Effects of aspen and spruce densities on tree and stand growth in the western boreal region of Canada:
Results from the WESBOGY Long-Term Study to age 31

Report to the Western Boreal Growth and Yield Project Team

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by

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Abstract

Mixtures of aspen and white spruce are common and widespread in the boreal plains of western Canada, with pure spruce stands historically resulting through succession of mixedwood stands. An aspen overstory can facilitate growth of young spruce by reducing competition from shrubs and grasses, frost injury and insect damage. However, growing spruce in mixtures is expected to result in longer rotations and lower spruce yields than growing it in pure stands.

The Long-Term Study was initiated by the Western Boreal Growth and Yield Association (WESBOGY) in 1990 to provide quantitative information needed to support decisions relating to mixedwood management. The 15 treatments established in this study represent combinations of six aspen densities (0, 200, 500, 1500, and 4000 stems·ha^{-1} plus an unthinned control) created by thinning at age 5 and three densities of planted spruce (0, 500, and 1000 stems·ha^{-1}) densities. The oldest of the 21 installations were 31 years old at the most recent (2021) measurement included in this report.

At age 20 and 28 spruce size was increased by removal of aspen with both spruce height and diameter declining with increasing aspen density. At age 28 spruce diameter with no aspen was 2.6x that of spruce in unthinned , and 1.8x that of the unthinned following thinning to 1500 stems·ha^{-1}. Spruce merchantable yield at age 90, estimated using the Mixedwood Growth Model (MGM21), declined with increasing initial aspen density, with the complete removal of aspen resulting in more than double that of unthinned plots and more than 1.3x that of the 1500 aspen ha^{-1} treatment.

Thinning resulted in significant increases in aspen DBH and crown size, with DBH and CW declining with increasing aspen density while slenderness and HTLC increased with increasing aspen density. Aspen DBH at age 28 averaged 40% larger in the 200 aspen ha^{-1} treatment and 22% larger in the 1500 aspen ha^{-1} relative to the unthinned. Thinning had only small and variable effects on the height of the 200 largest aspen·ha^{-1}.

Aspen yields and mixed stand yields were largest in stands with aspen densities of 1500 stems·ha^{-1} or higher. Carbon storage in stemwood at age 90 was also higher in mixed stands with 1500 aspen ha^{-1} or more than in pure spruce stands, with this occurring in addition to the benefits of mixed stands in terms of mitigating early competition, frost and insect issues, and risks, improvements in habitat values and increased resistance and resilience of stands to climate change.

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GOA Plot 1 @age 20

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Introduction

Early juvenile spacing of aspen has been shown to accelerate the growth of residual aspen (Bickerstaff 1946; Steneker 1976; Perala 1978; Bokalo et al. 2007; Kabzems et al. 2016) and achievement of merchantable diameter while reducing aspen densities also increases white spruce growth in mixed stands (Bokalo et al. 2007; Kabzems et al. 2016; Bjelanovic et al. 2021; Comeau 2021a). In addition, enhancing spruce yields through tending of mixedwood stands could help mitigate future conifer timber supply shortages resulting from fire and insect damage to other stands in the region, as well as from other causes.

Mixed stands of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss occur across a range of mid- to late-seral successional stages (Chen and Popadiouk 2002; Bergeron et al. 2014) and are a prominent component in the boreal forest of western Canada. During the early stages of succession following disturbances such as wildfire or harvesting aspen grows more rapidly than spruce and forms an overstory above spruce. After 50 to 80 years, white spruce begins to grow through the canopy and aspen decreases in dominance and basal area (Bergeron et al. 2014).

Mixedwood stands typically have greater species and structural diversity than monocultures and provide better habitat for many species of wildlife (Peterson and Peterson 1995; Macdonald et al. 2010). Long-term site productivity may also be enhanced by the presence of aspen (Pastor 1990; Macdonald et al. 2010). Physical, phenological, and successional differences in growth of aspen and white spruce can result in higher yields from mixedwood stands than from single-species stands (Man and Lieffers 1999; Kabzems et al. 2016; Kweon and Comeau 2019; Comeau 2021a). The risk of white pine weevil (*Pissodes strobi* Peck) damage is lower in mixedwood than pure spruce stands (Stiell and Berry 1985; Taylor et al. 1996) as is damage by *Armillaria* root disease (Morrison et al. 1991; Gerlach et al. 1997). Mixedwood stands may also be more resilient to drought and other climate related stresses, (Forrester 2015; Ammer 2017) with thinning potentially leading to increased resilience of these stands (Bell et al. 2014; Comeau 2021a). In addition, overstory aspen can serve as a nurse crop for small understory spruce by reducing the impact of frost (Groot and Carlson 1996; Pritchard and Comeau 2004; Filipescu and Comeau 2011) and reducing the vigor of understory competitors such as bluejoint reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) (Lieffers and Stadt 1994). Mixedwoods may also produce higher quality spruce stems than result from the open conditions experienced during the first 25 years in spruce plantations (Middleton and Munro 2002; Comeau 2021b).

In 1990 the Western Boreal Growth and Yield Associated (WESBOGY) initiated the Long Term Study to advance our understanding of the dynamics of mixedwood stands following tending in response to an identified need for information on the effects of aspen density on spruce and aspen growth. Major objectives of this study were: a) to provide quantitative information on effects of aspen and spruce densities on tree growth, yield, and wood quality; b) demonstrate effects of aspen and spruce densities and of precommercial thinning in mixedwood stands; and c) provide data for calibration and validation of growth and yield models.

In this report we examine effects of aspen and spruce density on growth of both spruce and aspen during the first 17-31 years after regeneration as a followup to the age 9 results for four installations presented by Bokalo et al. (2007). In addition, we use the Mixedwood Growth Model ((MGM21; https://mgm.ucalberta.ca) to explore effects of aspen and spruce densities on stand dynamics and yield.

Methods

The WESBOGY Long Term Study used a randomized block design with each agency being responsible for establishing and maintaining one block of two installations, one installation on a superior site and one on a median site. Each installation consists of two replications of 15 plots representing the different combinations of spruce and aspen treatment densities. After the loss of one replicate in the Weyerhaueser Grande Prairie Superior installation due to a fire in 2016 the study currently includes a total of 615 plots in 21 installations distributed across Alberta, British Columbia, Manitoba, Saskatchewan and the Northwest Territories (Fig. 1).

Treatments were based on a matrix of six aspen (0, 200, 500, 1500, and 4000 stems·ha^{-1} plus an unthinned control) and three spruce (0, 500, and 1000 stems·ha^{-1}) densities. Initial planting of spruce was at twice the desired final density (1000 stems·ha^{-1} and 2000 stems·ha^{-1}) with spruce densities reduced to target densities at the time of thinning of the aspen. For the first 5 years, vegetation was controlled within a 40 to 50 cm radius of the spruce using plastic mulch mats or by hand clipping to minimize early spruce mortality. Table 1 describes the combinations of spruce and aspen densities of interest and their associated plot number. Treatments were randomly assigned to the 15 plots within each replicate.

In each installation, both replications are located on a common soil type. Each replication required a minimum area of 1.35 ha, that was relatively uniform in physical (slope and aspect) conditions. Study sites had been cutover within less than 24 months of the establishment date and had uniform natural aspen regeneration of greater than 4000 stems·ha^{-1}. Height of aspen regeneration was less than 1.5 m to ensure that competition would not become a serious factor for the initial survival of the planted spruce.

Measurement plots are 20 m by 20 m (0.04 ha) with the centers and corners permanently marked. A 5- or 10-meter treated buffer surrounded each plot. In plots where aspen were not thinned, all spruce were measured in a 20 m by 20 m fixed area plot, while aspen were measured in four 1 m by 1 m (0.0001 ha) subplots located in the southwest quadrant of the main plot due to extremely high initial aspen densities, (upwards to 300,000 stems·ha^{-1}). Within this southwest quadrant, the 1 m by 1 m subplots were located at the centre of the midpoints of each side of the quadrant. At year 5, the 1 m by 1 m subplots were expanded to 2 m by 2 m subplots, utilizing the initial 1m by

1m subplot as 1/4 of the new expanded subplot. At age 20 or 21 subplot size was further increased to 5 m x 5 m resulting in the four 2 m x 2 m subplots being combined into a single 5 m x 5 m subplot. The purpose of subplot expansion was to address the high mortality that naturally occurs on aspen plots.

At year 5, both aspen and spruce were thinned to target treatment densities (Table 1). This treatment was applied to all plots except the natural density aspen (plots 6, 12, and 15). Prior to thinning, the spruce and aspen trees that were designated as leave trees were tagged and measured.

In this report we present results from measurements collected from all 21 LTS installations established in 11 areas in western Canada.

Statistical analysis

Data analysis was completed using SAS9.4 (SAS Institute, Cary, NC). Repeated measures analysis of aspen and spruce height and diameter trends used a random coefficients quadratic polynomial model run with Proc Mixed. Analysis assumed an unstructured covariance model and numerator degrees of freedom were calculated using the Kenward-Roger method with year treated as a random effect. For ages 10, 20 and 28 effects of aspen and spruce treatment densities were analyzed as linear models using Proc Mixed, numerator degrees of freedom were calculated using the Kenward-Roger method, and agency, agency x installation, and replication nested within agency x installation were treated as random effects. Least square means were compared using Tukey's LSD test with alpha=0.05.

Growth Projections using MGM21

The Mixedwood Growth Model (MGM21; https://mgm.ucalberta.ca) was used to project stem volume growth of the 615 plots and to provide data for analysis of potential effects of treatment on future yields. Full tree lists, which included height and diameter of all trees present in each plot at age 12, were developed for each plot from collected data. The tree list for each plot included species, tree factor (number of trees per hectare represented for each tree), DBH and height. Tree factor was calculated for live trees based on the plot size used (TRF=10 000/plot area). Gross total stand volume was reported for all simulations. Stemwood biomass was also calculated by MGM21 based on application of the Lambert et al. (2005) biomass equations. Site index (at age 50) was calculated for each installation using the GYPSY Site Index equations (Huang et al. 2009), with aspen site index determined from unthinned plots (plots 6, 12 and 15) and spruce site index determined from plots with zero aspen density (plots 1 and 7). Climate Moisture Index values shown in Table 2 were assigned to each installation.

