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Early development of tended mixtures of aspen and spruce in western Canadian boreal forests

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Abstract

In 1992, the Western Boreal Growth and Yield Association (WESBOGY) began a long-term study to evaluate the dynamics of regenerated aspen (*Populus tremuloides* Michx.)—white spruce (*Picea glauca* (Moench) Voss) mixedwood stands following manipulation of aspen to a range of densities. In this study six levels of aspen (0, 200, 500, 1500, 4000 stems ha^{-1} and natural) and three levels of spruce (0, 500 and 1000 stems ha^{-1}) densities have been created.

Data from four locations demonstrate substantial variation in initial aspen densities following clearcutting of aspen dominated stands. After 9 years densities begin to converge with the highest rates of mortality associated with high starting densities. A model was developed that shows a significant relationship between the proportion of trees surviving to the end of a year and the density at the beginning of the year. Size-density relationships based on quadratic mean root collar diameter, mean tree volume and mean tree height are presented.

Three to four years following spacing of aspen to densities ranging from 200 to 4000 stems ha^{-1} there were no significant effects of density on aspen size. In addition, spacing of the aspen had no significant effect on spruce height at year 9 (3–4 years after spacing), but spruce root collar diameter (RCD) was significantly smaller in the unspaced compared to the spaced plots. The ratio of height to root collar diameter (HDR) for white spruce showed a significant and clear response to aspen density and increased with increasing aspen density.

Keywords: Juvenile spacing; Boreal mixedwood; Self-thinning; Maximum size-density relationship; White spruce; Trembling aspen

1. Introduction

Mixedwood forests are widespread in western Canada and represent some of the most productive forest lands within the boreal forest (Kabzems et al., 1986; Drew, 1988). The most important commercial species in western boreal mixedwood forests are white spruce (*Picea glauca* (Moench) Voss) and aspen (*Populus tremuloides* Michx.). Past management of these forests has tended to focus on growing only spruce or aspen by themselves. Current forest practices are now attempting to take advantage of these mixtures and are therefore searching for efficient and effective ways of creating and managing these mixedwood stands.

Following harvesting of upland mixedwood stands, aspen generally regenerates vigorously from root sprouts and dominates during early stages of development of the subsequent stand. When conditions are ideal, aspen can regenerate to very high densities, sometimes exceeding 100,000 stems per hectare at age 2 (Steneker, 1976; Bella, 1986). However, self-thinning generally occurs rapidly due to the shade intolerance of this species and its susceptibility to drought and disease (Peterson and Peterson, 1992). Although there have been numerous studies dealing with aspen self-thinning, few are based on annual re-measurements beginning immediately after harvest and others are limited by the number of re-measurements. More commonly juvenile aspen mortality is represented using chronosequence data or partial datasets using periodic re-measurements (Pollard, 1971; Ek and Brodie, 1975; Bella, 1986). Although insight into the self-thinning of juvenile aspen has been obtained from these studies, we currently lack juvenile aspen mortality functions for growth modeling. The lack of these functions is a major limitation in modeling the dynamics of young aspen and mixedwood stands.

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Mortality can be modeled at a stand level or at an individual tree level. At a stand level, future stand density can be predicted as a function of present stand density along with other site and stand characteristics. At an individual tree level, survival probability can be calculated based on tree size, social position, competitive status, site, and stand conditions. Because modeling mortality is so difficult, modelers often use a representation of the average rate of mortality (Flewelling and Monserud, 2002). These functions commonly underestimate mortality in very dense stands. Consequently, most models also use size-density relationships (maximum average tree size that can be achieved at a given density) to constrain stocking levels (Yang and Titus, 2002).

Reineke's (1933) stand density index (SDI) and the −3/2 power law of self-thinning[1] (Yoda et al., 1963) are two of the most commonly applied size-density relationships. Reineke's SDI relates density to quadratic mean diameter. By plotting the number of trees per unit area over the quadratic mean diameter on double log scale graph paper, a line fit through the upper points has a slope of approximately −1.605. The −3/2 power law represents an empirical relationship between the maximum achievable average plant weight that can be reached at a particular density for a particular species (Yoda et al., 1963; Drew and Flewelling, 1977). By plotting the average plant weight over the number of trees per unit area over on double log scale graph paper the line fit through the upper data points has a slope of −3/2 and is referred to as the maximum size-density line. Although biomass was the original variable used with the −3/2 power law, any measure of mean plant size can be used, but the slope of the relationship may deviate from −3/2. For both SDI and the −3/2 power law, the relationship was initially believed to be linear and apply to all species, although this has been challenged (Weller, 1987; Zeide, 1987; Cao et al., 2000). Lieffers and Campbell (1984) found that the slope of the relationship between tree biomass and stand density was −0.96 for 23–57 year-old aspen stands. Since the −3/2 power law was introduced, subsequent papers have focused on verifying the intercept and constancy of the slope for different species (Puettmann et al., 1993; Begin et al., 2001), the placement of the self-thinning line (Smith and Hann, 1984; Weller, 1990; Sackville Hamilton et al., 1995), the appropriateness of the fitting methods used (Puettmann et al., 1993; Begin et al., 2001) and whether the functions are linear or curvilinear in the log form (Zeide, 1987; Cao et al., 2000).

For the boreal forest Yang and Titus (2002) developed maximum size-density functions for aspen, white spruce and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm). However, several difficulties arise when attempting to apply these functions in juvenile stands. Due to the lack of data for young and very old stands, these functions do not provide reliable predictions in these age classes. In addition, models based upon diameter at breast height (DBH) cannot be used when some or all of the trees in the stand are smaller than 1.3 m in height.

