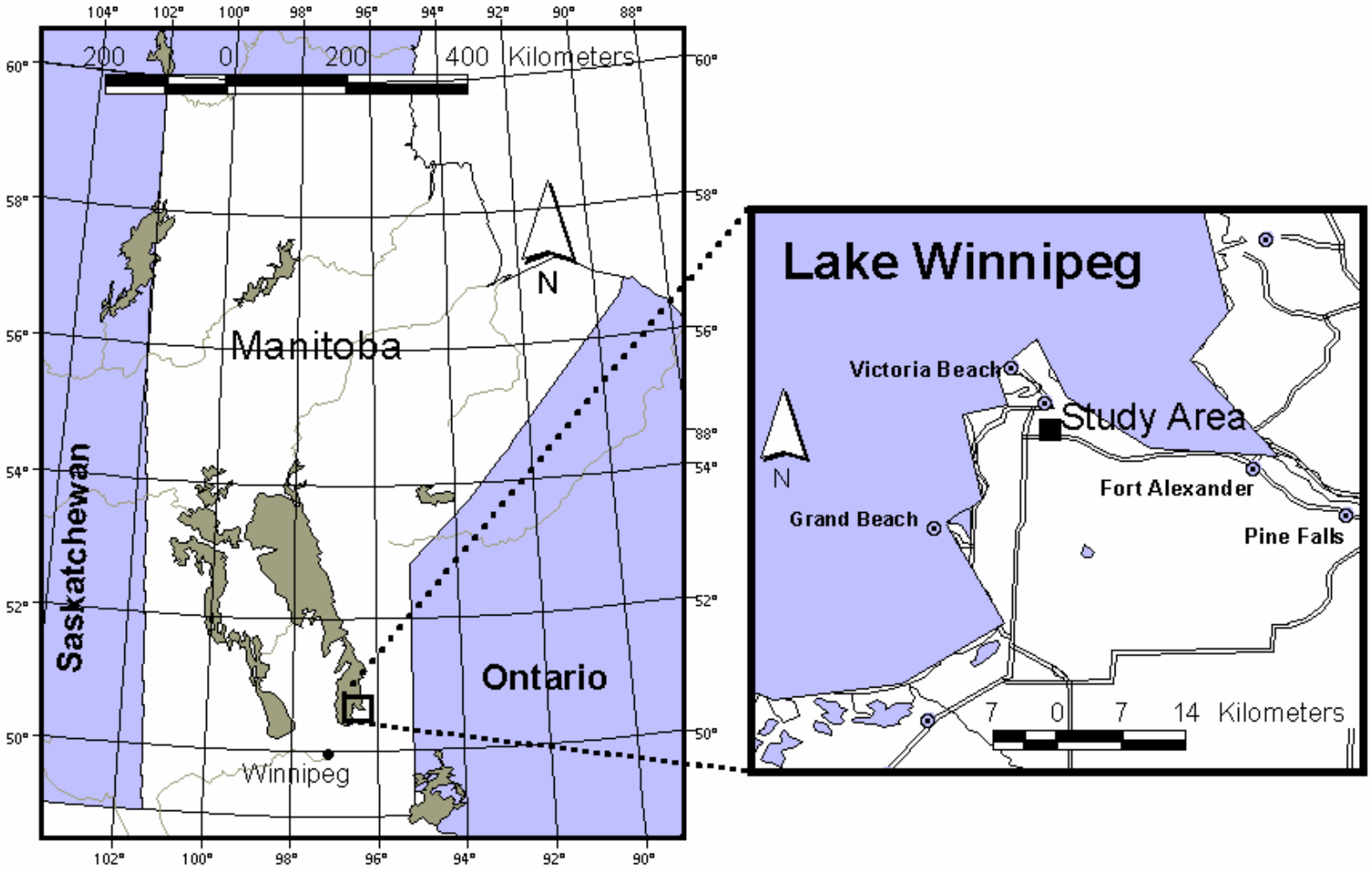

Figure 2: Location and general surroundings of study area. Area is indicated with a solid square in the expanded portion of the map. The closest meteorological station is located at Pine Falls.

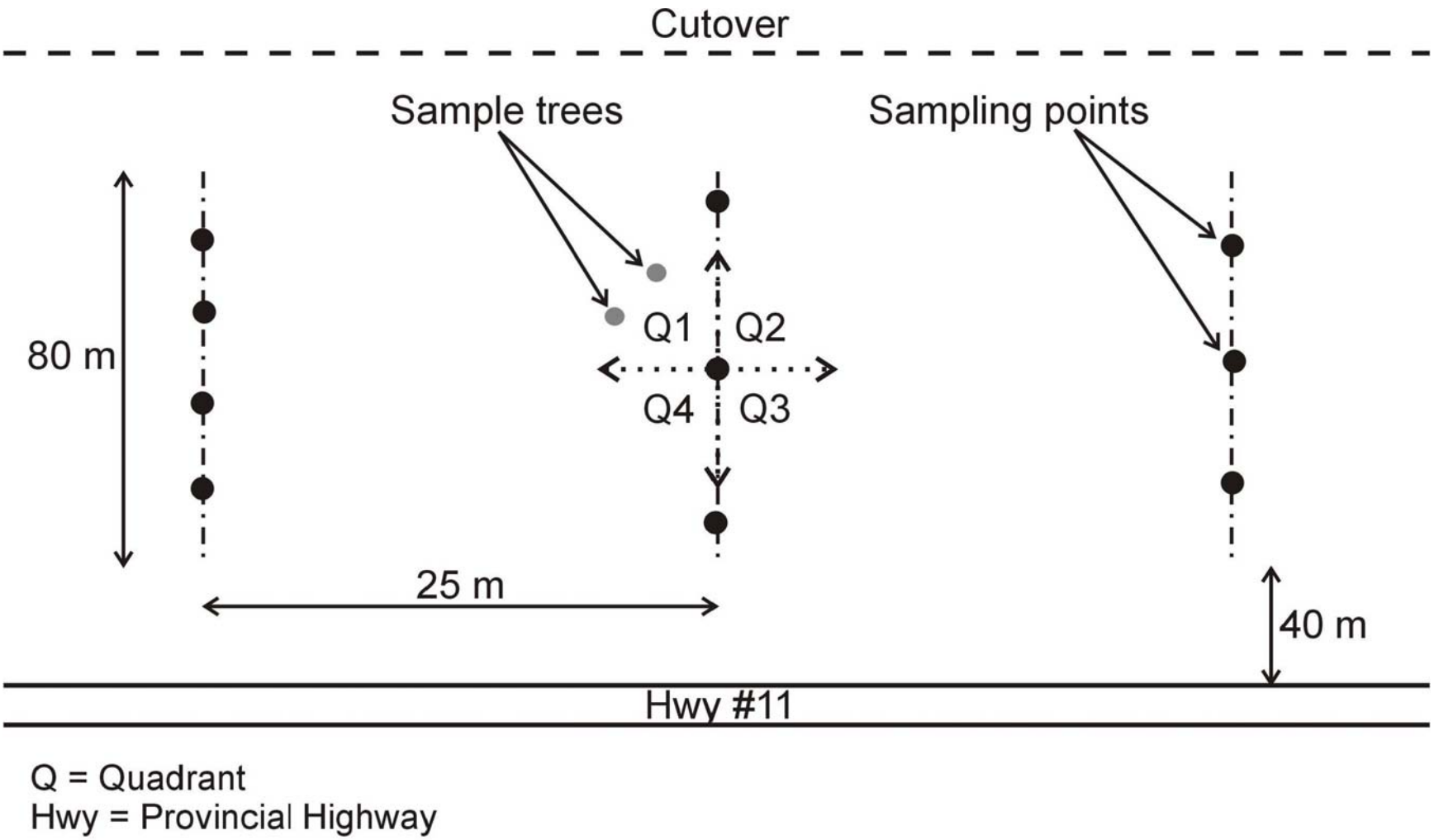

Figure 3: Description of the project sampling design. Layout is not to scale.

sampling points were randomly established along the three transects. Three points were located along two transects, and four points along one transect. Point position was selected with a random number table, with a condition that the number was between 40 and 100 m. to ensure the points were within the sample area with sufficient buffer zones to minimize edge effects from the recent cutover to the north, and the highway to the south. Each point represented the centre of a plot with no fixed area. The surrounding area was divided into four quadrants by projecting a line crossing perpendicular to the transect at the point. A number was randomly drawn to select the quadrant in which the two nearest trees to the point were selected; one heavily infected tree and the nearest lightly or non-infected tree between approximately 40 and 60 years of age. Tree age was roughly determined by counting the annual growth rings of core samples obtained by an increment borer, and trees with noticeable fire scars 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 for ease in stem analysis. If a suitable tree was not found within 50 m of the plot centre, sampling was done in the next quadrant in numerical order. Once candidate trees were selected, they were marked with a number (from 1 to 20), marked with a north-orientation line, and marked at 0.5 m and 1.3 m (breast height). Sampling took place from July 30 to August 2, 2002.