Table 1. Treatments associated with each of the 15 spruce and aspen density combinations created in the WESBOGY Long Term Study.

		Aspen Density (stems·ha^{-1})					
		0	**200**	**500**	**1500**	**4000**	**Natural**
Spruce Density (stems·ha^{-1})	**1000**	1	2	3	4	5	6
	500	7	8	9	10	11	12
	0	x	x	x	13	14	15

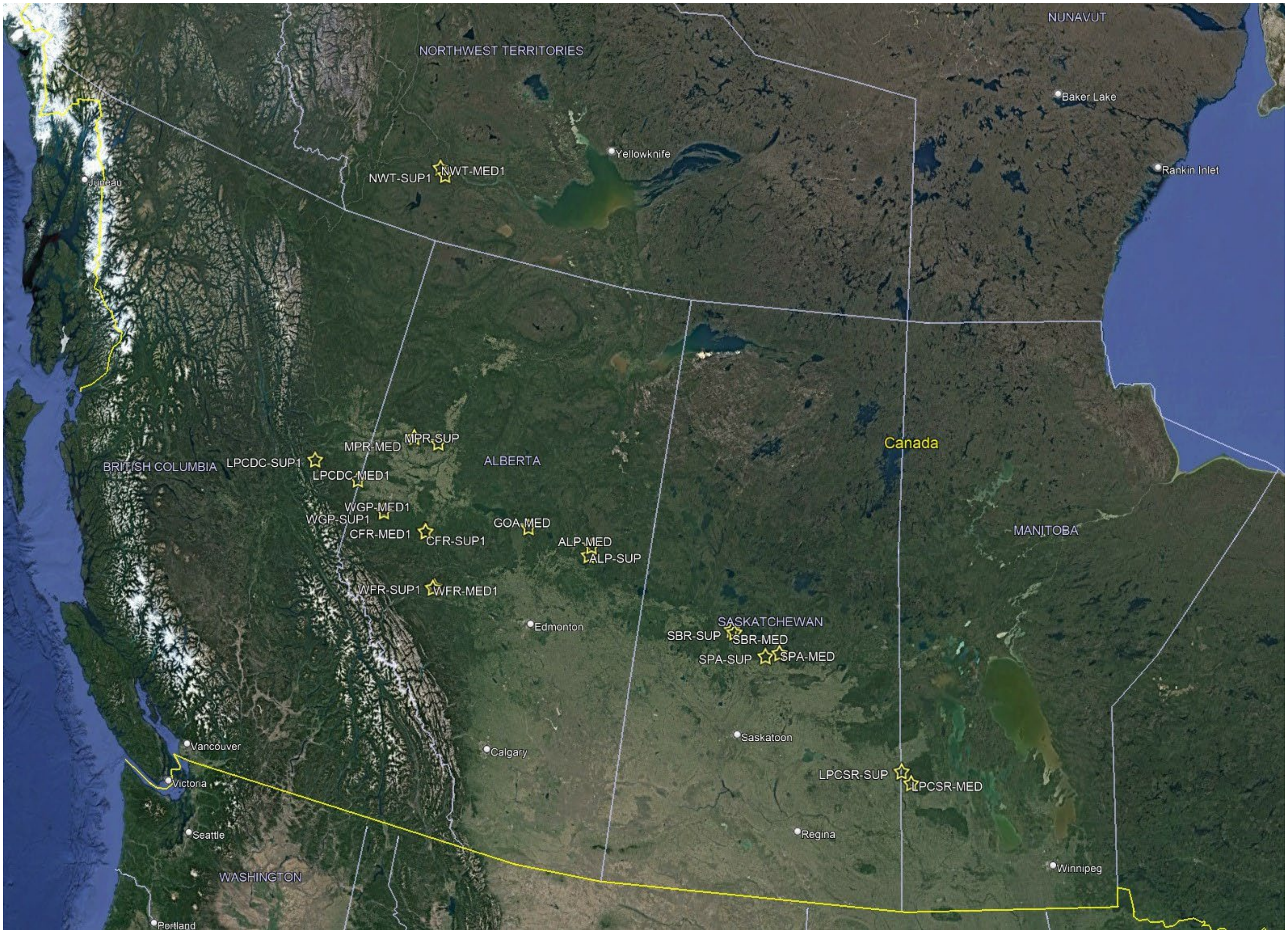


Figure 1. Locations of the 21 WESBOGY Long-Term Study Installations in western Canada. (generated using Google Earth).

Table 2. Location, climate and age of the 21 WESBOGY LTS installations. MAT=mean annual temperature (1991-2020), MAP=mean annual precipitation (1991-2020), CMI=mean climate moisture index (1991-2020). Climate values were generated using ClimateNA7.3 (climateNA.ca). Site index (height of the 100 largest diameter trees at breast height age 50) was calculated for each installation using the GYPSY Site Index equations (Huang et al. 2009), with aspen site index (SI-Aw) determined from unthinned plots (plots 6, 12 and 15) and spruce site index (SI-Sw) determined from plots with zero aspen density (plots 1 and 7) based on measurements at age 12.

Agency	**Installation**	**Est.**	**Lat.**	**Long.**	**Elev.**	**MAT (°C)**	**MAP (mm)**	**CMI (mm)**	**Last meas.**	**Age last meas.**	**SI-Sw**	**SI-Aw**
Government of Alberta	Median	1992	55.317	-114.070	622	1.7	477	4.38	2017	25	20.6	24.3
Alberta Pacific Forest Industries	Median	2001	55.216	-111.913	648	1.4	478	3.89	2020	19	19.4	22.6
Alberta Pacific Forest Industries	Superior	1993	55.041	-111.948	596	1.6	453	1.09	2019	26	18.8	24.2
Canadian Forest Products	Median	2001	54.760	-117.400	755	2.5	530	7.47	2021	20	19.1	19.4
Canadian Forest Products	Superior	2001	54.754	-117.369	800	2.5	533	7.83	2020	20	22.6	22.0
Louisiana Pacific Canada – Dawson Creek	Median	2000	53.758	-120.051	900	2.2	481	6.08	2020	20	12.9	23.4
Louisiana Pacific Canada – Dawson Creek	Superior-Rep1	2000	55.392	-121.687	671	3.1	499	4.57	2020	20	11.4	18.2
Louisiana Pacific Canada – Dawson Creek	Superior-Rep2	2003	55.222	-121.663	730	3.0	511	7.88	2020	17	18.5	19.1
Louisiana Pacific Canada – Swan River	Median	1998	56.485	-101.251	640	1.0	519	7.47	2021	23	23.1	17.4
Louisiana Pacific Canada – Swan River	Superior	1998	51.702	-101.550	619	1.0	511	5.61	2021	23	25.9	20.9
Mercer Peace River Pulp	Median	1992	56.385	-118.589	788	1.0	436	3.28	2019	27	22.1	20.9
Mercer Peace River Pulp	Superior	1992	56.414	-117.729	728	1.1	423	-0.22	2019	27	22.1	21.9
NWT	Median	1993	61.342	-120.749	240	-2.2	388	-2.34	2015	22	15.5	20.3
NWT	Superior	1993	61.239	-120.469	270	-2.3	369	-3.08	2015	22	17.9	23.6
Saskatchewan Environment-Prince Albert	Median	1990	53.759	-105.551	548	0.7	483	4.60	2021	31	21.9	22.0
Saskatchewan Environment-Prince Albert	Superior	1990	53.678	-105.937	535	1.0	476	2.68	2021	31	20.9	23.2
Saskatchewan Environment-Big River	Median	1992	54.092	-107.066	515	1.1	433	-1.19	2018	26	21.4	25.0
Saskatchewan Environment-Big River	Superior	1992	54.052	-106.979	505	1.2	436	-1.04	2018	26	19.6	25.1
WestFraser	Median	1992	53.760	-116.678	1050	2.9	544	10.76	2019	27	19.5	20.3
WestFraser	Superior-Rep1	1992	53.804	-116.644	1100	2.9	555	13.33	2019	27	21.2	19.8
WestFraser	Superior-Rep2	1994	53.796	-116.610	1085	2.9	551	12.28	2019	25	19.0	18.5
Weyerhaeuser Canada – Grand Prairie	Median	1991	54.886	-118.898	703	2.4	476	1.01	2018	27	15.7	19.6
Weyerhaeuser Canada – Grand Prairie	Superior	1991	54.913	-118.919	711	2.35	466	-0.74	2018	27	16.0	20.1

Results

Height and diameter trends for aspen and spruce

Figures 3 and 4 show observed trends in aspen height and DBH for the top 200 stems·ha^{-1}. The top 200 aspen were selected for comparison as this is the lowest density of aspen retained in the study and this provides a useful metric for comparison of treatment effects. Repeated measures analysis indicates a significant (α=0.05) quadratic trend with age, but no significant effects of thinning or spruce density on aspen top height (Table 3, Figure 5). A gradual decline in aspen height growth after age 20 is reflected in the quadratic term being negative. DBH of the top aspen (Table 3, Figure 5) shows a linear trend with age, significant effects of thinning, and significant interactions between age and aspen density and between age and spruce density. These interactions indicate that influences of aspen and spruce densities on aspen top tree DBH change with age, with changes in treatment ranking occurring over time.

Figures 6 and 7 show trends in mean height and DBH for white spruce. Repeated measures analysis of spruce height (Table 3, Fig 8) shows significant effects of age (linear and quadratic terms) and aspen density. The quadratic term for age was positive, reflecting increasing spruce height growth rates with age. The significant interaction between age and aspen density for spruce height reflects cumulative effects of aspen density with age and some changes in treatment rank. The model for spruce DBH shows significant effects of age (linear and quadratic terms), aspen density and spruce density with the positive quadratic term for age showing increasing height growth rates with age. The significant interactions between age and aspen density and age and spruce density for spruce DBH indicate cumulative effects of aspen density and spruce density with age and reductions in spruce size at the higher spruce densities at the lowest aspen densities. Figure 8 shows little difference between 0 and 200 stems·ha^{-1} of aspen on spruce height, but with spruce height and DBH decreasing noticeably after age 15 with increasing aspen density.