Although results from past studies are sometimes contradictory (Peterson and Peterson, 1992), in some stands early juvenile spacing of aspen can accelerate the growth of residual trees (Bickerstaff, 1946; Steneker, 1976; Perala, 1978), accelerating achievement of merchantable diameter and improving the quality of the stand. However, thinning of aspen (as with most other species) typically results in reduced total standing volumes at harvest (Bella and Yang, 1991). Rice et al. (2001) found that, while thinning of young aspen (5–15 years old) resulted in reduced gross stand volume, it did not significantly change merchantable volumes 15 years after treatment. They also found that thinning resulted in significant increases in diameter growth of the remaining trees. Height and height growth were increased by thinning in 3 of the 7 stands that they studied. In contrast, a study by Penner et al. (2001) found no benefit to thinning a stand with 4000–5000 stems per hectare at age 20, due to the fact that unspaced plots had self-thinned to densities (1000–2000 stems ha^{-1}) similar to those of treated plots by age 36. During the 16 years following thinning to 1100 stems ha^{-1} very little mortality was observed. In their study, frequency distributions of tree diameters 16 years after thinning showed substantial reductions in the number of trees in smaller size classes and only some increases in the numbers of trees in larger size classes on the good site.

Treatments which reduce competition from aspen and other broadleaved trees can provide substantial increases in growth of white spruce (e.g. Lees, 1966; Biring et al., 1999; Biring and Hays-Byl, 2000; Jobidon, 2000; Pitt et al., 2004). Reducing aspen densities by selective removal of aspen by manual, mechanical, or chemical spacing treatments or removal of aspen around crop conifers, is widely used to improve growing conditions for white spruce. Studies in northern B.C. and Alberta indicate that light levels underneath aspen canopies are related to the basal area of aspen (Comeau, 2001; Lieffers et al., 2002). Comeau (2001) suggests that maintaining total aspen basal area below 8 m^2 ha^{-1} may provide near optimal conditions for growth of white spruce.

Competition has an immediate effect on diameter growth of conifers, while impacts upon height growth do not generally appear until severe competition levels are reached or competition remains at sufficient intensity for a period of time. As a result, the ratio of height to root collar diameter (HDR) increases in response to increases in level of competition (Tesch et al., 1993; Wagner et al., 1999; Coopersmith and Hall, 1999; Coopersmith et al., 2000; Opio et al., 2000). For white spruce, HDR values exceeding 55–60 are considered to indicate stress. In addition to competition, HDR is influenced by a range of environmental factors, including variations in spring, summer and fall growing conditions, soil resource availability, and stem sway and bending (Opio et al., 2000).

This paper presents results from analysis of 9 years of measurement of natural self-thinning of regenerated aspen and the early dynamics and growth of tended mixtures. The objectives of this manuscript are to: (a) quantify self-thinning of naturally regenerated aspen and develop survival and size-density functions; (b) evaluate the effects of thinning of aspen

[1] From this point onward the −3/2 power law of self-thinning will be referred to as the −3/2 power law.

on aspen size after 4 years; and (c) examine the effects of thinning of aspen on spruce size after 4 years.

2. Methods

2.1. Data

Data from four locations established as part of the Western Boreal Growth and Yield Association (WESBOGY) Long-Term Study (LTS) providing 9 years of annual re-measurements of spruce and aspen are used in this paper. The installations are the Weyerhaeuser Prince Albert (WPA), installations located near Prince Albert, Saskatchewan (52°13′N and 105°41′W), the Weyerhaeuser Grande Prairie (WGP) installations located near Grande Prairie, Alberta (55°11′N and 118°53′W), the Daishowa-Marubeni (DMI) installations located near Peace River, Alberta (56°15′N and 117°17′W) and the Hinton Wood Products (HWP) installations located near Hinton, Alberta (53°25′N and 117°34′W). This study involved planting white spruce in recently clearcut areas where aspen natural regeneration had already established. Treatments are based on a matrix of aspen and spruce densities. There are six aspen densities—0, 200, 500, 1500, 4000 and natural (untreated) stems ha^{-1} and three spruce density levels—0, 500 and 1000 stems ha^{-1}. Initial planting of spruce was at twice the desired final density (1000 and 2000 stems ha^{-1}) with spruce densities reduced to target densities at the time of thinning of the aspen. Two installations on median (MED) and superior (SUP) site conditions were established. The criteria used to differentiate between median and superior sites were subjective, based on regional productivity. Each of the 15 treatments was replicated twice in each of two installations at each of the four locations. DMI, WPA and HWP maintained 60 plots (2 installations by 2 replicates of 15 plots) while WGP lost (were destroyed) one replicate installation, reducing their total to 45 plots Treatments were randomly assigned to plots.

Study sites were established within a 24-month period of the cutover and had a uniform distribution of natural aspen regeneration of greater than 4000 stems ha^{-1}. The maximum height of aspen regeneration on selected study sites had to be less than 1.5 m to ensure that competition would not become a serious factor for the initial survival of the planted spruce. Initial aspen age was set relative to harvest year and month while white spruce age was set based on planting year and month.

For the first 5 years, vegetation was controlled by clipping or using plastic mulch mats within a 40–50 cm radius of the spruce in order to minimize early mortality. Planted white spruce seedlings on all plots were measured annually. For aspen, only the natural (untreated) plots were measured annually. Measurements were taken in the late fall after diameter and height growth ceased for the season. The following individual tree characteristics were measured: species, root collar diameter, diameter at breast height (when height >1.3 m), total height, height increment, height to live crown, crown diameter (north and south), up to three tree condition codes, age and spatial location (distance and azimuth). At year 5, both aspen and spruce were thinned using brush saws to target treatment densities. Soil, site and vegetation were also assessed.

Within each treatment plot a 20 m by 20 m (0.04 ha) fixed area permanent measurement plot was established. Each plot had a minimum 5 m treated buffer to separate plots and minimize the effects of neighboring plots. Although the natural density plots were also 20 m by 20 m fixed area plots, the extremely high initial aspen densities (upwards to 300,000 stems ha^{-1}) required the use of four, 1 m by 1 m subplots located in the southwest quadrant of the main plot to monitor changes in aspen density over time. At year 5, each of these 1 m by 1 m subplots was expanded to 2 m by 2 m in size.