Data Collection

Prior to felling, the infestation index of the trees was estimated using the Hawksworth 6-class system (Hawksworth, 1977). With this method, the tree crown was divided into thirds, and the level of infection in each third was rated on as scale from 0 to 2; where 0 means there was no visible infection, 1 means there was less than 50% of

the branches infected, and 2 means there was more than 50% of the branches infected. Ratings for each third of the crown were then summed to give the infection rating for the entire tree. Presence of infection was most easily determined from the ground by the presence of "witches' broom"-like growth. Trees with an infestation index of 0 to 3 were placed within the non- to lightly infected group, and trees with an infestation index of 4 to 6 were placed in the moderately to heavily infected group. The GPS position of each tree was recorded, and in order to take into account the competition of other trees, the dbh and distance of the nearest competitor tree in each direction (N, E, S, W) were measured.

Following felling of the trees, the stems were marked with paint in the following sequence so they could be sectioned: base (0 m), 0.5 m, 1.3 m, 2 m, 3 m, 4 m, etc., continuing in approximately 1-metre intervals along the stem until stem diameter was less than 1 cm. For ease of stem analysis, I avoided taking sections at points of the stem where branches emerge, and the adjusted height was recorded. The north-orientation line was extended to the tip of the stem, and the total tree height was recorded. The stem was then divided at each mark; from 0 m. to the tip, and a cross-section slab was removed at the base of each segment. Tree number and stem position were then marked on the upper side of each cross-section, as well as a mark indicating the north-orientation. For each cross-section, diameter inside bark and diameter outside bark were measured along two diameters crossing perpendicular to each other at the centre. At the laboratory, the lower side of each cross-section was sanded and polished, and the age at the cross-section height was recorded. The pointer-year method of cross-dating was used to validate the age of each cross-section (Yamaguchi, 1991). Pointer years with unusual characteristics such as narrow growth rings or thin latewood were indicated in a skeleton plot. Strong

pointer years were used to verify dating between the cross-sections. Following dating, the width of each annual growth ring was measured electronically using the WinDENDRO™ v. 2002a program (Régent Instruments Inc., 2002). Each cross-section was scanned with a high-resolution flatbed scanner and saved as a digital image in "*.tiff" format. Where possible, an image resolution of 800 dpi was used, and for cross-sections exhibiting high levels of suppression, a resolution of 1600 dpi was used. For one tree (Tree 5), suppression was too great for ring detection by the WinDENDRO™ program, so measurements were performed manually using a Velmex measuring stage. Ring widths were measured, starting at the pith, along four radial paths in the north, east, south and west directions.

Data analysis

Data obtained in the field was used to determine the significance of differences between the two infection groups with regards to infestation index, age, competition, dbh, basal area, total height, total volume and stem form at the time of sampling. The competition index was determined using a modification of 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 simply by using the formula for the area of a circle:

$$BA = \frac{\pi \cdot dbh^2}{4(10,000)}$$

Where *BA* is basal area square meters, and *dbh* is the field measurement of diameter (at breast height) in centimetres. Total tree volume without bark was calculated by determining the volume of each stem segment between the cross sections taken for stem analysis. The volume of each segment was then combined to get the total stem volume. This was accomplished by applying Smalian's formula for volume (Avery and Burkhart, 2002) to each segment:

$$V = \frac{A_b + A_u}{2} \cdot L$$

Where V is the volume of the stem segment, A_b is the area of the base of the segment, A_u is the area of the top of the segment, and L is the length of the segment, determined by taking the difference in height between the cross-sections taken at the upper and lower ends of the segment. Smalian's formula was selected for ease of execution. Tree stem form expressions were determined using the Girard form class (Avery and Burkhart, 2002):

$$F = \frac{Q_5}{Dob_{1.3}}$$

Where F is the Girard form class, Q_5 is the quadratic mean diameter inside bark at 5 metres, and $Dob_{1.3}$ is the diameter outside bark at breast height. In this case, the quadratic mean diameter was taken at the section nearest 5 metres. All variables were then tabulated in a spreadsheet, and grouped by their infection class (low infection or high infection). 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 the

significance of differences between the populations of each infection group. This test also minimizes the importance of outliers in the calculations. U-test calculations were made using the statistical analysis program SPSS for Windows, Release 11.0.0 (SPSS Inc., 2001).

Stem analysis was performed on each tree to determine tree growth over time for the following variables: Dbh, basal area, height, and volume. Annual growth increments were calculated using XLSTEM™ 1.3a (Régent Instruments Inc., 1999). The program calculates cumulative radial growth from the data obtained from the WinDENDRO™ program using the following methods. Average radial growth was calculated from the four measurement paths using the quadratic mean method:

$$R_{Ave} = \sqrt{\frac{\sum R^2}{4}}$$

Where R_{Ave} is the quadratic mean radius, and R is the cumulative radius of a measurement path for any given tree age. Basal area is then calculated from the quadratic mean radius by using the formula for calculating the area of a circle. Annual height increment for each segment was calculated using a linear interpolation method:

$$H_i = \frac{\Delta h}{\Delta a}$$

Where H_i is annual height increment for the stem segment, Δh is the difference in height between the upper end and base of the segment, and Δa is the difference in age between the upper end and base of the segment. Annual volume increment for each segment was calculated by using the formula for the volume of a frustum of a cone:

$$V_{cone} = \frac{\left(R_b^2 + R_b \cdot R_u + R_u^2\right) h \cdot \pi}{3}$$

Then volume increment for the entire tree:

$$V_{tree} = \sum \left(\frac{V_{cone}}{1000} \right)$$

Where R_b is the radius at the base of the segment (mm), R_u is the radius at the upper end of the segment (mm), and h is the length of the segment (m).

Once annual growth increments were calculated for each variable, mean height was plotted against the mean radius of each individual growth year along the length of the stem. The resulting graphs (Figure 4, Appendix 1) illustrate annual volume growth over time, as a function of height and radial growth. Average growth curves were then compared for each infection group with regards to cumulative dbh, basal area, height and volume growth. Tree growth was compared through time with reference to tree age, rather than calendar year. The mean cumulative growth of 10 trees for each infection group was then calculated by computing the average cumulative growth for each year, as well the standard error of the mean, up to a maximum tree age of 45 to retain a sufficient N value (minimum: $N = 9$) for each growth year. This was repeated for each variable. The average cumulative growth data and standard error of the mean for each variable was then plotted in a graph, with separate curves for each infection group. Predicted growth curves were then calculated for each tree using a non-linear regression model. The 3-parameter logistic regression model was found to best fit the actual growth curves for each variable:

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

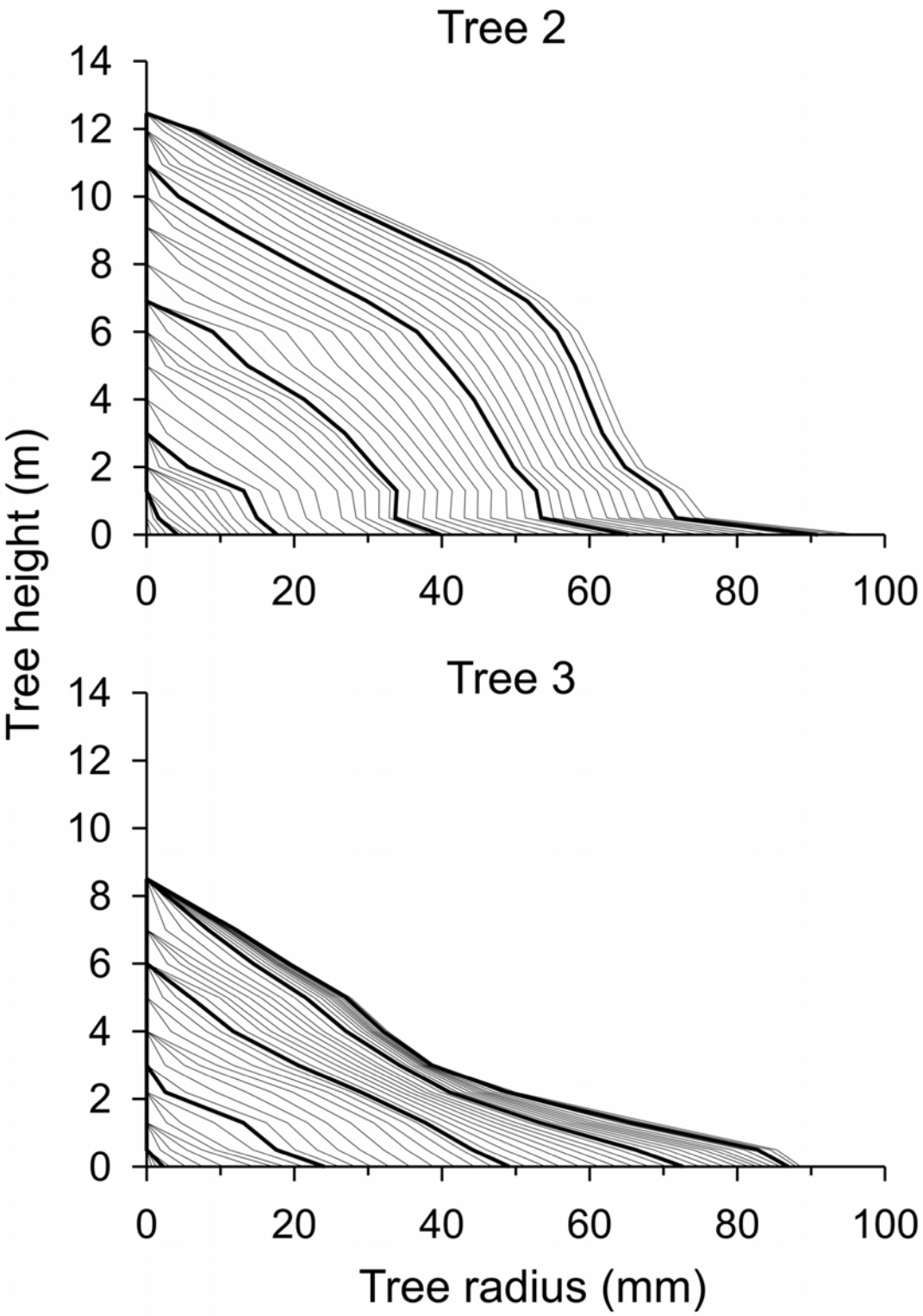

Figure 4: Stem profiles for a typical tree from the low infection group (Tree 2) and from the high infection group (Tree 3). Individual lines represent a single growth year. Bold lines indicate decades, with the year 2000 being at the far right of the graph.

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. Since each of these three parameters define the shape of the cumulative growth curves, the significance of differences between the means of each of the three values between infection groups was calculated using the Mann-Whitney U-test ($\alpha = 0.05$). The logistic regression model was then applied to the ten replicates for each infection group, and the resulting predicted growth curves were then plotted, extending the maximum number of growth years to $N = 60$. This was repeated for each cumulative growth variable.

Results

Total tree growth

Results from the Mann-Whitney U-tests that had been performed on the field data confirmed that the Hawksworth Infestation Indices were significantly different between the two infection groups (Table 1). The two infection groups showed no significant difference in age, despite one sample in the high infection group being much older (Table 1). There was also no significant difference in competition index between the two infection groups, revealing that trees in both groups had experienced similar levels of competition. The U-test showed no significant difference between the two infection groups with regards to diameter at breast height, and basal area in 2002. The two infection groups, however, showed a significantly different height, volume and form class (Table 1). Specifically, trees in the high infection group showed a 20.2% lower height, and a 31.9% lower volume on average, as well as a higher amount of stem taper. It was interesting to note that the tree with the highest volume and the tree with the lowest volume both belonged to the high infection group (Table 1).

Cumulative tree growth

Analysis of the three growth parameters of the logistic regression model showed results that were generally reflective of the total tree growth at age 45 (Table 2). Results showed that the high infection group had significantly lower maximum height and volume, as predicted by the asymptotic values of the regression model. In contrast to total growth at age 45, however, the maximum basal area was also lower for the high infection group (Table 2). Maximum dbh did not differ significantly at the 5% significance level, but the high infection group was significantly lower at the 10%

Table 1: General characteristics of heavily infected and non-infected trees at time of sampling (age 45). Significance of Mann-Whitney U-test differences are shown as a probability (*P*) value ($\alpha = 0.05$).

		Low infection				*High infection*				
	N	Max.	Min.	$\overline{X}$	s	Max.	Min.	$\overline{X}$	s	***P***
Infestation index	20	2.0	0.0	1.2	0.92	6.0	4.0	5.2	0.63	0.000
Tree age	20	48.0	42.0	46.3	1.95	82.0	44.0	50.0	11.35	0.728
Competition index	20	3.34	0.77	1.85	0.95	1.89	0.66	1.29	0.47	0.257
Dbh (cm)	20	19.20	13.10	16.17	1.19	19.60	11.50	15.45	2.61	0.544
Basal area (m^2)	20	0.022	0.012	0.017	0.00	0.024	0.007	0.016	0.01	0.544
Height (m)	20	14.10	10.90	12.65	1.23	13.30	8.30	10.10	1.70	0.004
Volume (m^3)	20	0.16	0.09	0.12	0.02	0.17	0.04	0.08	0.04	0.019
Form coefficient	20	0.83	0.64	0.73	0.06	0.76	0.35	0.56	0.13	0.004

Table 2: Results of Mann-Whitney U-test on significance of differences between four sets of logistic growth parameters for each infection group. Significance is based on a probability (*P*) value (α=0.05). The three growth parameters of the predicted logistic curve are *a* (theoretic maximum), *b* (growth) and x_0 (inflection point).

		Low infection group					**High infection group**					
		N	Max	Min	$\overline{X}$	**s**	**N**	Max	Min	$\overline{X}$	*s*	*P*
Dbh (cm)	a	10	22.03	14.12	17.29	2.70	10	20.97	8.87	13.97	3.83	0.059
	b	10	-1.84	-3.30	-2.46	0.41	10	-2.46	-4.29	-3.26	0.60	0.005
	x_0	10	3.62	2.33	2.85	.47	10	2.85	1.92	2.32	.38	0.023
BA (m^2)	a	10	0.071	0.019	0.038	0.019	10	0.032	0.007	0.016	0.0082	0.002
	b	10	-2.32	-3.51	-2.84	0.41	10	-3.07	-5.27	-3.84	0.62	0.001
	x_0	10	0.0093	0.0034	0.0054	0.0017	10	0.0039	0.0025	0.0032	0.0005	0.001
Height (m)	a	10	24.37	14.99	19.59	3.20	10	20.63	9.28	13.90	3.83	0.008
	b	10	-1.71	-2.64	-1.98	0.29	10	-1.44	-2.65	-2.07	0.39	0.326
	x_0	10	42.01	24.38	32.66	5.50	10	49.34	20.56	27.58	8.56	0.034
Volume (m^3)	a	10	3.237	0.120	0.604	0.939	10	0.214	0.042	0.097	0.065	0.001
	b	10	-2.98	-4.36	-3.60	0.42	10	-3.12	-6.07	-4.09	0.80	0.082
	x_0	10	0.112	0.040	0.060	0.021	10	0.049	0.031	0.036	0.006	0.001

significance level (Figure 5). The logistic regression model, projected to an age of 60, predicts that there will a 21.1% lower basal area (Figure 6), 23.4% lower height (Figure 7), and 42.1% lower volume (Figure 8).

Results showed that there was a significantly higher growth rate for dbh (Figure 5) and basal area (Figure 6) in the high infection group, as indicated by the growth constant (Table 2), but there was no significant difference in the growth rate for height and volume. However, all four cumulative growth variables of the high infection group reached their inflection point sooner than the low infection group (Table 2), suggesting that the high infection group reached its maximum growth rate sooner. Dbh (Figure 5) and basal area (Figure 6) of the two infection groups were not predicted to diverge until after 45 years of age, but growth curves showed that height growth began to diverge after approximately 20 years of age (Figure 7), and volume growth began to diverge after approximately 35 to 40 years of age (Figure 8).