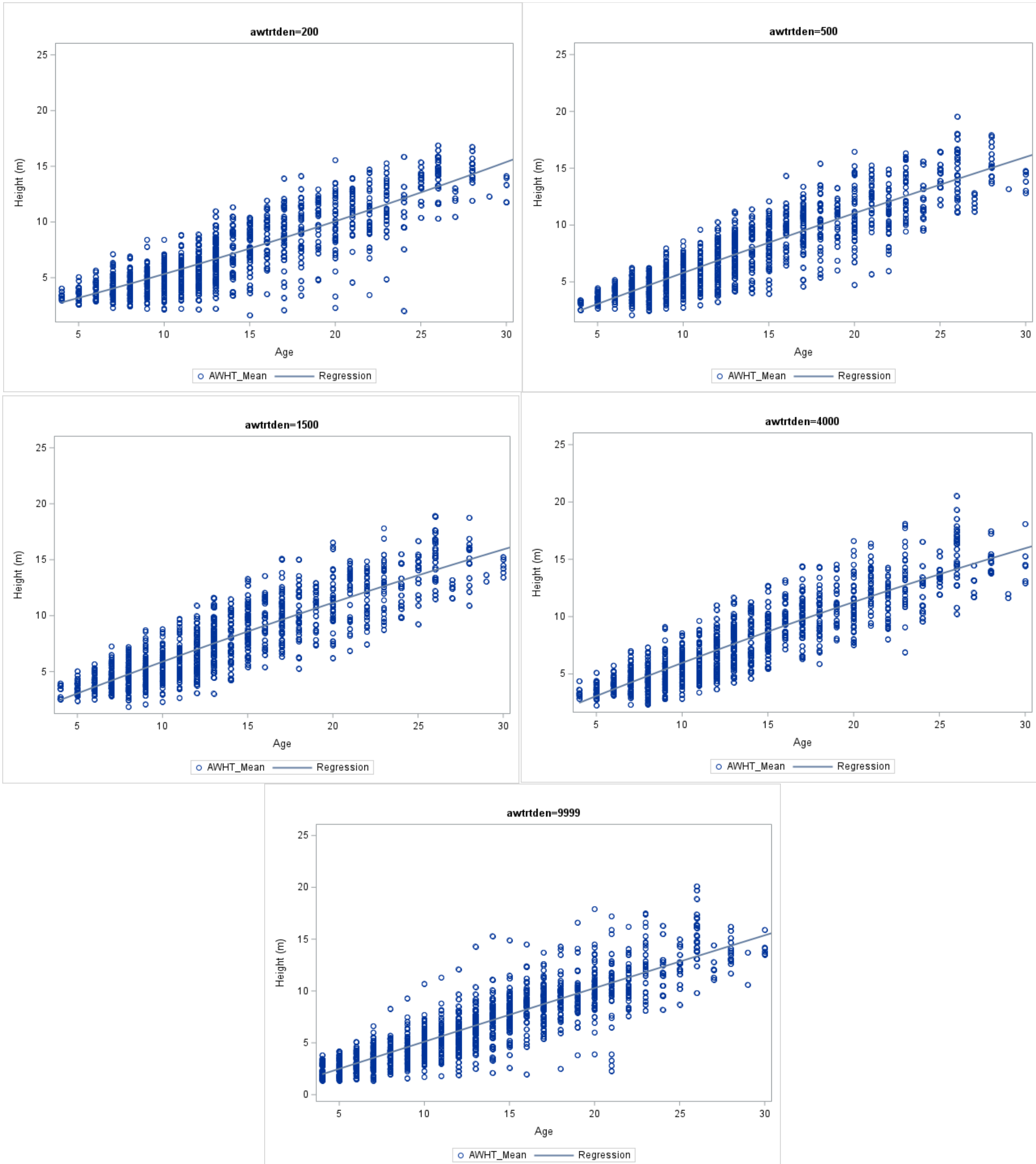


Figure 3. Aspen (top 200 trees per hectare) height trends for the five aspen treatment densities (awtrtden). Awtrtden of 9999 represents the unthinned.

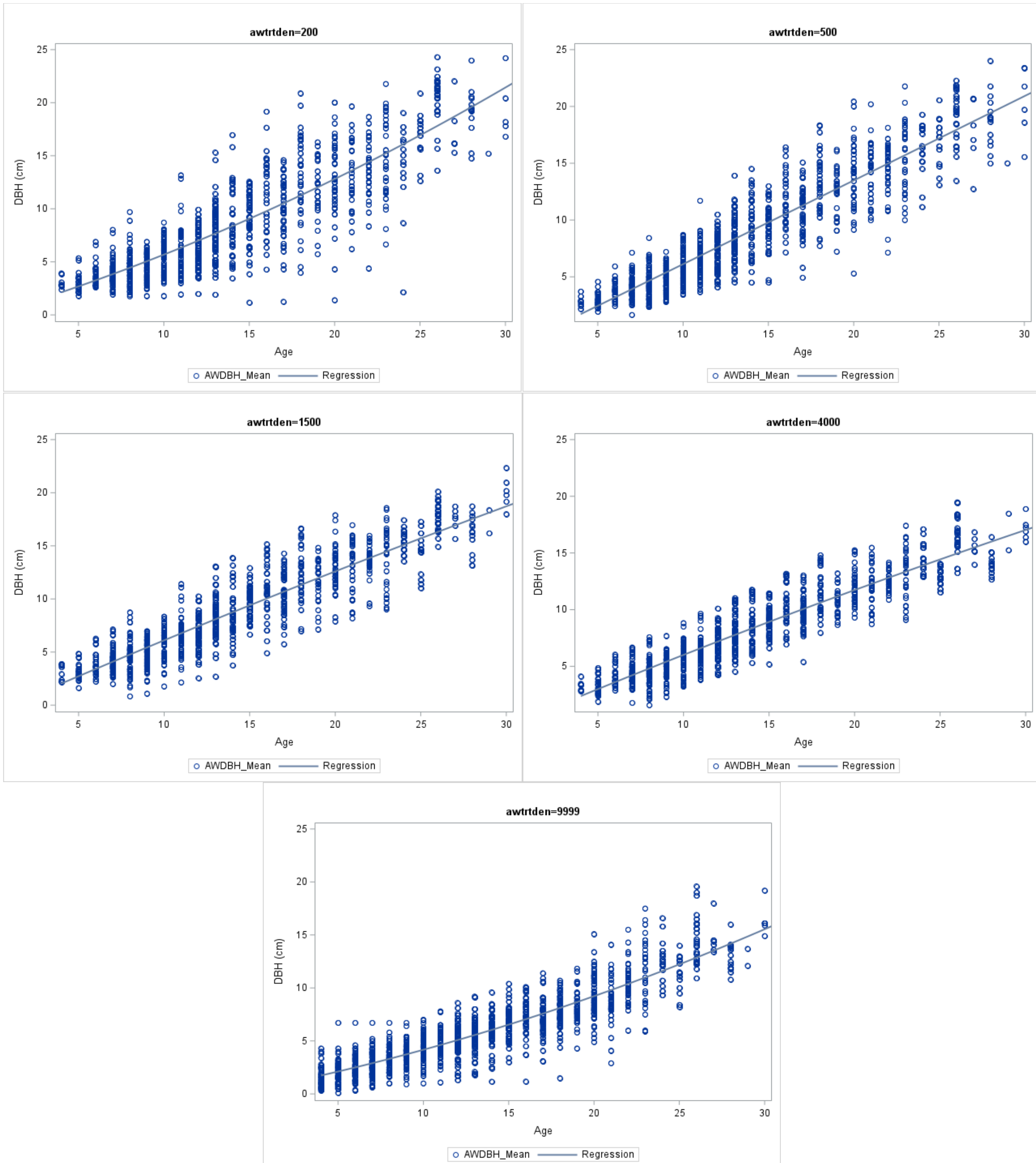


Figure 4. Aspen (top 200 trees per ha) DBH trends for the five aspen treatment densities (awtrtden). Awtrtden of 9999 represents the unthinned.

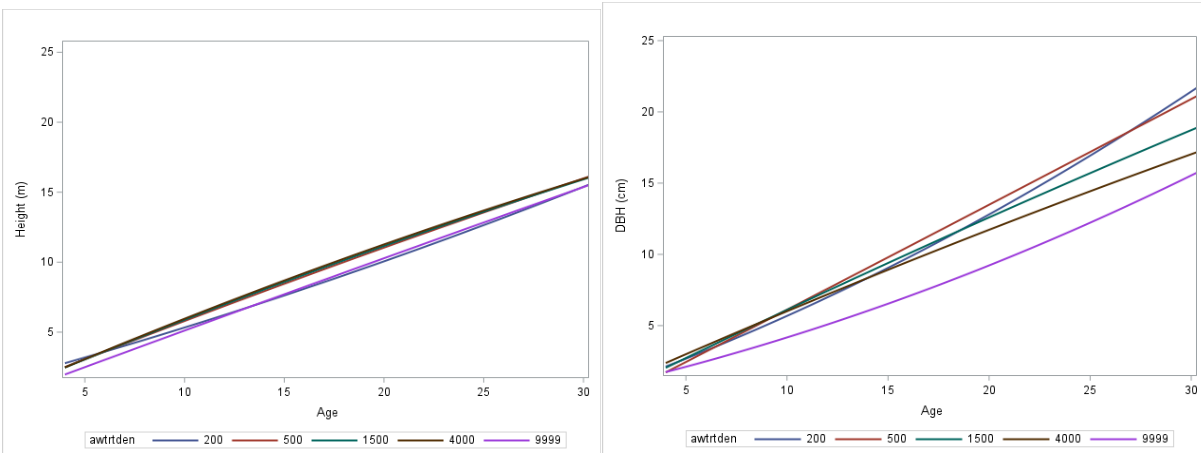


Figure 5. Results from quadratic models (Table 3) summarizing trends for aspen (top 200 trees per ha) height and DBH for the five aspen treatment densities (awtrtden).