2.2. Naturally regenerated aspen mortality

Data from the unthinned (natural density) plots were used to examine aspen survival and to fit maximum size-density relationships. Because each of the natural plots contains four smaller subplots, the subplots were aggregated and the plot level means used for analysis. There were 45 untreated plots available for analysis, each with a minimum of nine re-measurements.

2.2.1. Mean survival rate

The mean survival rate was calculated as the ratio of density at the end of a given growth period to the density at the beginning of the growth period (Eq. (1)). More formally;

$$S_R = \frac{\text{Density}_{t2}}{\text{Density}_{t1}} = \frac{\text{Density}_{t1} + \text{Ingrowth} - \text{Mortality}}{\text{Density}_{t1}} \quad (1)$$

where S_R is the mean survival rate representing the ratio between the density at the end of the period and the density (stems ha^{-1}) at beginning of the period; Density_{t1} is density at beginning of the period; Density_{t2} is density at the end of the period; Ingrowth is ingrowth of any tree (no minimum diameter) during the period; Mortality is mortality during the period.

S_R values include ingrowth therefore values greater than one indicate that ingrowth was larger than mortality during the period. S_R equal to one indicate no change in density during the period. S_R below one indicates that mortality was greater than ingrowth during the period.

Following the general approach of Ek and Brodie (1975), an exponential decay function using density at the beginning of the year to predict S_R (Eq. (2)) was fit using non-linear least square methods.

$$S_R = \beta_0 \times \exp^{-(\beta_1 \times \text{Density}_{t1})} \quad (2)$$

Because the data used to fit the survival rate equation were from repeated measurements, the Durbin–Watson test was used to test for the presence of first order autocorrelation. Although the Durbin-Watson test is most appropriate for linear regression it is approximately valid for non-linear regression (Serber and Wild, 1988, pp. 318–319).

2.2.2. Maximum size-density

Maximum size-density functions were fit using quadratic mean root collar diameter (QMRCD), mean tree volume (TVOL) and mean tree height (TH) as dependant variables. The maximum size-density function for quadratic mean root collar diameter was a modification of Reineke's (1933) stand density index where root collar diameter (RCD) was used in place of breast height diameter. The maximum size-density functions for mean tree volume (tree volume for these young trees was calculated using an adaptation of Honer's equation (Pitt et al., 2004)) and mean tree height are based on the −3/2 power law (Yoda et al., 1963; Drew and Flewelling, 1977). For each mean plot characteristic, two maximum-density functions are presented, the mean maximum size-density function and the biological maximum size-density function. The mean maximum size-density functions were fit by first placing the plots into 5000 stems ha^{-1} classes and ranking each observation within each class. For each density class plots that were above the 90th percentile were used for fitting using least squares methods. *T*-tests were done to determine if the slopes of the fitted equations were significantly different then those presented in the literature for each of the given relationships. The second function fit was the biological maximum size-density function, and was positioned by adding the value of the largest positive residual (obtained from reviewing the residuals of the mean maximum size-density function) to the intercept of the maximum size-density function. This shifted the maximum size-density function upward an amount equal to the largest residual and forced all data points to be below the biological maximum line.

The maximum size-density function for QMRCD is presented in two ways, the first regresses ln(Density) on ln(QMRCD) (Eq. (3)). This representation is similar to Reineke's original SDI.

$$\ln(\text{Density}) = \beta 0 + \beta 1(\ln(\text{QMRCD})) \quad (3)$$

A second model that regresses ln(QMRCD) on ln(Density) (Eq. (4)) was done to present the relationship of QMRCD to Density in a similar fashion as the self-thinning line.

$$\ln(\text{QMRCD}) = \beta 0 + \beta 1(\ln(\text{Density})) \quad (4)$$

For mean tree volume and mean tree height, the ln(TVOL) (Eq. (5)) and ln(TH) (Eq. (6)) were regressed on ln(Density).

$$\ln(\text{TVOL}) = \beta 0 + \beta 1(\ln(\text{Density})) \quad (5)$$

$$\ln(\text{TH}) = \beta 0 + \beta 1(\ln(\text{Density})) \quad (6)$$

The SAS Proc Mixed procedure (SAS Institute, Cary, NC) was used to carryout a mixed model ANOVA to test ($\alpha = 0.05$) whether or not there was a treatment (thinning) effect on aspen and white spruce size, 9 years after establishment and 4 years after treatment. If differences were detected, Tukey's multiple comparisons for differences in treatments were used to group similar treatment densities.

Analysis of aspen response to thinning was based on the top aspen trees or four largest DBH trees from the thinned plots (100 largest DBH trees ha^{-1}). The untreated plots were not included in the statistical comparisons because top height could not be adequately approximated (the single largest tree represented 625 trees ha^{-1}) which would introduce a negative bias in the estimate of top height. The response variables tested included mean top height (HT), mean diameter at breast height (DBH), mean height increment (HTI) and mean slenderness (height to diameter ratio).

The statistical analysis for spruce was based on all the trees on the plot. The response variables tested included mean height (HT), mean root collar diameter (RCD), mean height increment (HTI) and mean height–diameter ratio (HDR).