Results indicate a higher level of variability in the dbh, 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. Examination of the stem profiles also revealed that some trees in the high-infection group exhibited little or no evidence of suppression despite a high infection index (Tree 16 and 18 in Appendix 1). This may have been due to these subjects being only recently infected by mistletoe.

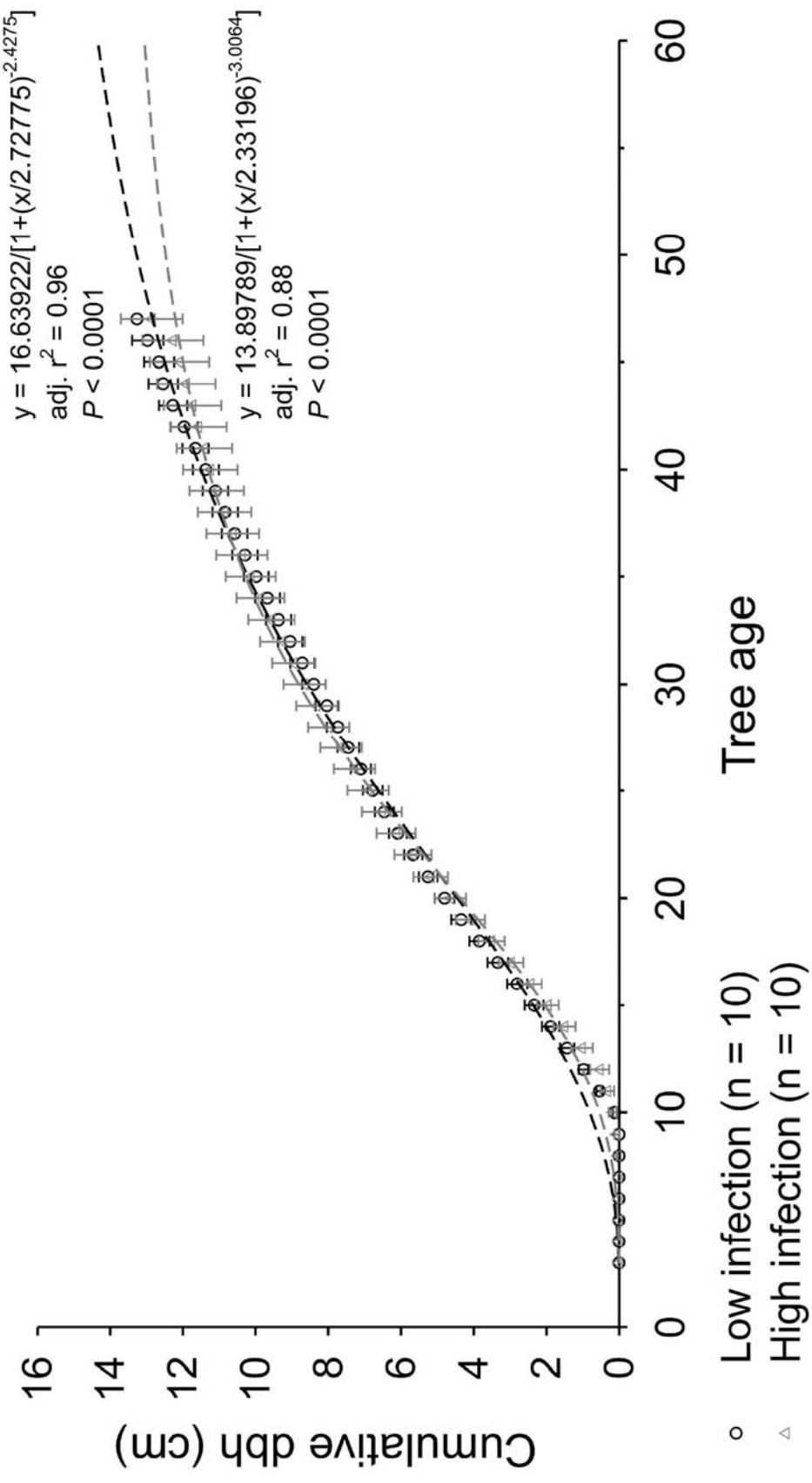

Figure 5: Average cumulative dbh growth of the two infection groups. Dashed lines represent predicted height growth to year 60 for the infection groups. Predicted growth curves were obtained using a 3-parameter logistic regression model which is presented next to the growth curves. Vertical bars represent standard error of the mean.

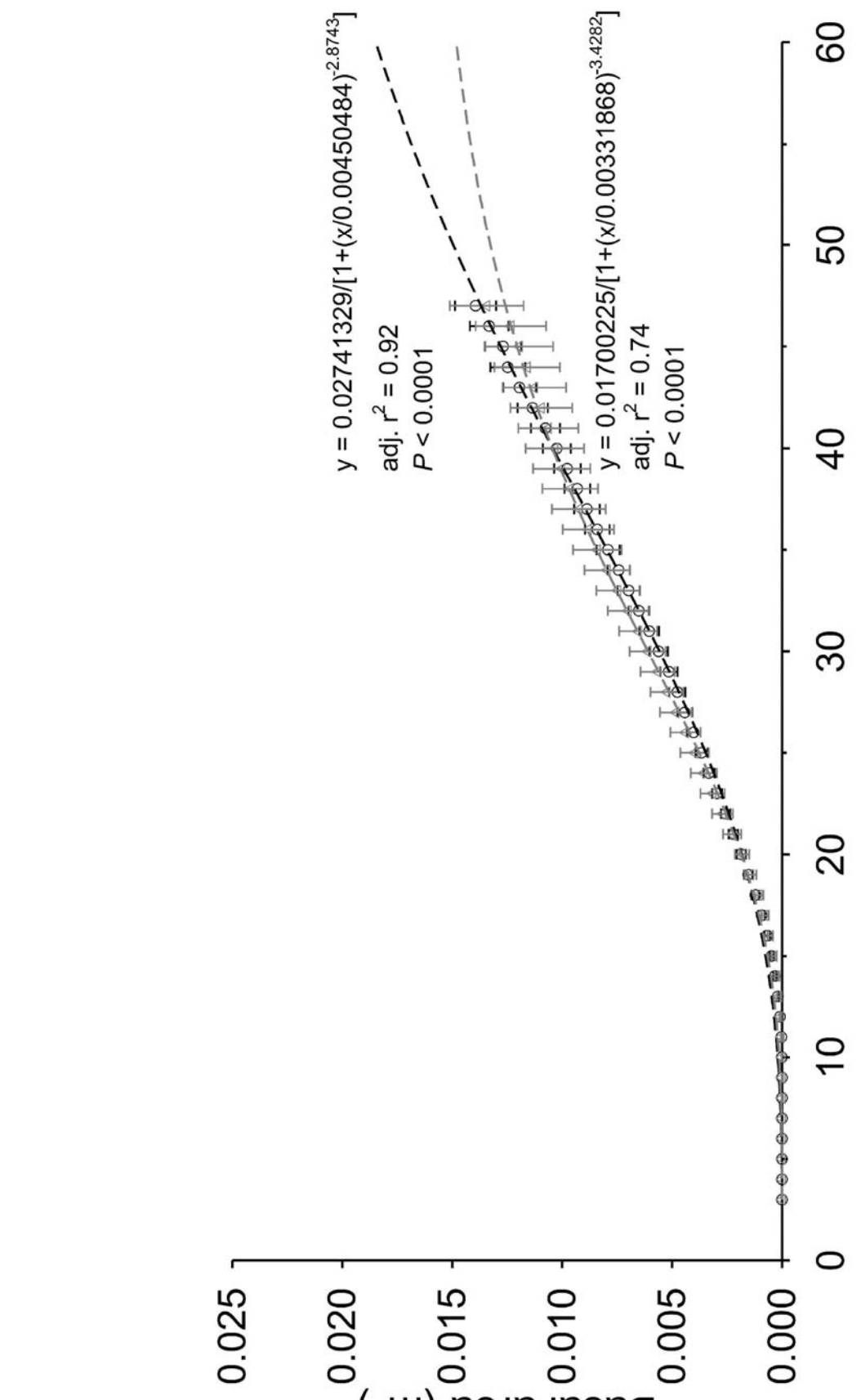

Figure 6: Average cumulative basal area growth for the two infection groups. Dashed lines represent predicted height growth to year 60. Predicted growth curves were obtained using a 3-parameter logistic regression model which is presented next to thegrowth curves. Vertical bars represent standard error of the mean.