Table 3. Results from repeated measures analysis testing effects of age, aspen treatment density, spruce treatment density, and interaction terms on aspen and spruce height and DBH. Significant ($p<0.05$) values are shown in bold.

Species:	**Aspen (top 200 trees ha^{-1})**						**Spruce**					
Variable:	**Height**			**DBH**			**Height**			**DBH**		
Source	**Num df**	**Den df**	**P-value**	**Num df**	**Den df**	**P-value**	**Num df**	**Den df**	**P-value**	**Num df**	**Den df**	**P-value**
Age	1	804	***<0.0001***	1	791	***<0.0001***	1	771	***<0.0001***	1	718	***<0.0001***
Age^2	1	2704	***0.0008***	1	2737	*0.6001*	1	2855	***<0.0001***	1	2521	***<0.0001***
Aspen Treatment Density *(Aw)*	4	371	*0.8091*	4	397	***0.0465***	5	470	***<0.0001***	5	456	***<0.0001***
Spruce Planting Density *(Sw)*	1	372	*0.3702*	1	398	*0.1366*	1	470	*0.7155*	1	456	***0.0026***
*Aw * Sw*	4	372	*0.9185*	4	*398*	*0.8268*	5	469	*0.8771*	5	456	*0.1926*
*Age * Aw*	4	343	*0.7916*	4	352	***0.0003***	5	469	***<0.0001***	5	456	***<0.0001***
*Age * Sw*	1	344	*0.2020*	1	353	***0.0349***	1	469	*0.9822*	1	456	***0.0121***
*Age * Aw * Sw*	4	344	*0.9054*	4	353	*0.5805*	5	469	*0.9072*	5	456	*0.4198*

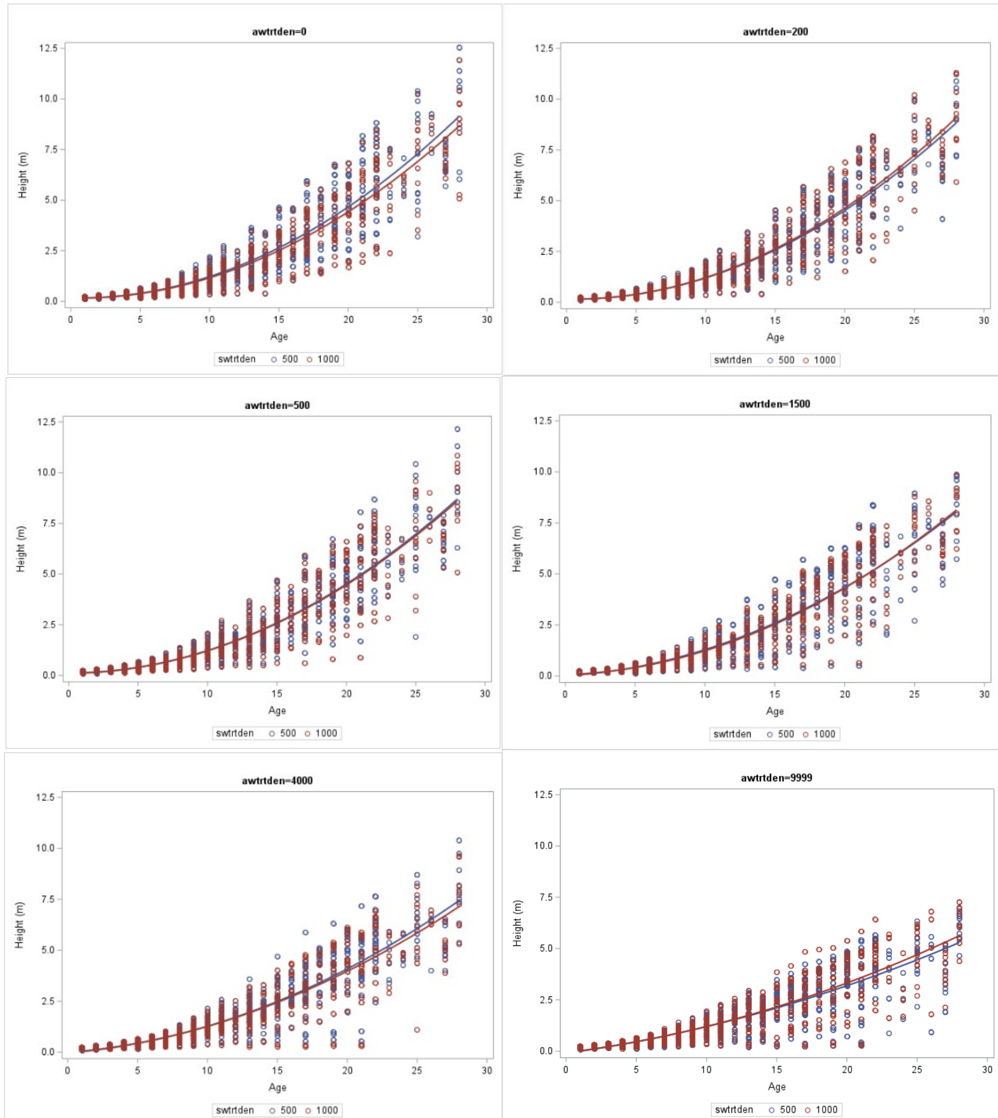


Figure 6. Spruce height trends for the five aspen treatment densities (awtrtden) and two spruce densities (swtrtden). Awtrtden of 9999 represents the unthinned.

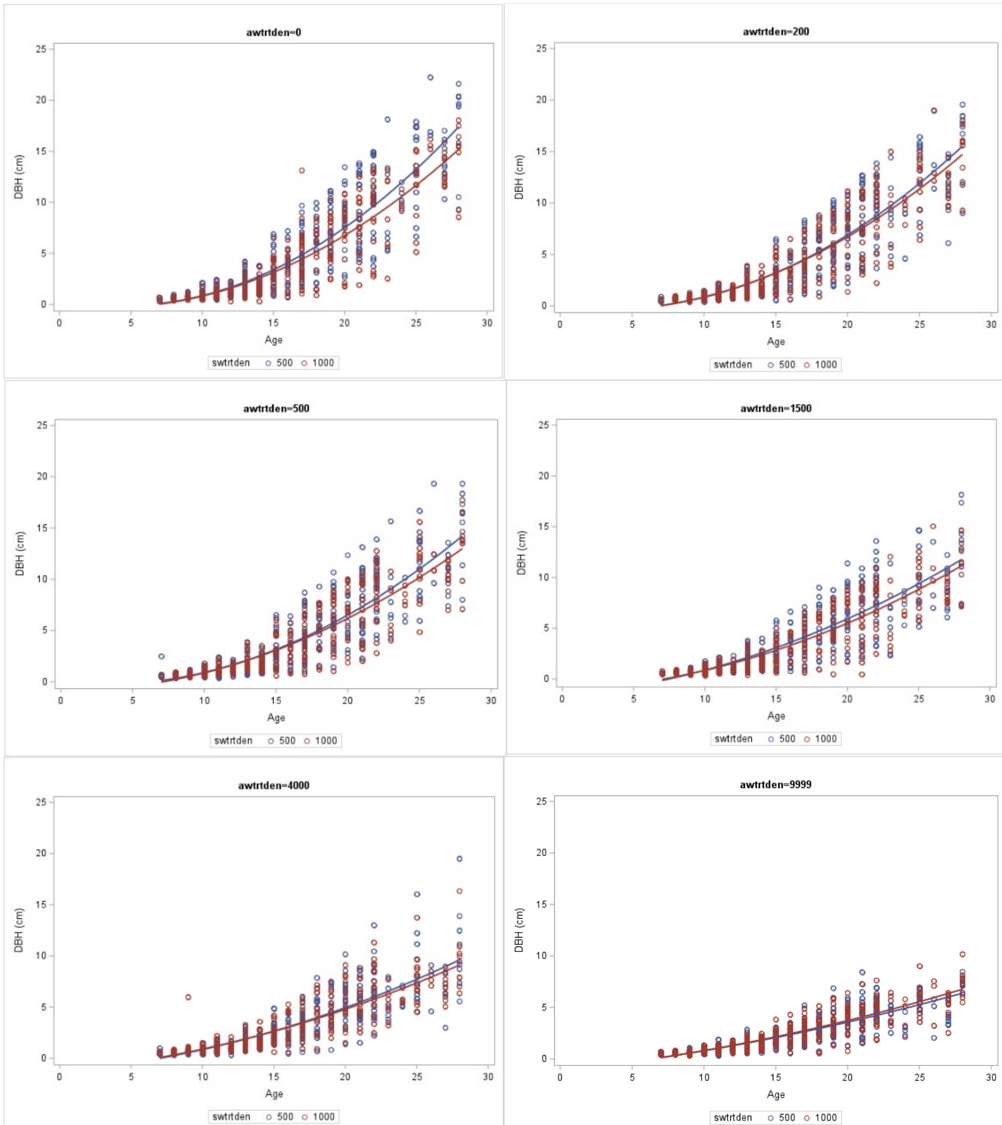


Figure 7. Spruce DBH trends for the five aspen treatment densities (awtrtden) and two spruce densities (swtrtden). Awtrtden of 9999 represents the unthinned.