The statistical model for both aspen and spruce was as follows:

$$\begin{aligned} Y_{ijklm} = {} & \mu + A_i + I_j + R_k(A \times I)_{ij} + Aw_l + Sw_m + A_i \times I_j \\ & + Aw_l \times Sw_m + Aw_l \times I_j + Sw_m \times I_j + Aw_l \times Sw_m \\ & \times I_j + \varepsilon_{ijklm} \end{aligned}$$

where Y_{ijklm} is the response; μ is the overall mean; A_i is the random effect of *i*th a*gency*; I_j is the fixed effect of the *j*th *installation*; $R_k(A \times I)$ is the random effect of the *k*th replication nested within *agency* and *installation*; Aw_l is the fixed effect of the *l*th *aspen treatment*; Sw_m is the fixed effect of the *m*th *spruce treatment*; $A_i \times I_j$ is the random effect of the interaction between the *i*th *agency* and *j*th *installation*; $Aw_l \times Sw_m$ is the fixed effect of the interaction between the *l*th *aspen treatment* and *m*th *spruce treatment*; $Aw_l \times I_j$ is the fixed effect of the interaction between the *l*th *aspen treatment* and *j*th i*nstallation*; $Sw_m \times I_j$ is the fixed effect of the interaction between the *m*th *spruce treatment* and *j*th i*nstallation*; $Aw_l \times Sw_m \times I_j$ is the fixed effect of the interaction between the *l*th *aspen treatment the m*th *spruce treatment* and *j*th *installation*; ε_{ijklm} is the residual

3. Results

3.1. Density of natural aspen plots

Changes in aspen density with age for each location are illustrated in Fig. 1. WPA began with an average density of 122,500 stems ha^{-1} decreasing to 22,343 stems ha^{-1} at year 9. DMI began with 98,958 stems ha^{-1} and decreased to 29,062 stems ha^{-1} at year 9. At the lower end of the starting density scale, HWP began at 38,750 stems ha^{-1} and declined to 22,000 stems ha^{-1} while WGP began at 22,500 stems ha^{-1} and decreased to 15,555 stems ha^{-1} at year 9. The mean density over all agencies began at 73,888 stems ha^{-1} and decreased to 22,782 stems ha^{-1} at year 9. The results shown in Fig. 1 represent net density, the combined effect of both ingrowth and mortality. When starting densities are very high, mortality exceeds ingrowth and densities drop from year to year. When starting densities are lower, densities increase for the first 4 or 5 years, with ingrowth exceeding mortality. At some point, after year 5, mortality generally exceeds ingrowth, and densities begin to decrease.

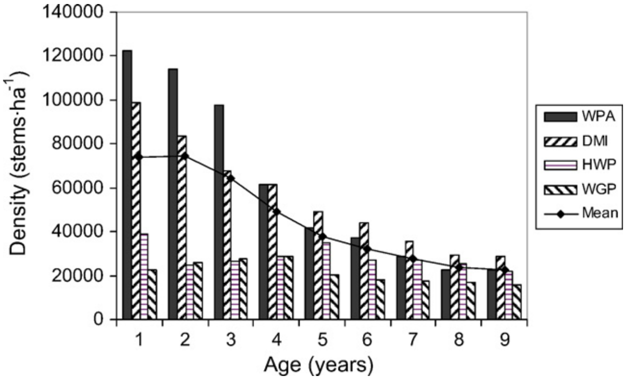

Fig. 1. Trends in density (stems ha^{-1}) of natural regeneration of trembling aspen with age (years). Histogram values shown are averages for each of the four locations. The line represents the mean of the four locations.

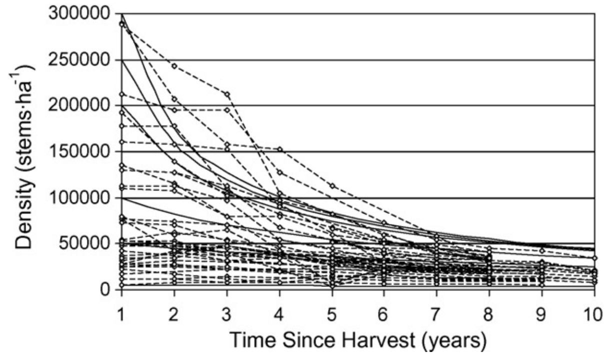

Fig. 3. Changes in observed densities (stems ha^{-1}) with time (years) (dashed lines) and five representations of model predictions using Eq. (7) (solid lines), for starting densities of 5000, 50,000, 100,000, 200,000, 250,000 and 300,000 stems ha^{-1}.

3.2. Mean survival rate

Fitting of the non-linear mean survival rate function yielded the following model:

$$S_E = .9893 \times \exp^{-(0.000001760 \times \text{Density}_{t1})} \tag{7}$$

($n = 310$, MSE = .086, $P < .0001$), both the slope and intercept were significant. The Durbin–Watson statistics of 2.027 is higher than the upper critical value for a single parameter model indicating the absence of positive first order autocorrelation. Fig. 2 illustrates the distribution of the actual survival rate (S_R) in relation to starting densities. As expected, $S_R > 1.0$ occurs only where starting densities are low, and represents plots where initial suckering was delayed. The four plots with $S_R > 2.0$ were examined closely and were considered realistic since the majority of suckering appeared over the 5-year period after harvest. This is not in agreement with the general belief that suckering all but stops after 2 or 3 years (Peterson and Peterson, 1992). The general trend of the scatter plot shows that as starting densities increase, the S_R decreases. This is consistent with results presented by Yao et al. (2001). When starting densities are low, for example 5000 stems ha^{-1}, 98% of the initial density remains after one year. At extremely high densities, for example 250,000 stems ha^{-1}, 64% of the density at the beginning of the year remains after 1 year. Fig. 3 uses the predicted S_R to estimate final densities for some typical starting densities (5000, 50,000, 100,000, 200,000, 250,000 and 300,000 stems ha^{-1}). The non-linear model predicts that for the plot with 300,000 stems ha^{-1} the density would drop by 41% to 175,041 stems ha^{-1} by the end of the first year. By year 9, still within the bounds of the data, the survival probability reaches 91% with a residual density of 49,498 stems ha^{-1}. Similarly, plots starting with very low densities (i.e. 5000 stem ha^{-1}) show a net increase in density for the first 5 years, with densities declining gradually after this point. This trend is consistent with what one would expect and is supported by the data.