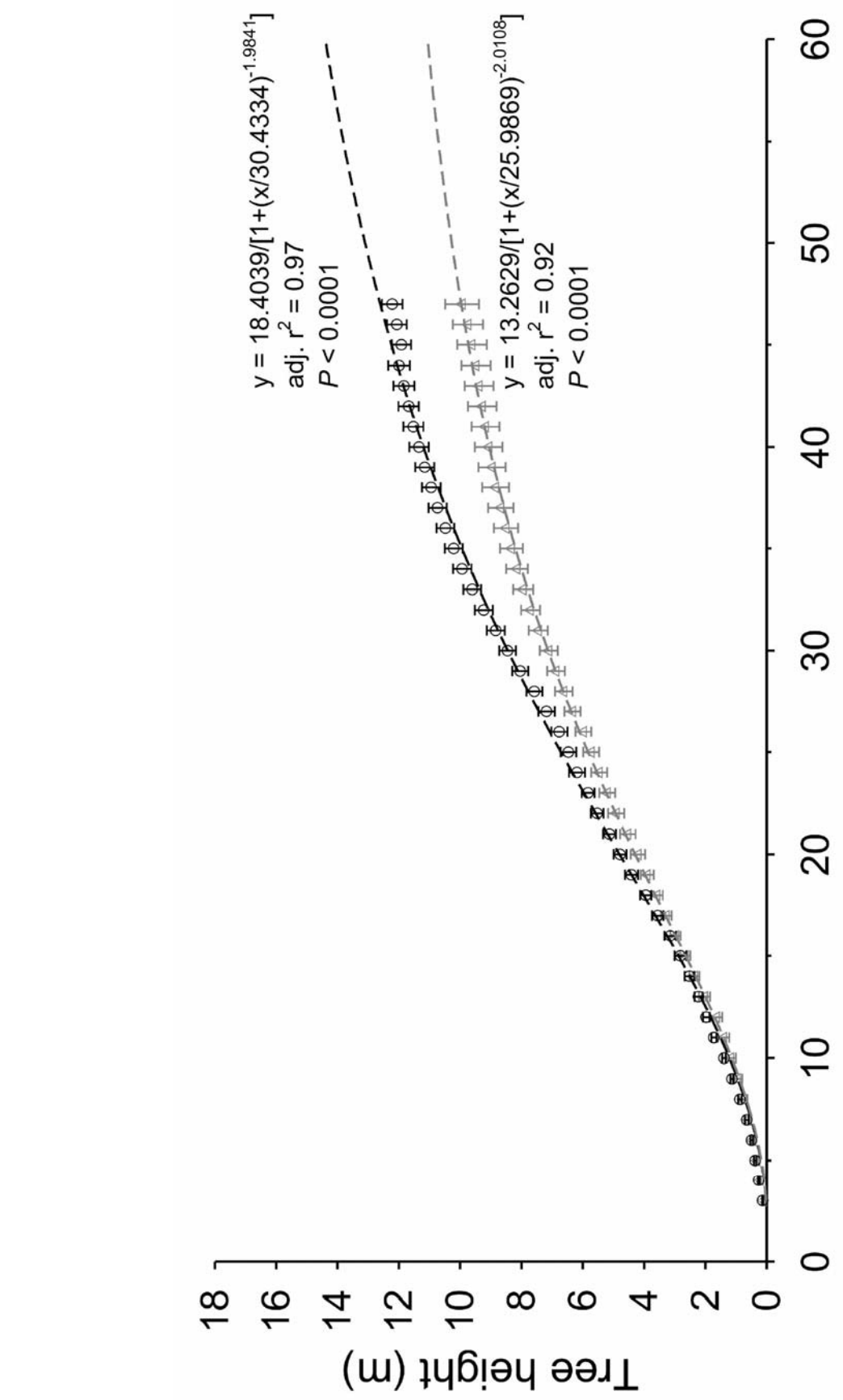

Figure 7: Average cumulative height growth of the two infection groups. Dashed lines represent predicted height growth to year 60. Predicted growth curves were obtained using a 3-parameter logistic regression model which is presented next to the growthcurves. Vertical bars represent standard error of the mean.

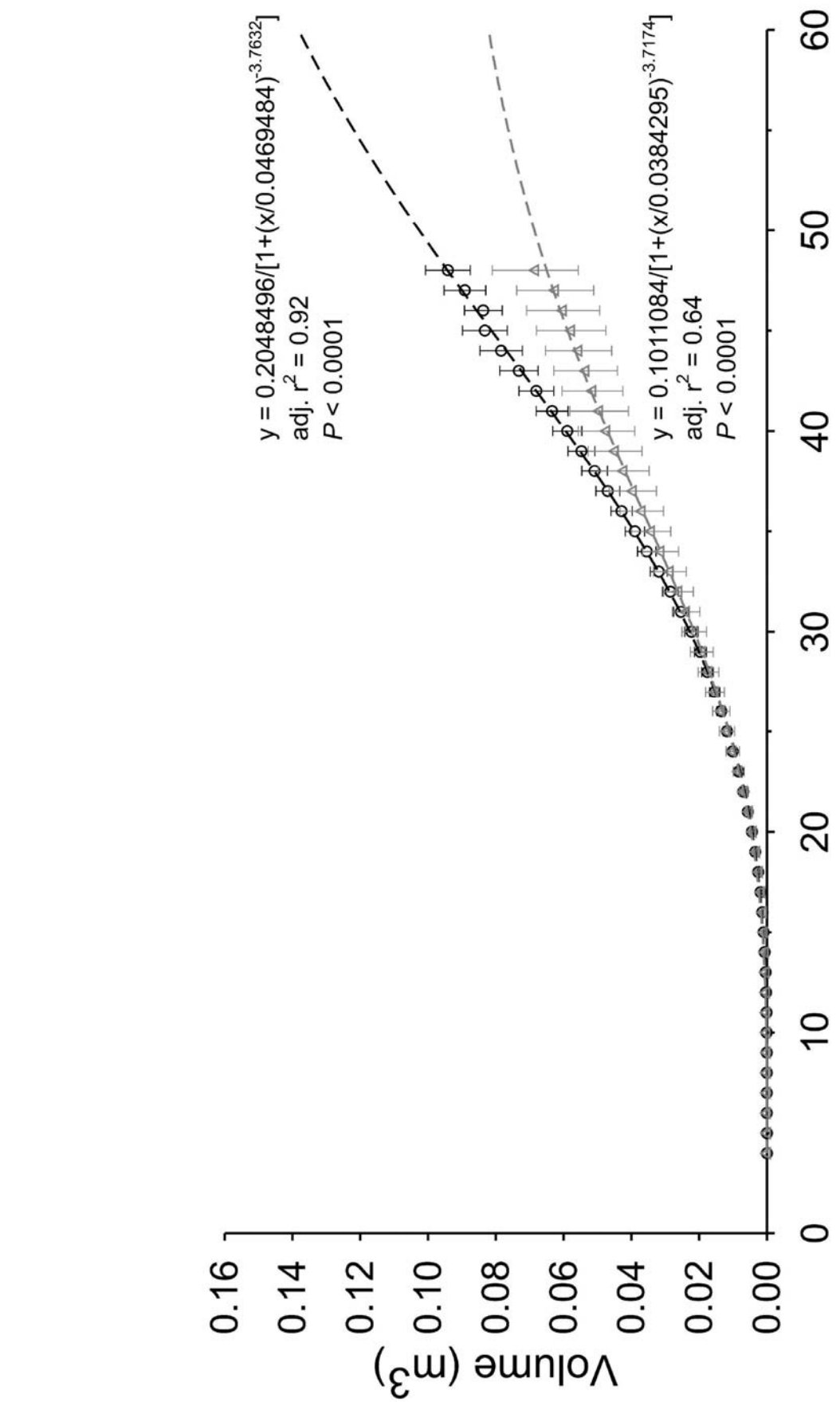

Figure 8: Average cumulative volume growth of the two infection groups. Dashed lines represent predicted height growth to year 60 for the infection groups. Predicted growth curves were obtained using a 3-parameter logistic regression model which is presented next to the growth curves. Vertical bars represent standard error of the mean.