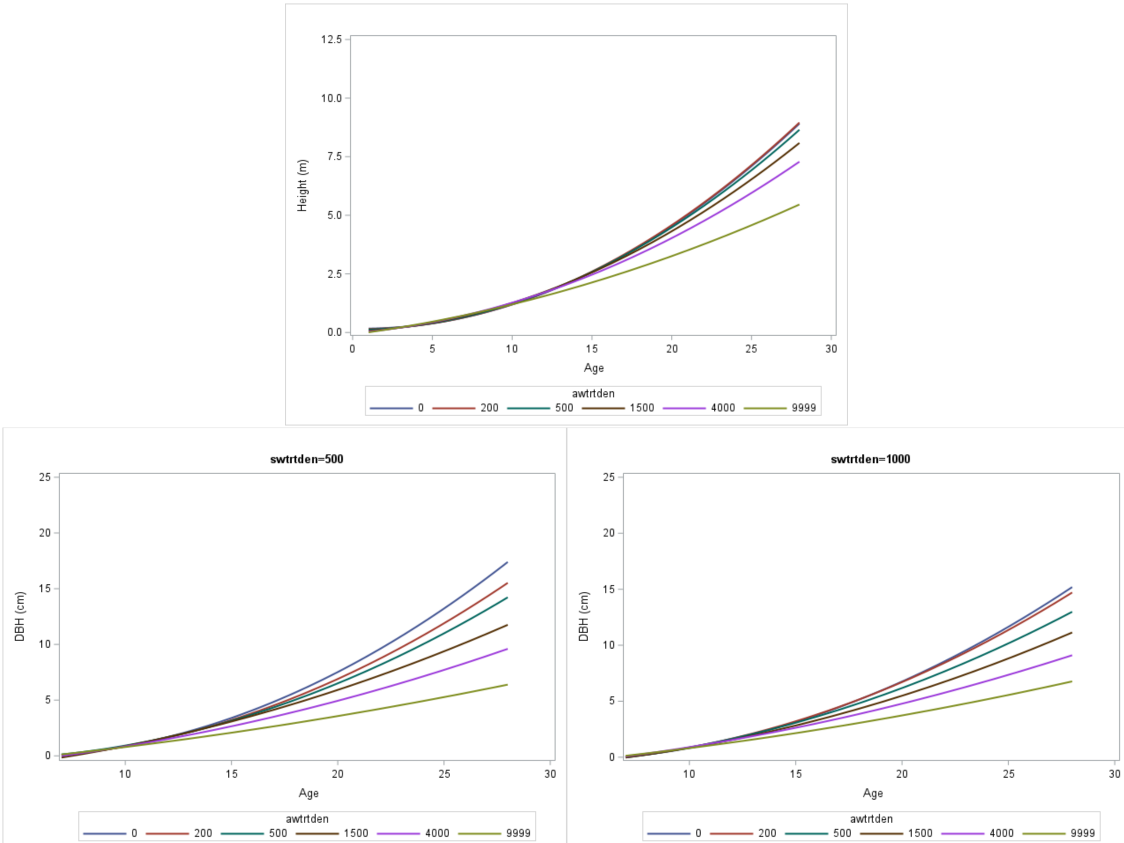


Figure 8. Results from quadratic models (Table 3) summarizing trends for spruce height and DBH for the five aspen treatment densities (awtrtden). Since spruce density was significant in the models for DBH, separate plots are shown for the two spruce densities.

Effects of thinning on aspen growth

Analysis of results at selected specific ages provides a better understanding of effects of precommercial thinning on aspen sizes than does repeated measures analysis. Tables 4, 5 and 6 provide results for analysis at ages 10, 20 and 28, respectively. Figure 9 illustrates effects of aspen densities on aspen height and DBH at the three ages and table 7 summarizes the least-square means for each treatment. At all ages, aspen density had significant effects on mean top height, DBH, slenderness, crown width (CW), height to live crown base (HTLC), aspen stems$\cdot$ha^{-1} and aspen basal area. At age 28, differences in responses across installations result in significant interactions between installations and aspen density for DBH and slenderness, and a significant 3-way interaction between installations, aspen density and spruce density for aspen mean top height.

Aspen top height was smaller in the 200 aspen density than in the 1500 or 4000 but did not differ from unthinned at all 3 ages, and was larger in the 1500 and 4000 than the unthinned at ages 10 and 20 but not at age 28 (Table 7). Aspen DBH was increased significantly by thinning at all ages, with a clear trend of decreasing DBH with increasing density at age 28 (Figure 9), but with differences between 200 and 500 stems$\cdot$ha^{-1} not being significant. Aspen slenderness is significantly higher in the unthinned than the other treatments with slenderness at age 28 declining with decreasing aspen density. Thinning resulted in increased CW at all ages, with all but the 200 and 500 stems$\cdot$ha^{-1} treatments differing at age 28, while HTLC declined with thinning intensity, but with poor differentiation between the unthinned and 4000 stems$\cdot$ha^{-1} treatments. Aspen density and basal area in the unthinned differed between all treatments at each age, but show only a small decline in aspen density between ages 10 (17 775 stems$\cdot$ha^{-1}) and age 28 (16 490 stems$\cdot$ha^{-1}) and a small increase in aspen basal area (12.01 m$^{2}\cdot$ha^{-1} at age 10, 12.94 m$^{2}\cdot$ha^{-1} at age 28).

Table 4. Mixed model ANOVA results (α=0.05) for aspen, testing differences in mean HT(m), DBH (cm), Slenderness, crown width (CW) (m), height to live crown base (HTLC) (m), SPH (#/ha) and basal area (BA) (m^2/ha) by treatment at year 10.

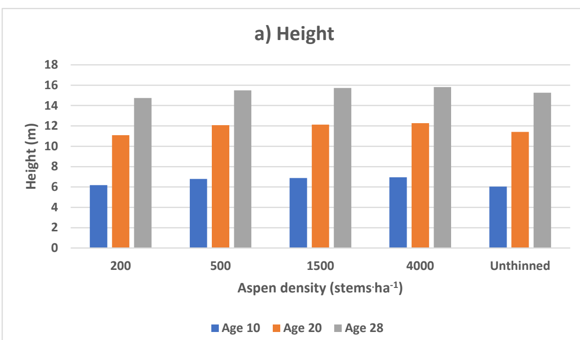
Source	df	HT P-value	DBH P-value	Slendernes P-value	CW P-value	HTLC P-value	SPH P-value	BA P-value
Agency *(A)*	10	-	-	-	-	-	-	-
Installation*(I)*	1	0.2073	0.3467	0.5691	0.6068	0.1742	0.3300	0.6683
Aspen Treatment Density *(Aw)*	3	***<0.0001***	***0.0109***	***<0.0001***	0.4947	***<0.0001***	***<0.0001***	***<0.0001***
Spruce Planting Density *(Sw)*	1	0.7137	0.2358	0.6205	0.4446	0.9486	0.3300	0.7211
*A * I*	9	-	-	-	-	-	-	-
Replicate*(A*I)*	20	-	-	-	-	-	-	-
*Aw * Sw*	3	0.2765	0.1504	0.3674	0.6113	0.4175	0.4190	0.8348
*I*Aw*	3	0.3653	0.6592	0.7982	0.9297	0.3922	0.0851	0.8719
*I*Sw*	1	0.9301	0.6139	0.5167	0.9994	0.7343	0.0905	0.8783
*I*Aw*Sw*	3	0.2199	0.9002	0.1516	0.6781	0.4960	0.0353	0.9462
Residual Error	272	-	-	-	-	-	-	-
Total	326	-	-	-	-	-	-	-

Table 5. Mixed model ANOVA results (α=0.05) for aspen, testing differences in mean HT(m), DBH (cm), Slenderness, crown width (CW) (m), height to live crown base (HTLC) (m), SPH (#/ha) and basal area (BA) (m^2/ha) by treatment at year 20.

Source	df	HT P-value	DBH P-value	Slendernes P-value	CW P-value	HTLC P-value	SPH P-value	BA P-value
Agency *(A)*	10	-	-	-	-	-	-	-
Installation*(I)*	1	0.6718	0.4282	0.3710	0.9925	0.3438	0.5983	0.5819
Aspen Treatment Density *(Aw)*	4	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***
Spruce Planting Density *(Sw)*	1	0.8226	0.3320	0.5397	0.7923	0.2371	0.3899	0.9749
*A * I*	9	-	-	-	-	-	-	-
Replicate*(A*I)*	19	-	-	-	-	-	-	-
*Aw * Sw*	4	0.9769	0.3390	0.4685	0.1364	0.7584	0.5927	0.7405
*I*Aw*	4	0.1650	0.2471	0.5172	0.5511	0.3283	0.3918	0.9368
*I*Sw*	1	0.8730	0.8840	0.7671	0.8982	0.0625	0.1383	0.8510
*I*Aw*Sw*	4	0.7850	0.9976	0.9200	0.8057	0.9570	0.0782	0.9932
Residual Error	340	-	-	-	-	-	-	-
Total	397	-	-	-	-	-	-	-

Table 6. Mixed model ANOVA results (α=0.05) for aspen, testing differences in mean HT(m), DBH (cm), Slenderness, crown width (CW) (m), height to live crown base (HTLC) (m), SPH (#/ha) and basal area (BA) (m^2/ha) by treatment at year 28.

Source	df	HT P-value	DBH P-value	Slenderness P-value	CW P-value	HTLC P-value	SPH P-value	BA P-value
Agency *(A)*	6	-	-	-	-	-	-	-
Installation*(I)*	1	0.2329	0.3441	0.0720	0.2537	0.4929	0.2103	0.6716
Aspen Treatment Density *(Aw)*	4	***0.0010***	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***
Spruce Planting Density *(Sw)*	1	0.1346	0.1762	0.8035	0.1909	0.2978	0.2533	0.2227
*A * I*	4	-	-	-	-	-	-	-
Replicate*(A*I)*	10	-	-	-	-	-	-	-
*Aw * Sw*	4	0.5198	0.4927	0.1084	0.8385	0.4933	0.2627	0.5223
*I*Aw*	4	0.3651	***0.0021***	***0.0056***	0.7459	0.5860	0.0521	0.4855
*I*Sw*	1	0.6091	0.5043	0.3445	0.8205	0.2995	0.2823	0.7067
*I*Aw*Sw*	4	***0.0111***	0.7156	0.3293	0.9275	0.1254	0.4036	0.3505
Residual Error	178	-	-	-	-	-	-	-
Total	217	-	-	-	-	-	-	-



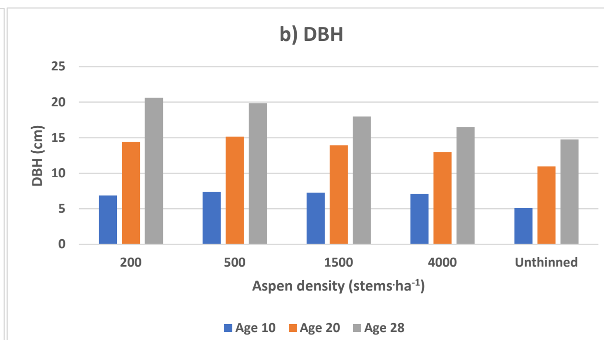


Figure 9. Effects of aspen treatment density on a) height and b) DBH of the 200 largest aspen per hectare at ages 10, 20 and 28.