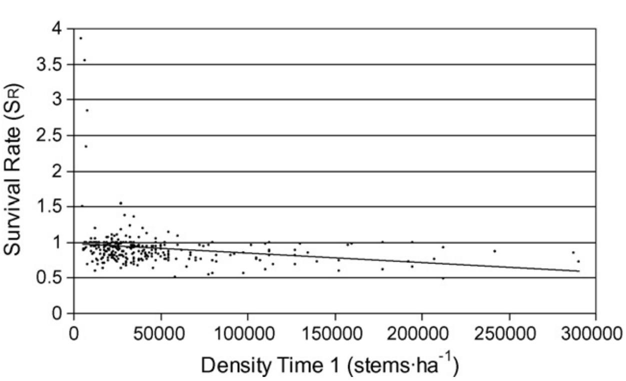

Fig. 2. Relationship between the proportion of trees surviving a growing season (survival rate, S_R) and density (stems ha^{-1}) at the beginning of the growing season. Points indicate observed data and the line represents a least squares regression fit of the observed data represented by Eq. (7).

3.3. Maximum size-density

Fig. 4a–c show the maximum size-density relationships for QMRCD (cm), TVOL (m^3), and HT (m). The trend lines show how each of the plots used in fitting the maximum size-density functions tracked over time.

The traditional representation of Reineke's SDI, ln(Density) was regressed on ln(QMRCD) (Eq. (8)). This model had an intercept of 11.904 and a slope of −1.408 ($n = 48$, MSE = 0.049, adjusted $R^2 = 0.94$). The t-test ($\alpha = 0.05$) determined that the slope of the fitted line (−1.408) was significantly different from −1.605. The mean maximum size-density line for ln(QMRCD) regressed on ln(Density) (Eq. (9)) is simply Reineke's SDI equation expressed in an analogous way to the self-thinning line. It had an intercept of 7.992 and a slope of −0.665 ($n = 48$, MSE = 0.023, adjusted $R^2 = 0.94$). The t-test ($\alpha = 0.05$) determined that the slope of the fitted line (−0.665) was not significantly different than the slope of −0.623.

The biological maximum size-density line for ln(QMRCD) (Eq. (10)) was obtained by shifting the intercept from Eq. (9) (7.992) upward by a value of 0.432, a value equivalent to the largest positive residual obtained from fitting the mean maximum size-density function.

$$\ln(\text{Density}) = 11.904 - 1.408(\ln(\text{QMRCD})) \tag{8}$$

$$\ln(\text{QMRCD}) = 7.992 - .665(\ln(\text{Density})) \tag{9}$$

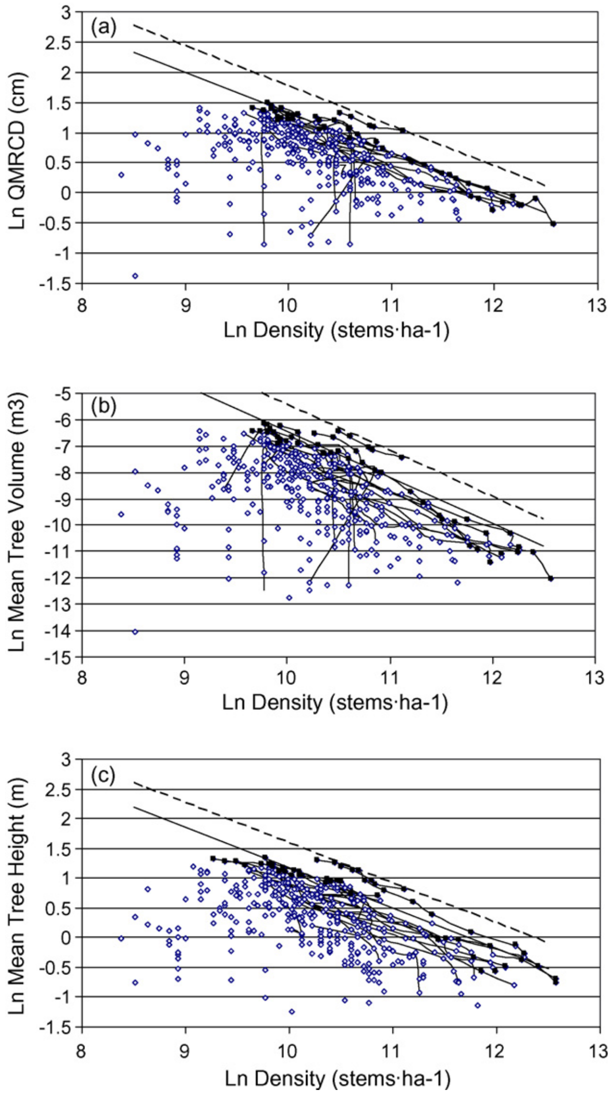

Fig. 4. Maximum mean (solid straight lines) and biological maximum (dashed lines) size-density lines for juvenile aspen based on natural log of density (stems ha^{-1}) vs. (a) natural log of quadratic mean root collar diameter (QMRCD) (cm), Eqs. (9) and (10) (b) natural log of mean tree volume (TVOL) (m^3), Eqs. (11) and (12) (c) natural log of mean tree height (TH) (m), Eqs. (13) and (14). The trajectory of plot values for the upper 10% of observed data points are joined by a fine solid line.

$$\ln(\text{QMRCD}) = 8.424 - .665(\ln(\text{Density})) \quad (10)$$

The mean maximum size-density regression line for ln(TVOL) (Eq. (11)) has an intercept of 10.847 and a slope of -1.731 ($n = 48$, MSE = 0.215, adjusted $R^2 = 0.92$). The t-test ($\alpha = 0.05$) determined that the slope of the fitted line (-1.731) was significantly different than the $-3/2$ slope. The biological maximum size-density line for ln(TVOL) (Eq. (12)) was a obtained by shifting the intercept from Eq. (11) (10.847) upward by a value of 1.023, a value equivalent to the largest positive residual obtained from fitting the size-density line.