Discussion

Site Characteristics

Statistical analysis confirmed that the major factor affecting jack pine growth in this study was dwarf mistletoe. There was no significant difference between the two groups (low infection, high infection) with regards to tree age or competition levels, and the site chosen for sampling had generally homogeneous terrain with regards to stand origin, slope variation and understory cover type. These characteristics greatly reduced the possibilities of any other factors than dwarf mistletoe contributing to differences in growth between the two infection groups.

Diameter at Breast Height

Statistical analysis did not reveal any significant difference in total dbh at the time of sampling, which did not support our hypothesis. This lack of significant difference between the two infection groups may have been due to 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 heavily infected trees (infection index = 5 and 6) when compared to non-infected trees (infection index = 0) for trees having mean age of between 78 and 84 years. Furthermore, Baranyay and Safranyik (1970) reported that the nature of diameter reduction of lodgepole pine was such that infected trees tend to exhibit a greater taper. Their study showed that diameter growth was not significantly affected at stump height, but significant decreases in diameter growth were apparent at heights further up the stem. In this study, a significantly higher level of stem taper for the high infection group confirms this. A significantly lower inflection point for cumulative volume growth of the heavily infected

trees in this study suggests that dbh growth should diverge, but at 45 years of age, growth had not yet diverged significantly. This appears to be because the divergence has been offset by a higher growth rate. Baranyay and Safranyik (1970) reported that infected trees, prior to heavy levels of infection, exhibited a higher radial growth rate. This, however, was not a result of mistletoe infection, but a cause of mistletoe infection, as the more vigorous and therefore larger trees had a greater chance of intercepting mistletoe seeds. This could explain why heavily infected trees in this study appear to have a greater initial growth rate. Variation in growth rate may also be reflective of the uncertainty of environmental conditions affecting the tree in the past. Previous openings, or lack of competition may have increased the availability of light for the subject, increasing the rate of diameter growth. It is likely that the lack of significance of diameter growth reduction at breast height may be due to a combination of variability in environmental conditions and proximity of dbh to the base of the stem. Studies have shown (Pierce, 1960; Baranyay and Safranyik, 1970) that there is a lack of significance in differences of dbh growth between adjacent infection levels. Our study area was within a center of severe mistletoe infection, and there were, in fact, few trees that did not have any detectable level of infection. Considering the findings of Pierce (1960) and Baranyay and Safranyik (1970), it must be considered that between the indexes of 2 and 4, there was a much lower significance of growth differences than there would be between indexes of 0 and 6. Inclusion of the "near" indexes may reduce the significance of the results. Although the results weren't significant at the 5% level, at the 10% level there was approximately a 19% reduction in the projected maximum dbh. This falls within the 15% to 20% reduction in diameter growth that Tinnin *et al.* (1999) found for heavily infected Douglas fir trees.

Basal Area

The arguments for field dbh may also be applied to the basal area variable, as it is determined by the value of the diameter variable. Similarly, the growth pattern of basal area for the high infection group was significantly different than that of the low infection group. This would be expected, as basal area should exhibit a similar growth pattern to that of dbh. In this case, however, the hypothesis is supported in that it is predicted that basal area growth of the high infection group will become significantly lower than the basal area of the low infection group as the trees continue to grow after the age of 45. From the logistic regression model, the projected maximum basal area of the high infection group was approximately 57% lower than that of the low infection group. The greater difference in basal area as tree age increases is also to be expected, due to the exponential relationship of area to diameter. Pierce (1960) found a 68.5% reduction in basal area for heavily infected Douglas fir, and a 41.0% reduction in intermediately infected Douglas fir. Again, the findings of this study fall between this range, particularly considering that the subject trees in the high infection group fell into infection indices between a moderately high 4, and a heavily infected 5.

Height

With respect to the height of the trees at the time of sampling, the heavily infected subject trees at an age of 45 exhibited a significantly lower total height as was hypothesized earlier. Pierce (1960) found that differences in height were significant between all infection classes, in contrast to diameter. This corresponds with the strongly significant, 20% 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 mistletoe

infections. Tinnin and Knutson (1980) found that infected trees accumulate a high level of biomass in their brooms, which detracts the allocation of resources from biomass production elsewhere in the tree. This resulting disruption in apical dominance favours growth in lateral buds and branches over terminal growth that will favour elongation of the stem. Therefore, a marked reduction in height growth should be apparent with the appearance of large witches' brooms, which would not be expected prior to mistletoe infestation. 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 was likely due to the sensitivity of height to site quality, and its lack of responsiveness to other variables such as stand density and competition (Avery and Burkhart, 2002). The other growth variables were more sensitive to changes in stand density and competition, and as a result, exhibited greater variability. Lack of variability in height further confirms the homogeneity of the sampling site. Height growth over time showed that there was a significant reduction in height at a much earlier age than significant reductions in volume, diameter or basal area. This further suggests that height growth begins to show significant decreases shortly after the development of brooms and loss of apical dominance (Tinnin and Knutson, 1980).

Volume

At the time of sampling, the heavily infected subject trees exhibited a significant decrease in total height and volume as was hypothesized earlier. At the time of sampling, there was a significant 31.90% lower average total volume of in the high infection group. Because of a lack of significant difference in diameter and basal at this

age, this volume reduction was due to a significant reduction in tree height. This figure very closely corresponds with the amount of volume reduction found by Baranyay and Safranyik (1970), where a group of lodgepole pine trees with an average age of 37 showed a 35.5% reduction in the volume of the infected tree class. This figure is less than the minimum estimated volume loss of 53.4% in infected jack pine stands in Manitoba (Baker *et al.*, 1992). This was under the assumption that all trees in the infected stands are infected by mistletoe, and average minimum loss in volume for each tree was 53.4%. However, this comparison may not be valid, as the average age class of the subject stands in Baker *et al.* (1992) study was in the mature to overmature range. In addition, our study does not take into account tree mortality, which is an important factor in loss of volume. In this respect, the 31.90% lower volume may underestimate actual volume loss at the stand scale. From the logistic growth model, it was found that the predicted maximum average volume of trees in the high infection group was approximately 84% lower than that of 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. Again, it was important to remember that these findings reflected the volume loss in individual trees, and not the volume loss as averaged through an entire stand. The study of Baker *et al.* (1992) also incorporated stand openings and mortality, both of which were not taken into account in this study.

Conclusions

Our results showed that the growth rate of jack pine trees with heavy dwarf mistletoe infections were significantly reduced when compared to non- and lightly-infected trees. In addition, reduction in the growth rate of jack pine is similar to that observed in other species studied, and corresponded with aerial estimates of volume loss in other studies in Manitoba. In this study, by the age of 60, there was predicted to be up to a 21% lower basal area, a 23% lower height, and a 42% lower volume for individual jack pine trees with severe dwarf mistletoe infections. However, it was important to remember that these figures assumed that actual tree growth would continue to follow the growth predicted by the logistic regression model after the age of 45 years. These figures also did not make allowances for factors such as tree mortality, or further opening of the stand. Diameter at breast height was less significantly affected by the dwarf mistletoe infections; instead a higher level of taper can be expected. This 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 infections. Of the three significantly affected growth variables, height was the variable that showed cumulative growth reduction first, between the ages of 20 and 25 years. This likely followed the initial development of broom growth. Despite early reduction in cumulative height growth, cumulative volume growth of the heavily infected trees was not significantly affected until between 30 and 40 years of age. This suggested that cumulative volume of heavily infected trees may have continued to increase at a similar rate as lightly to non-infected trees for 5-20 years after cumulative height growth had been affected. This was because dbh and basal area were not yet significantly affected in the heavily infected

trees at an age of 45 years, as divergence in growth appears to have been offset by a greater growth rate at an earlier age.

If wood quality, with respect to strength, resistance to warp and shrinkage were desirable, the presence of mistletoe infection would have severely reduced the merchantability of the wood, depending on the length of time that individual trees had been affected. However, if the desired end use of the wood was for production of pulp, where the structural properties of the wood were not as important, infected trees may have been allowed to grow for as much as twenty years prior to salvaging the wood without significant loss in volume. This is provided that sufficient precautions were taken to prevent further spread of the mistletoe to uninfected areas. Further study on the effects of dwarf mistletoe over a wider range of age classes would be beneficial in modelling the impact of the parasite. Also, studies that incorporate tree mortality due to the mistletoe infections would help to better predict the impact of dwarf mistletoe throughout the entire jack pine stands, or over the forest landscape.