Table 7. Summary of treatment means (least square means) for aspen height (HT), DBH, Slenderness, crown width (CW), height live crown base (HTLC) for top trees, density (SPH, stems·ha^{-1}) and basal area (BA) by treatment and age. Values within each row with different letters were found to be significantly (α=0.05) different using Tukey's test.

		Treatment				
Variable	**Age**	**200**	**500**	**1500**	**4000**	**Unthinned**
HT (m)	**10**	6.18b	6.79a	6.88a	6.95a	6.04b
HT (m)	**20**	11.09c	12.08ab	12.13a	12.28a	11.42bc
HT (m)	**28**	14.74b	15.49ab	15.73a	15.82a	15.26ab
DBH (cm)	**10**	6.87a	7.38a	7.29a	7.09a	5.09b
DBH (cm)	**20**	14.44ab	15.14a	13.93b	12.95c	10.96d
DBH (cm)	**28**	20.62a	19.86a	17.99b	16.50c	14.76d
Slenderness	**10**	0.93c	0.92c	0.94bc	0.98b	1.22a
Slenderness	**20**	0.85bc	0.80c	0.88bc	0.95b	1.07a
Slenderness	**28**	0.72e	0.79d	0.88c	0.97b	1.05a
CW (m)	**10**	1.20a	1.24a	1.23a	1.18a	0.86b
CW (m)	**20**	1.97ab	2.06a	1.81bc	1.68c	1.41d
CW (m)	**28**	2.68a	2.48a	2.14b	1.83c	1.61d
HTLC (m)	**10**	1.58c	1.68bc	1.70bc	1.87ab	2.02a
HTLC (m)	**20**	2.96e	3.45d	3.97c	4.71b	5.27a
HTLC (m)	**28**	4.97d	5.75c	6.91b	7.41ab	7.86a
SPH (# ha^{-1})	**10**	182c	492c	1364c	3599b	17775a
SPH (# ha^{-1})	**20**	160c	467c	1354c	3590b	17466a
SPH (# ha^{-1})	**28**	150c	464c	1356c	3507b	16490a
BA (m^{2}ha^{-1})	**10**	1.25e	2.70d	5.21c	8.72b	12.01a
BA (m^{2}ha^{-1})	**20**	1.26e	2.70d	5.23c	8.86b	11.94a
BA (m^{2}ha^{-1})	**28**	1.62e	3.16d	6.18c	10.10b	12.94a

Effects of thinning on spruce growth

At age 10 aspen density had significant effects on spruce height, root collar diameter and height: diameter ratio (HDR) but not on crown width (CW) or height to live crown (HTLC) (Table 8). At age 20 (Table 9) and 28 (Table 10), spruce density had significant effects on spruce DBH and CW but not on other variables. Significant interaction terms (Aw*Sw) for slenderness at age 20 (Table 9) and for DBH, CW and HTLC at age 28 (Table 10) indicate a need for separate analysis of aspen density effects for each spruce density.

Table 11 summarizes treatment means (least squares means) for spruce at ages 10, 20 and 28. Spruce height declined with increasing aspen density at all ages, with differences being most apparent and significant between the lowest and highest densities and with the magnitude of these differences increasing with age. At age 28, spruce in the unthinned are 59 % of the height of spruce without aspen (Fig. 10) while they were 70% at age 20 and 94% at age 10. DBH was reduced by both increasing spruce density and increasing aspen density at ages 20 and 28 (Tables 9 and 10, Fig. 10) ($p<0.01$). At age 20, spruce DBH was 77% and 44% of the 0 aspen density values and in the 1500 and unthinned (U) treatments, respectively, at 500 stems·ha^{-1} spruce and 81% and 51% at 1000 stems·ha^{-1} spruce. Differences between aspen densities were larger at age 28, spruce DBH was 66% and 34% of the 0 aspen density values in the 1500 and U treatments, respectively, at 500 stems·ha^{-1} spruce and 72% and 42% at 1000 stems·ha^{-1} spruce.

HDR and slenderness increased with increasing aspen density at the three ages with differences being most apparent and significant between the lowest and highest densities. At age 20, slenderness was higher with 1000 spruce than 500 spruce for aspen density of 0 stems·ha^{-1}. Crown width at both ages 20 and 28 was smaller for the higher (1000 stems·ha^{-1}) spruce density and declined with increasing aspen density. For HTLC, analysis of both spruce densities combined at age 20 indicated that HTLC was significantly higher for thinned than for 0 aspen, however, the difference in HTLC between these two treatments was only 12 cm. At age 28, differences appear inconsistent, with HTLC in the 0 aspen not differing from that in the unthinned. This inconsistency results from more rapid growth of trees and tree crowns in the lower aspen densities leading to crown closure and intraspecific competition, and a reversal of the effects of aspen densities.

Table 8. Mixed model ANOVA results (α=0.05) for spruce, testing differences in mean height (HT) (m), root collar diameter (RCD) (cm), height:diameter ratio (HDR), crown width (CW) (m) and height to live crown base (HTLC) (m) by treatment at year 10.

Source	df	HT P-value	RCD P-value	HDR P-value	CW P-value	HTLC P-value
Agency *(A)*	10	-	-	-	-	-
Installation*(I)*	1	0.2180	0.1263	0.2348	0.1662	0.7794
Aspen Treatment Density *(Aw)*	5	***0.0064***	***<0.0001***	***<0.0001***	0.0832	0.0852
Spruce Planting Density *(Sw)*	1	0.2822	0.7305	0.2739	0.0962	0.9316
*A * I*	9	-	-	-	-	-
Replicate*(A*I)*	20	-	-	-	-	-
*Aw * Sw*	5	0.7804	0.7928	0.8974	0.5788	0.8032
*I*Aw*	5	***0.0049***	***0.0059***	0.1714	***0.0022***	0.6081
*I*Sw*	1	0.3241	0.3296	0.3034	0.3630	0.4518
*I*Aw*Sw*	5	0.3074	0.0554	0.3393	0.4178	0.7897
Residual Error	429	-	-	-	-	-
Total	491	-	-	-	-	-

Table 9. Mixed model ANOVA results (α=0.05) for spruce, testing differences in mean height HT(m), DBH(cm), Slenderness, crown width (CW) (m) and height to live crown base (HTLC) (m) by treatment at year 20.

Source	df	HT P-value	DBH P-value	Slenderness P-value	CW P-value	HTLC P-value
Agency *(A)*	10	-	-	-	-	-
Installation*(I)*	1	0.7536	0.4082	0.6940	0.9849	0.3533
Aspen Treatment Density *(Aw)*	5	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***
Spruce Planting Density *(Sw)*	1	0.5258	***0.0019***	0.9190	***0.0001***	0.1422
*A * I*	9	-	-	-	-	-
Replicate*(A*I)*	19	-	-	-	-	-
*Aw * Sw*	5	0.5492	0.2767	***0.0448***	0.1009	0.0932
*I*Aw*	5	***0.0396***	0.5296	***0.0196***	***0.0475***	0.8642
*I*Sw*	1	0.2304	0.4760	0.1300	0.7081	0.0775
*I*Aw*Sw*	5	0.7703	0.5308	0.4156	0.9048	0.4306
Residual Error	418	-	-	-	-	-
Total	479	-	-	-	-	-

Table 10. Mixed model ANOVA results (α=0.05) for top spruce, testing differences in mean height (HT) (m), DBH(cm), Slenderness, crown width (CW) (m) and height to live crown base (HTLC) (m) by treatment at year 28.

Source	df	HT P-value	DBH P-value	Slenderness P-value	CW P-value	HTLC P-value
Agency *(A)*	6	-	-	-	-	-
Installation*(I)*	1	0.0839	0.8733	0.6394	0.9675	0.5502
Aspen Treatment Density *(Aw)*	5	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	0.2009
Spruce Planting Density *(Sw)*	1	0.6546	***0.0057***	0.9711	***0.0056***	***<0.0001***
*A * I*	4	-	-	-	-	-
Replicate*(A*I)*	10	-	-	-	-	-
*Aw * Sw*	5	0.1834	***0.0415***	0.6557	***0.0300***	***0.0117***
*I*Aw*	5	0.1018	0.3381	0.4640	***0.0326***	0.1337
*I*Sw*	1	0.5789	0.7092	0.2405	0.9036	0.9675
*I*Aw*Sw*	5	0.8171	0.9803	0.9884	0.9382	0.1071
Residual Error	220	-	-	-	-	-
Total	263	-	-	-	-	-

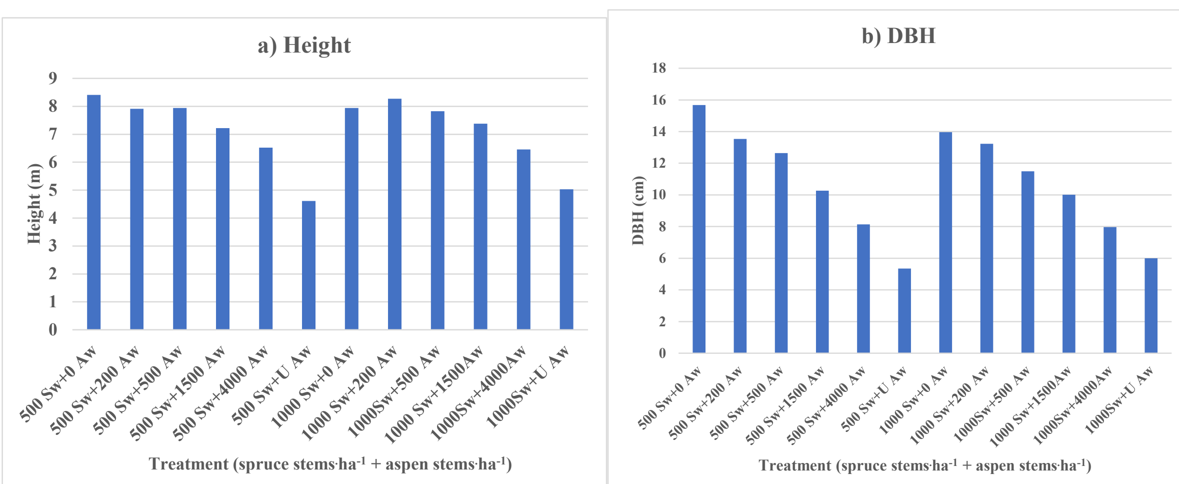


Figure 10. Effects of aspen (Aw) and spruce (Sw) treatment densities on a) spruce height and b) spruce DBH at age 28.