$$\ln(\text{TVOL}) = 10.847 - 1.731(\ln(\text{Density})) \quad (11)$$

$$\ln(\text{TVOL}) = 11.870 - 1.731(\ln(\text{Density})) \quad (12)$$

The mean maximum size-density line for (HT) (Eq. (13)) has an intercept of 7.946 and a slope of -0.677 ($n = 48$, MSE = 0.049, adjusted $R^2 = 0.85$). The biological maximum size-density line for ln(TH) (Eq. (14)) was obtained by shifting the intercept from Eq. (13) (7.946) upward by a value of 0.406, a value equivalent to the largest positive residual obtained from fitting the mean maximum size-density function.

$$\ln(\text{TH}) = 7.946 - 0.677(\ln(\text{Density})) \quad (13)$$

$$\ln(\text{TH}) = 8.351 - 0.677(\ln(\text{Density})) \quad (14)$$

3.4. Aspen size relative to aspen density

Table 1 shows the mean HT, DBH, HTI and slenderness, at year 9, calculated for the top trees. The results of the mixed model ANOVA using the top trees show no significant ($\alpha = 0.05$) effects of density (excluding the untreated) on HT, DBH, HTI and slenderness of aspen, 4 years after spacing treatments had been applied (Table 2).

3.5. Spruce size relative to aspen density

Substantial differences in spruce size are evident at year 9 between the different locations (Agency) (Fig. 5). The DMI installations have the highest average – HT, RCD and HTI over all treatment densities followed by HWP, WPA and WGP. Within each location, treatment effects on HT are small. HTI at year 9 show that although there are HTI differences between

Table 1
Summary of treatment means for aspen HT (m), DBH (cm), HTI (cm) and slenderness by treatment for top trees

Treatment density	HT	DBH	HTI	Slenderness
200	4.551	5.002	43.925	0.927
500	4.955	5.428	43.931	0.922
1500	4.883	5.523	48.786	0.901
4000	5.054	5.489	50.594	0.933

Table 2
Mixed model ANOVA results ($\alpha = 0.05$) for aspen, testing differences in mean HT (m), DBH (cm), HTI (cm) and slenderness by treatment at year 9

Source	d.f.	HT *P*-value	DBH *P*-value	HTI *P*-value	Slenderness *P*-value
Agency (*A*)	3	–	–	–	–
Installation (*I*)	1	0.875	0.998	0.628	0.630
Aspen treatment density (*Aw*)	3	0.061	0.141	0.141	0.616
Spruce planting density (*Sw*)	1	0.466	0.283	0.758	0.364
$A \times I$	3	–	–	–	–
Replicate ($A \times I$)	6	–	–	–	–
$Aw \times Sw$	3	0.944	0.949	0.808	0.715
$I \times Aw$	3	0.378	0.734	0.530	0.919
$I \times Sw$	1	0.624	0.734	0.880	0.066
$I \times Aw \times Sw$	3	0.468	0.791	0.380	0.684
Residual error	84	–	–	–	–
Total	111	–	–	–	–

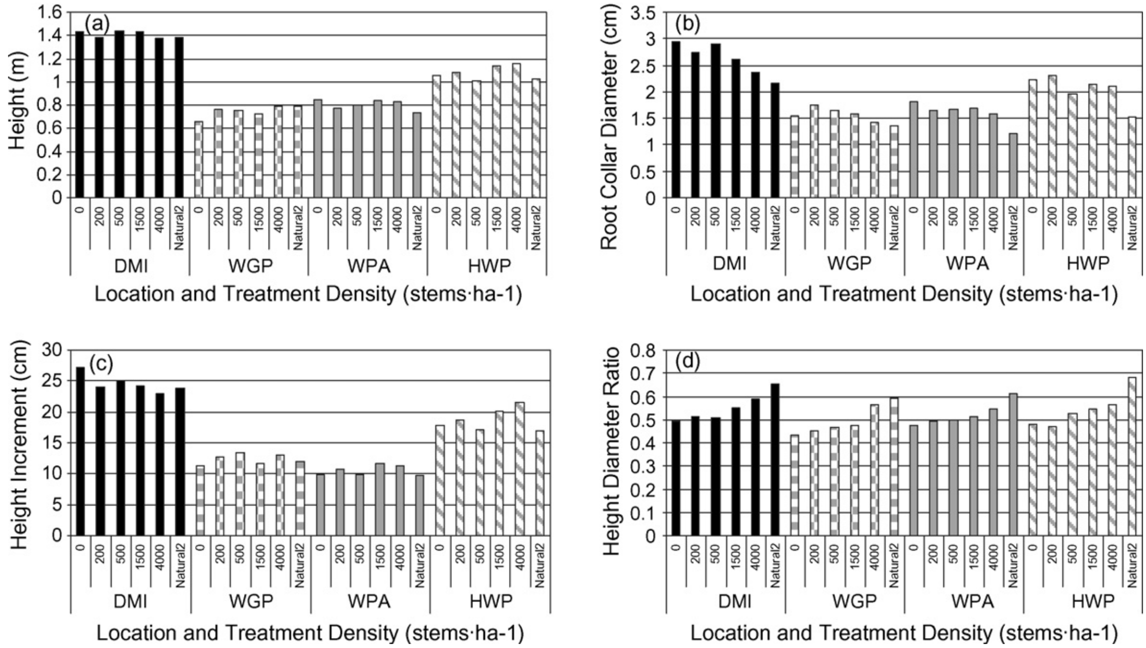

Fig. 5. Effects of aspen density on white spruce height (HT) (m), root collar diameter (RCD) (cm), height increment (HTI) (cm) and slenderness at age 9 for the four study locations.

locations, there are no aspen treatment effect on HTI within each location. At all locations spruce RCD tends to decrease as aspen density increases. Strong trends in HDR are evident with HDR increasing as aspen density increases.