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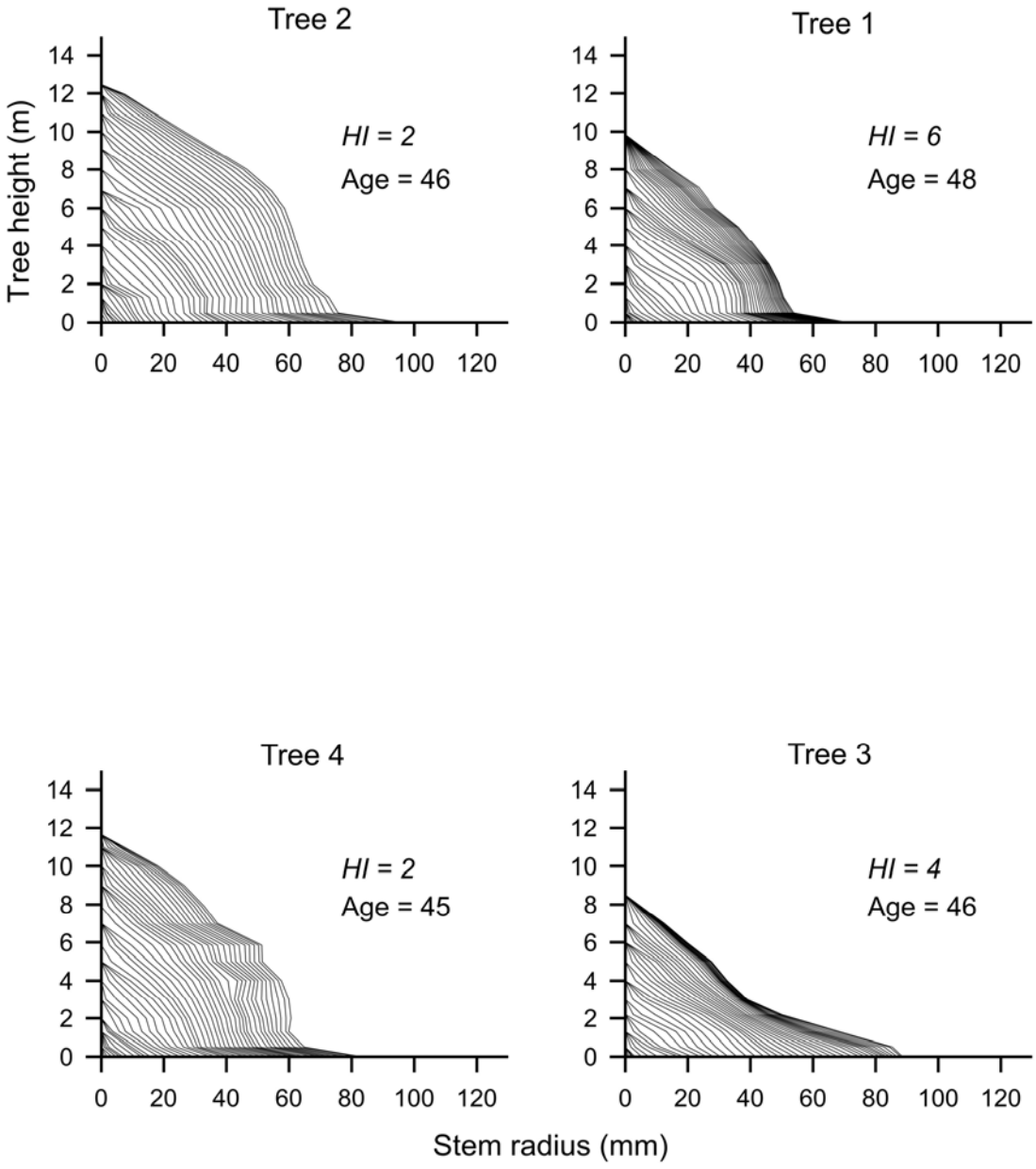
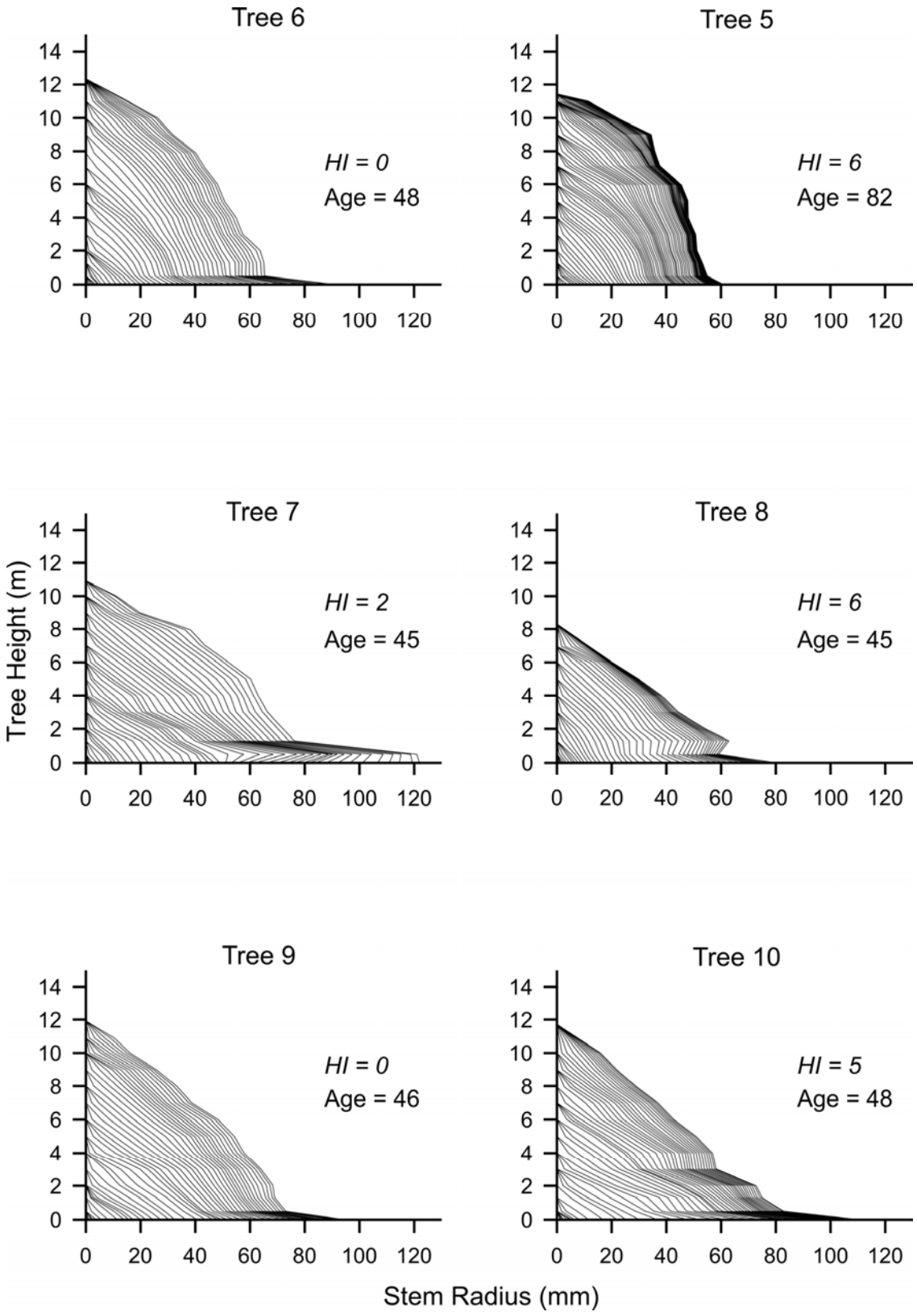
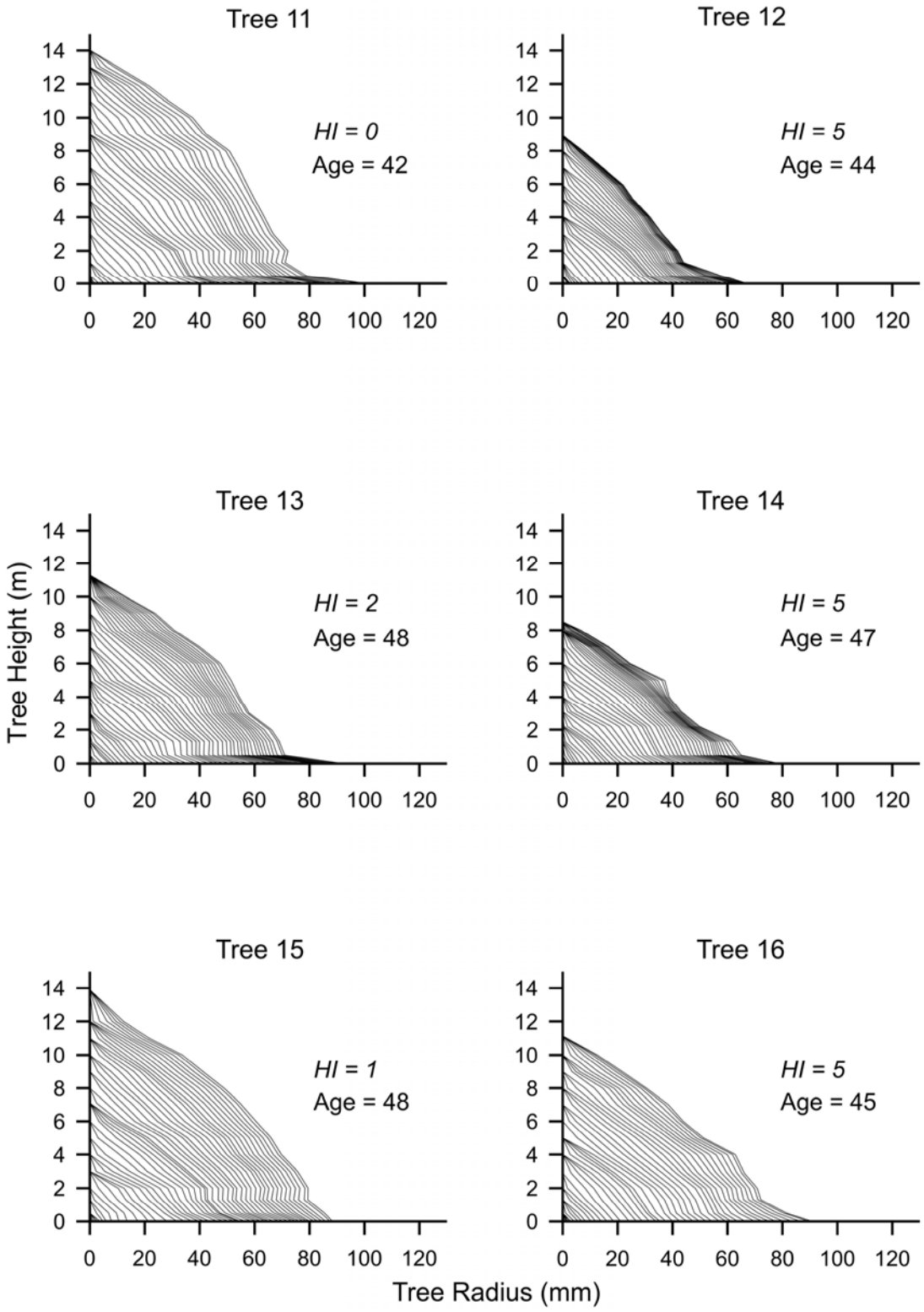
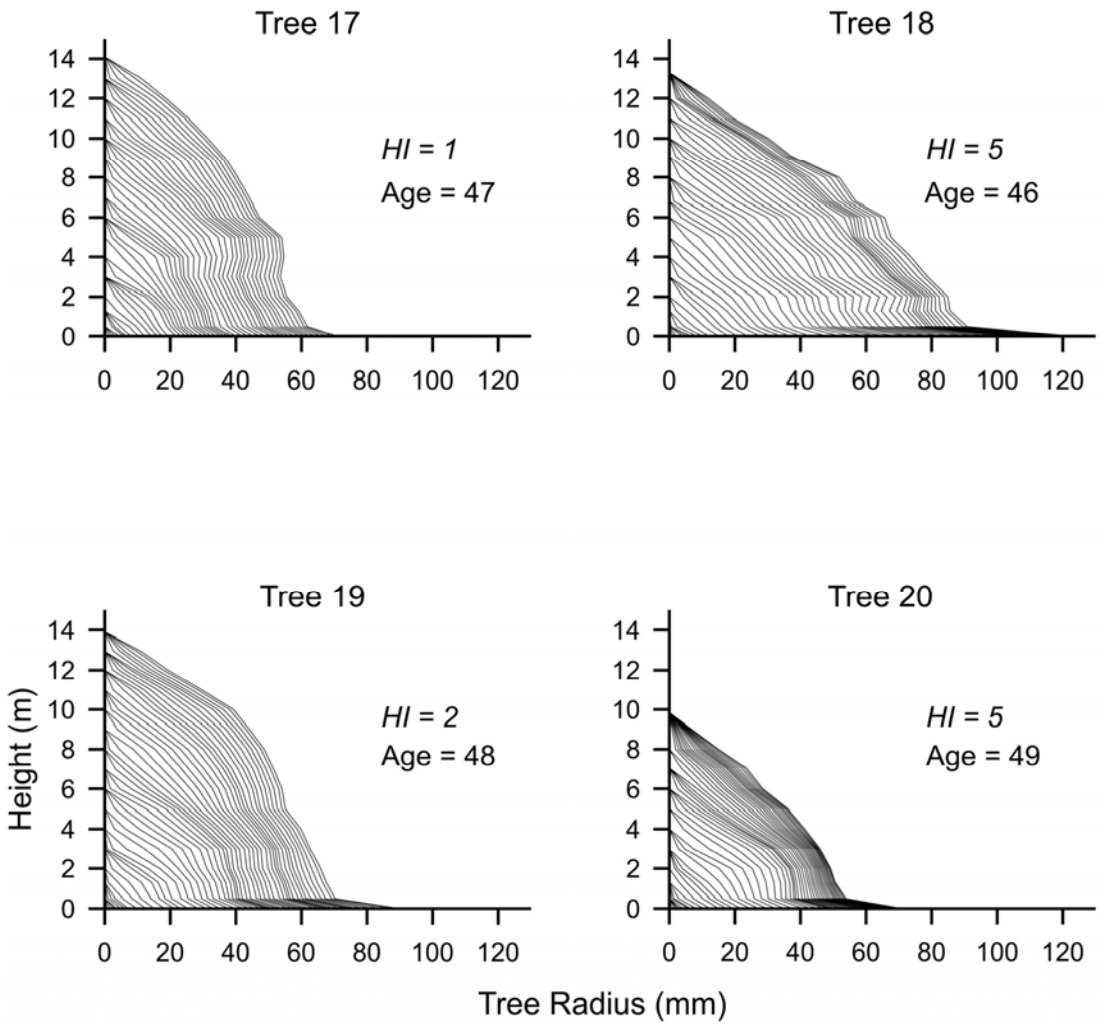
Appendix

1. Stem profiles of individual subject trees including the Hawksworth Index rating (*HI*) and tree age. Trees from the high infection group are in the right-hand column.




Tree 6
HI = 0
Age = 48
Tree 5
HI = 6
Age = 82
Tree 7
HI = 2
Age = 45
Tree 8
HI = 6
Age = 45
Tree 9
HI = 0
Age = 46
Tree 10
HI = 5
Age = 48
Tree Height (m)
Stem Radius (mm)
0
2
4
6
8
10
12
14
0
20
40
60
80
100
120


Tree 11
HI = 0
Age = 42
Tree 12
HI = 5
Age = 44
Tree 13
HI = 2
Age = 48
Tree 14
HI = 5
Age = 47
Tree 15
HI = 1
Age = 48
Tree 16
HI = 5
Age = 45
Tree Height (m)
Tree Radius (mm)
0
2
4
6
8
10
12
14
0
20
40
60
80
100
120


Tree 17
HI = 1
Age = 47
Tree 18
HI = 5
Age = 46
Tree 19
HI = 2
Age = 48
Tree 20
HI = 5
Age = 49
Height (m)
Tree Radius (mm)
0
2
4
6
8
10
12
14
0
20
40
60
80
100
120