Table 11. Summary of treatment means for spruce height (HT), height increment (HI), root collar diameter (RCD), DBH, height:diameter ratio (HDR), slenderness (Slen), crown width (CW) and height to live crown base (HTLC) by treatment at years 10, 20 and. Values within each row within each spruce density (Sw density) with different letters were found to be significantly (α=0.05) different using Tukey's test. Yellow highlighting indicates cases where the two spruce densities should be examined separately due either to significant interactions between aspen and spruce densities (age 20 slenderness, age 28 DBH, CW, and HTLC) or significance of both spruce and aspen densities (age 20 DBH and CW, age 28 DBH, CW and HTLC). U represents the unthinned treatment.

		Sw density=500						**Sw density=1000**						**Sw density=both**					
		Aspen Density (stems·ha^{-1})						**Aspen Density (stems·ha^{-1})**						**Aspen Density (stems·ha^{-1})**					
Var	**Age**	**0**	**200**	**500**	**1500**	**4000**	**U**	**0**	**200**	**500**	**1500**	**4000**	**U**	**0**	**200**	**500**	**1500**	**4000**	**U**
HT (m)	**10**	1.49ab	1.44ab	1.49ab	1.50ab	1.53a	1.34b	1.41ab	1.46ab	1.45ab	1.46ab	1.48a	1.37b	1.45ab	1.45ab	1.47ab	1.49a	1.51a	1.36b
HT (m)	**20**	5.28a	5.18a	5.11a	4.93ab	4.57b	3.54c	4.97ab	5.23a	5.07a	4.85ab	4.51ab	3.68c	5.06a	5.14a	5.03a	4.83ab	4.48b	3.54c
HT (m)	**28**	8.41a	7.91ab	7.94ab	7.22bc	6.52c	4.61d	7.94ab	8.27a	7.83ab	7.38b	6.46c	5.03d	8.13a	8.05a	7.84a	7.26b	6.45c	4.78d
RCD (cm)	**10**	3.08a	2.92ab	2.78abc	2.69bc	2.45c	2.04d	2.93a	2.92a	2.81a	2.73a	2.46b	1.99c	3.04a	2.95ab	2.83ab	2.74b	2.48c	2.05d
DBH (cm)	**20**	8.72a	8.07ab	7.48bc	6.75c	5.60d	3.83e	7.76a	7.76ab	7.20b	6.29c	5.39d	3.94e	8.23a	7.91ab	7.34b	6.51c	5.49d	3.88e
DBH (cm)	**28**	15.68a	13.53ab	12.64b	10.27c	8.14d	5.35e	13.96a	13.23b	11.49c	10.01d	7.97e	6.00f	14.82a	13.38b	12.06c	10.14d	8.05e	5.67f
HDR	**10**	0.46c	0.46c	0.50bc	0.52b	0.58a	0.62a	0.45e	0.47de	0.48d	0.52c	0.57b	0.62a	0.45e	0.46de	0.49d	0.52c	0.57b	0.62a
Slen.	**20**	0.66b	0.72b	0.74b	0.81b	0.90b	1.32a	0.73e	0.75de	0.80cd	0.92bc	0.95b	1.11a	0.69d	0.74cd	0.77bcd	0.86bc	0.92b	1.22a
Slen.	**28**	0.55c	0.65bc	0.65bc	0.78ab	0.83ab	0.97a	0.58d	0.65cd	0.72bc	0.76b	0.84ab	0.92a	0.56e	0.65de	0.68cd	0.77bc	0.83b	0.94a
CW	**10**	0.47	0.45	0.47	0.46	0.47	0.42	0.45	0.45	0.44	0.45	0.45	0.43	0.46	0.45	0.46	0.45	0.46	0.43
CW	**20**	1.21a	1.18a	1.14ab	1.12ab	1.03b	0.78c	1.08a	1.13a	1.09a	1.05ab	0.98b	0.81c	1.15a	1.15a	1.12a	1.09a	1.00b	0.80c
CW	**28**	1.90a	1.74ab	1.64b	1.53b	1.28c	1.02d	1.67a	1.66ab	1.60b	1.44c	1.27d	1.07e	1.79a	1.7ab	1.62b	1.48c	1.28d	1.04e
HTLC (m)	**10**	0.28	0.27	0.27	0.27	0.28	0.29	0.28	0.30	0.30	0.29	0.31	0.32	0.29	0.3	0.3	0.29	0.31	0.32
HTLC (m	**20**	0.53	0.52	0.51	0.53	0.55	0.60	0.49c	0.52c	0.56bc	0.55bc	0.62ab	0.66a	0.51c	0.52c	0.54bc	0.54bc	0.59ab	0.63a
HTLC (m	**28**	0.96	0.88	0.91	0.97	0.95	0.89	1.10ab	1.23a	1.13a	1.03b	1.00b	0.99b	1.03	1.06	1.02	1	0.97	0.94

Aw density * Sw density interaction significant for: age 20 slenderness, age 28 DBH, CW and htlc
Sw density significant for: age 20 DBH and cw, age 28 DBH, CW and htlc

Table 12. Summary of treatment means for spruce density (SPH) and spruce basal area (BA) by treatment at years 10, 20 and 28. Values within each row within each spruce density (Sw density) with different letters were found to be significantly (α=0.05) different using Tukey's test. U represents the unthinned treatment.

		Sw density=500						Sw density=1000						Sw density=all					
		Aspen Density (stems·ha^{-1})						Aspen Density (stems·ha^{-1})						Aspen Density (stems·ha^{-1})					
Variable	**Age**	**0**	**200**	**500**	**1500**	**4000**	**U**	**0**	**200**	**500**	**1500**	**4000**	**U**	**0**	**200**	**500**	**1500**	**4000**	**U**
SPH	**10**	640ab	630ab	647a	616ab	629ab	615b	1306	1287	1278	1285	1298	1255	973	959	963	950	964	935
SPH	**20**	641ab	631ab	648a	617ab	630ab	614b	1308	1288	1280	1286	1301	1255	975a	959ab	964ab	951ab	965ab	935b
SPH	**28**	605a	591ab	591ab	573ab	589ab	560b	1231	1214	1187	1208	1209	1159	918a	902ab	889ab	890ab	899ab	859b
BA	**10**	1.82a	1.43b	1.33b	0.90c	0.63cd	0.29d	2.97a	2.60ab	2.22b	1.69c	1.25c	0.66d	2.39a	2.01b	1.78b	1.29c	0.94d	0.47e
BA	**20**	1.82a	1.43b	1.31b	0.89c	0.62cd	0.26d	2.97a	2.59ab	2.21b	1.65c	1.21c	0.61d	2.40a	2.01b	1.76b	1.26c	0.92d	0.43e
BA	**28**	2.45a	1.82b	1.60b	1.03c	0.72cd	0.22d	3.93a	3.40ab	2.79b	2.03c	1.41c	0.68d	3.19a	2.61b	2.20b	1.53c	1.06d	0.45e

Aw * Sw interaction not significant for sph at ages 10, 20, or 28 but significant for BA at ages 10, 20 and 28.

MGM projections.

Figures 11 and 12 summarize effects of aspen density, spruce density and site index on volume-age trends for eight selected treatments (plots 1, 4, 6, 7, 10, 12, 13 and 15) for site index values covering the range between minimum and maximum values observed in the 21 installations (Table 2). Volumes of both aspen and white spruce increased with increasing site index. Trends for white spruce (Fig. 11) show reductions in volume with increasing aspen density and increases in volume with increasing spruce density. In addition, increases in aspen density result in narrowing differences between the lowest and highest site index values. Adding spruce to aspen stands generally resulted in decreases in aspen volume (Fig. 12). Table 13 provides the parameter estimates for the non-linear (Chapman-Richards) equations fit to the data generated from MGM simulations for all plots.

Table 14 provides results for analysis of effects of aspen and spruce densities on culmination ages and associated MAI values. Both aspen and spruce densities have significant effects on culmination age and culmination age MAI. The interaction between aspen and spruce densities was significant for conifer and stand MAI but not significant for deciduous MAI or culmination ages. Table 15 shows least-square means and results from Tukey's tests for culmination age values. Conifer culmination ages ranged between 89 and 104 years, with culmination age being lower overall at the higher conifer density and shortest with 4000 aspen.