Table 3
Summary of treatment means for spruce HT (m), RCD (cm), HTI (cm) and HDR by treatment

Treatment density	HT	RCD	HTI	HDR
0	1.004	2.138 a	16.623	0.473 d
200	1.000	2.104 a	16.447	0.485 d
500	1.004	2.056 ab	16.332	0.500 dc
1500	1.036	2.005 ab	16.853	0.522 c
4000	1.033	1.863 b	16.977	0.565 b
Untreated	0.980	1.553 c	15.638	0.635 a

Values within each column with different letters were found to be significantly ($\alpha = 0.05$) different using Tukey's test.

Table 4
Mixed model ANOVA results ($\alpha = 0.05$) for spruce, testing differences in mean HT (m), RCD (cm), HTI (cm) and HDR ratios by treatment at year 9

Source	d.f.	HT *P*-value	RCD *P*-value	HTI *P*-value	HDR *P*-value
Agency (*A*)	3	–	–	–	–
Installation (*I*)	1	0.683	0.474	0.448	0.416
Aspen treatment density (*Aw*)	5	0.706	**<.0001**	0.829	**<.0001**
Spruce planting density (*Sw*)	1	0.128	0.537	**0.010**	0.325
$A \times I$	3	–	–	–	–
Replicate ($A \times I$)	6	–	–	–	–
$Aw \times Sw$	5	0.421	0.153	0.324	0.465
$I \times Aw$	5	0.700	0.908	0.751	0.951
$I \times Sw$	1	0.634	0.863	0.118	0.993
$I \times Aw \times Sw$	5	0.626	0.869	0.432	0.305
Residual error	132	–	–	–	–
Total	167	–	–	–	–

Table 3 presents the overall means for HT, RCD, HTI and HDR, at year 9. Mixed model ANOVA (Table 4) indicated that there was no significant aspen treatment effect on HT. For RCD there was a significant ($P < .0001$) aspen treatment effect with RCD decreasing as aspen density increases. Tukey's pairwise comparisons indicated that three aspen treatment groups exist. The 0, 200, 500 and 1500 aspen treatment densities formed the first group, the 500, 1500 and 4000 formed the second group and the untreated represented the third group.

For HTI there was a significant spruce planting density effect but no effect of aspen density. However, the size of this difference is small (the mean HTI was 17.25 and 15.70 cm for 500 and 1000 aspen per hectare, respectively).

HDR displayed the strongest aspen treatment effect and increased as density increases, suggesting that at higher aspen densities the trees have a smaller RCD in relation to their height. Tukey's pair wise comparison indicated that for HDR four aspen treatment groups exist, one group comprising the 0, 200,500 treatment densities, the second was made up of the 500 and 1500 aspen treatment densities, the third group was the 4000 aspen treatment density and the fourth was represented by the natural or untreated.

4. Discussion

During the first 20 years of their development natural aspen stands are very dynamic. Although much is known about the individual factors that influence the growth and mortality of aspen, there has been little reported success in developing a predictive mortality model for juvenile aspen. The simplest approach to model juvenile aspen mortality is to use a stand level mortality model represented by Eq. (7). This function simply predicts the future survival rate for the stand based on the current stand density. Other stand characteristics such as mean stand height, mean root collar diameter and time since harvest (age) were evaluated as independent variables but did not significantly improve the model. The appeal of this type of whole stand approach is that it simply relies on current density and can be readily used within a growth model.

However, it is possible for Eq. (7) to yield biologically unlikely outcomes for final densities, such that they are above the biological maximum size-density line, suggesting that predicted survival rates for that period were too high (mortality not severe enough). In these cases mean maximum size-density Eqs. (9), (11) or (13), or biological maximum size-density Eqs. (10), (12) or (14), can be used as a guide to further reduce densities. It is also possible to use these equations directly to predict mortality/survival.

The slopes of the maximum size-density relationships in these young aspen stands are statistically different for TVOL (Eq. (9)) and QMRCD (Eq. (11)) when compared to the theoretical slope of $-3/2$. The slope of the relationship also differs from the slope of -0.96 which Lieffers and Campbell (1984) obtained for 23–57 year-old aspen stands. Several other studies have demonstrated substantial variation in the slope of maximum size-density lines with values ranging from about -0.9 to -2.1 (Weller, 1987; Zeide, 1987). It is very likely, as Cao et al. (2000) suggest, that the self-thinning relationship is a curve comprised of many smaller linear segments, each with a unique slope and this study is observing one of these segments.

The relationship between ln(QMRCD) and ln(Density) (Eq. (8)) also has a slope (-1.408) which differs significantly from Reineke's slope of -1.605. Zeide (1987) cites numerous examples of studies where similar deviations in the slope of this relationship occur. The use of root collar diameter in place of diameter at 1.3 m (DBH) is unlikely to be the cause of this deviation, since DBH and root collar diameter are strongly linearly correlated in young aspen (P. Comeau, unpublished data).

The choice of which maximum size-density function to use becomes a question of practicality. Using mean tree volume maintains a linkage to the original work by Yoda et al. (1963) and Drew and Flewelling (1977) but in juvenile stands this requires use of root collar diameter measurements which are not commonly available. Quadratic mean DBH cannot be used in juvenile stands since many or all trees are below 1.3 m. Our results indicate that height–density relationships may be an alternative to volume–density or diameter–density relationships in these young aspen stands.

Traditionally, height has not been used as a mean stand size parameter when fitting maximum size-density equations because it is not considered to be as sensitive to competition as other variables. The maximum size-density relationship that we obtain for TH (Fig. 4c) along with the tracking of the individual plots suggests that at least for juvenile aspen, mean height may be an alternative. Further testing is required to evaluate the application of height–density relationships across a broader range of stand ages and with other species.

Aspen size 4 years after thinning (based on a consistent subset of crop trees) showed no significant differences between 200, 500, 1500 and 4000 stems ha^{-1} spacings. However, since thinning from below selectively removes smaller trees, thinning did significantly increase the overall average diameter and height as observed by others (Penner et al., 2001). Coopersmith and Hall (1999) and Coopersmith et al. (2000) also showed no difference in early aspen growth between stands spaced to 5000 and 10,000 stems ha^{-1}. In contrast Bella and Yang (1991) and Rice et al. (2001) found that thinning resulted in significant increases in diameter growth of the remaining trees. In this study, mean height and diameter differed little between the treated and natural, and it is felt that if the bias resulting from the use of small plots in the natural stands could be removed, the means would not be significantly different.

White spruce height 4 years after thinning was unaffected by aspen density. The lack of height response is consistent with results presented by Coopersmith and Hall (1999). However, Coopersmith et al. (2000) found that spruce were significantly taller at year 9 when growing without aspen. Jobidon (2000) and Pitt et al. (2004) also report that spruce height and diameter growth over the 5 years following treatment was greatest with complete removal of all overtopping vegetation. Logan (1969) and Lieffers and Stadt (1994) report that height growth of white spruce reaches a maximum at 40–45% of full sunlight. However, total stem growth of white spruce was significantly higher at 100% full sunlight than at 45% of full sunlight. Wright et al. (1998) report that while diameter and height growth of white spruce are maximized at full sunlight, the relationship between height growth and light levels off substantially at light levels above 60%. Due to the non-linear and variable nature of height growth responses of white spruce, and the fact that spruce established in our study had received treatments to remove competition within a 40–50 cm radius of the crop tree it is not surprising that there are no significant treatment effects on height or height increment.

The existence of a significant effect of spruce planting density on spruce height increment is perplexing. Results indicate slightly (1.55 cm) greater height increment for the 1000 than for the 500 spruce ha^{-1} density (which had originally been planted at twice this density). Due to the small size of this effect, it should not be over interpreted, however similar effects of planting density resulting in early increases in seedling growth have been found with Douglas-fir (Reukema and Smith, 1987; Scott et al., 1998). The most likely explanations for this effect are: (1) greater likelihood of planting favourable microsites; (2) improvements in microenvironmental conditions (i.e. Reduced frost or winter injury); (3) reductions in competitive effects of other vegetation; (4) enhancement of beneficial intraspecific interactions (i.e. Root grafting and mycorrhizal interactions); and/or (5) red-far red signaling effects on shoot elongation (Scott et al., 1998). In our study, the effects of small differences due to any of these factors could be increased as a result of tree selection during the thinning of the spruce to final densities.

Spruce RCD was significantly lower in the unspaced treatment compared to the spaced plots. In the studies by Coopersmith and Hall (1999) and Coopersmith et al. (2000) there were no differences in RCD between the 5000 and the 10,000 stems ha^{-1} aspen densities but, as shown by our results

RCD was significantly smaller in the untreated than in all other aspen thinning treatments. Overall trends in spruce diameter in relation to levels of competition are consistent with findings from studies which have examined relationships between white spruce growth and broadleaf competition (Comeau et al., 2003; Jobidon, 2000). The lack of differences in spruce RCD between the three lowest aspen densities (0, 200 and 500) is likely related to the low levels of competition and substantial spatial variability within these plots. At the lowest densities of aspen, increased cover and vigor of *Calamagrostis canadensis* and other vegetation over that evident in the 4000 aspen ha^{-1} and untreated was observed, as well as some increase in duration of summer frost and may be negatively influencing spruce growth (Voicu and Comeau, 2006).

HDR of white spruce was sensitive to aspen density with data indicating four groups: (1) a low aspen density group (0, 200 and 500), (2) a 500 and 1500 stems ha^{-1} group, (3) a 4000 stems ha^{-1} group, and (4) a natural density group. This is consistent with results from other studies that show HDR increases in response to increases in level of competition (Tesch et al., 1993; Wagner et al., 1999; Coopersmith and Hall, 1999; Coopersmith et al., 2000; Opio et al., 2000). Spruce growing in the unspaced treatment had average HDR values of 0.64 at year 9, exceeding the HDR value of 0.60 which is considered to indicate stress. HDR values are 0.50 and lower when aspen density was below 500 stems ha^{-1}. Coopersmith and Hall (1999) found that HDR of white spruce planted with various densities of trembling aspen increased during the 4 years after planting presumably in relation to the growth of the aspen, the increase in aspen basal area, and the decline in light levels reaching these trees.

5. Conclusions

Data from four locations demonstrate the substantial variation in initial aspen densities that can occur following clearcut harvesting of aspen dominated stands. Re-measurement data also show that after 9 years, regardless of initial establishment densities, the densities begin to converge, with high rates of mortality associated with high starting densities and low mortality associated with low starting densities. A general model was developed that shows a significant relationship between the proportion of trees surviving to the end of a year, and the density at the beginning of the year. Three maximum size-density functions were fit for juvenile aspen using tree volume, tree height and root collar diameter as predictors of maximum density. In these young aspen stands the slope of the maximum mean tree volume – density line was -1.731 rather than $-3/2$. Although lines for the three measurements of tree size had different slopes, the strength of the fits were all very similar suggesting that input data availability would be the main reason for choosing one function over another.

No significant effects of density on aspen size were detected 4 years following spacing at year 5 when comparing densities created by spacing ranging from 200–4000 stems ha^{-1}. Aspen spacing had no significant effect on spruce height at year 9 (3–4 years after spacing), but spruce RCD was significantly smaller in the unspaced compared to the spaced plots. HDR showed a significant and clear response to aspen density and increased with increasing aspen density.

Although the WESBOGY long-term study has been in place for over 13 years, the benefits are only beginning to be seen. The study offers a unique opportunity to track the development of a series of spruce aspen mixedwood stands from establishment to harvest. Ongoing measurement of these installations, and analysis of collected data is expected to continue to yield interesting and useful insights into the dynamics of boreal mixedwood stands and the effects of these spacing treatments.

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