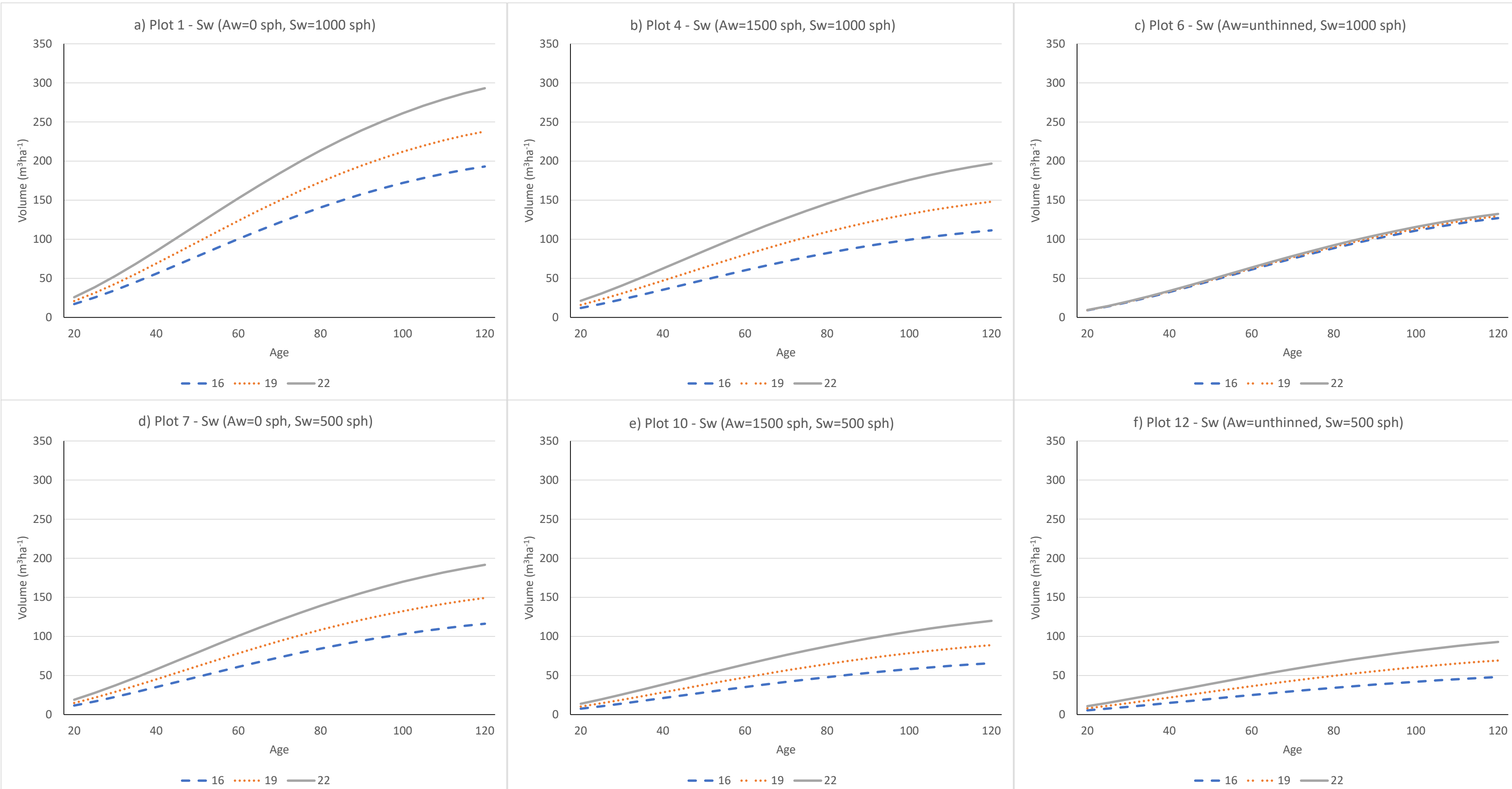


Figure 11. Yield curves showing volume-age trends for spruce in plots 1, 4, 6, 7, 10, and 12 for spruce site index values of 16, 19 and 22 m. sph=stems·ha^{-1}.

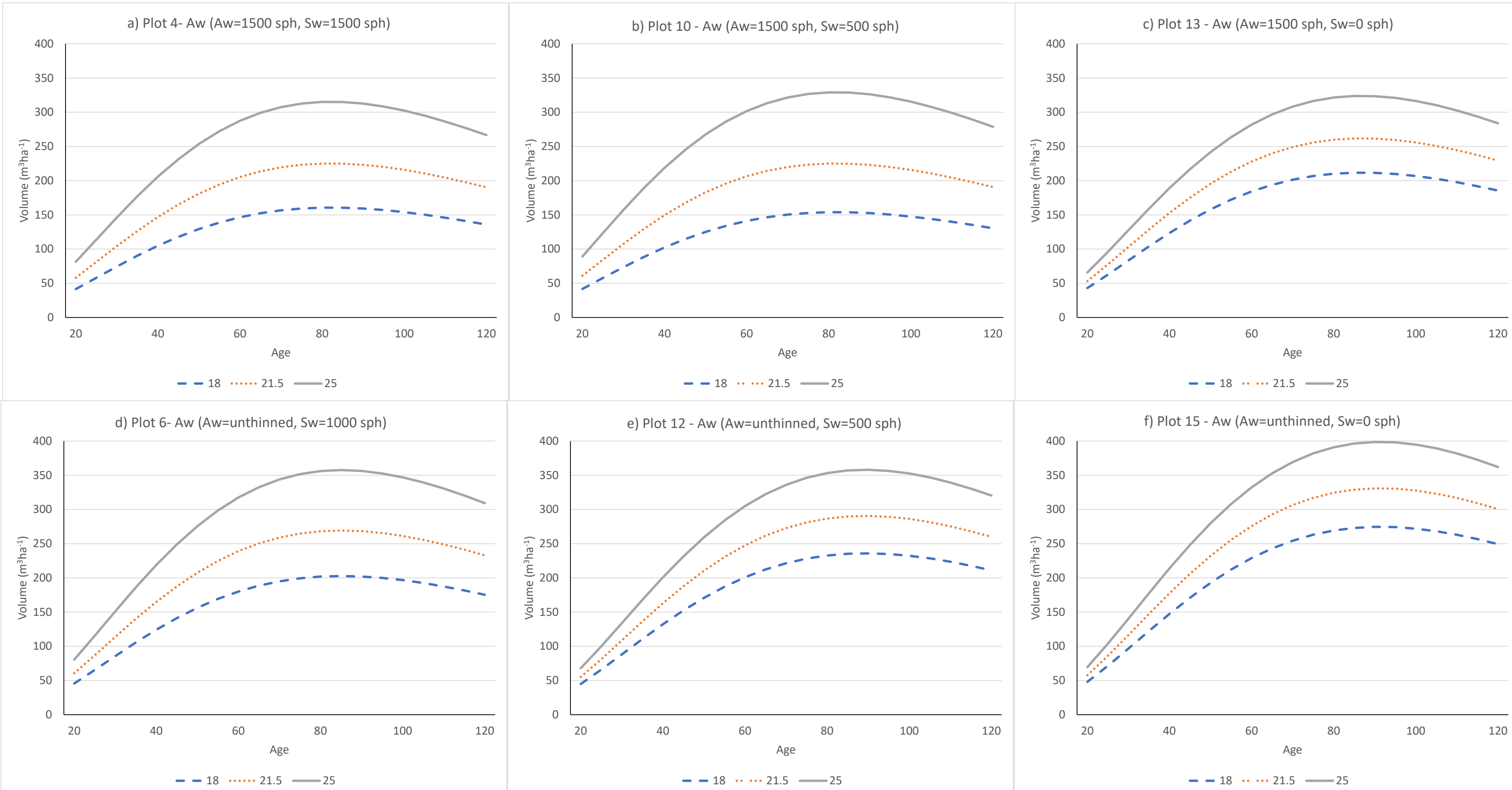


Figure 12. Yield curves showing volume-age trends for aspen in plots 4, 6, 10, 12, 13, and 15 for aspen site index values of 18, 21.5 and 25 m. sph=stems·ha^{-1}.

Table 13. Parameter estimates for non-linear models describing MGM based volume-age trends for the 15 treatments. The non-linear model fit using SAS Proc NLIN was: Vol=a*age^{b}*exp(-a*age + c*SI). SI was defined separately for each species. Parameters were significantly different from 0 (*p<0.01*) in all cases except for spruce site index (c) in plot 6.

			Spruce			Aspen		
PLOT	**Aspen density ((stems·ha^{-1}))**	**Spruce density (stems·ha^{-1})**	**a**	**b**	**c**	**a**	**b**	**c**
1	0	1000	0.013406	2.103442	0.069621			
2	200	1000	0.013013	2.055303	0.075101	0.024172	1.692271	0.107603
3	500	1000	0.012498	1.988504	0.083878	0.024681	1.925144	0.096546
4	1500	1000	0.011594	1.888494	0.094996	0.025084	2.062146	0.096351
5	4000	1000	0.010323	1.760039	0.113647	0.025401	2.106533	0.097945
6	unthinned	1000	0.013565	2.226961	0.006931***ns***	0.025652	2.182628	0.081048
7	0	500	0.011652	1.937034	0.083284			
8	200	500	0.011242	1.909724	0.083304	0.024831	1.744878	0.099654
9	500	500	0.011176	1.908504	0.077902	0.025498	1.978808	0.08919
10	1500	500	0.009829	1.751954	0.100082	0.02438	1.996066	0.108543
11	4000	500	0.008973	1.703911	0.098421	0.027075	2.251298	0.07519
12	unthinned	500	0.008933	1.714591	0.090917	0.025794	2.304432	0.059599
13	1500	0				0.026231	2.280332	0.06079
14	4000	0				0.027682	2.434509	0.043261
15	unthinned	0				0.025888	2.364609	0.053273

Table 14. Mixed model ANOVA results (α=0.05) for culmination ages, testing differences in conifer (Con), deciduous (Dec) and stand (Stand) culmination ages and associated MAI (Con MAI is associated with Con culmination age, Dec MAI with Dec culmination age and Stand MAI with stand culmination age).

Source	df	Con P-value	Dec P-value	Stand P-value	Con_MAI P-value	Dec_MAI P-value	Stand_MAI P-value
Agency *(A)*	6	-	-	-	-	-	-
Installation*(I)*	1	0.0919	0.7936	0.8584	0.2612	0.8213	0.6076
Aspen Treatment Density *(Aw)*	4	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***	***<0.0001***
Spruce Planting Density *(Sw)*	1	***<0.0001***	***0.0027***	***<0.0001***	***<0.0001***	***0.0003***	***<0.0001***
*A * I*	4	-	-	-	-	-	-
Replicate*(A*I)*	10	-	-	-	-	-	-
*Aw * Sw*	4	0.1650	0.4798	0.3387	***0.0324***	0.9326	***0.0393***
*I*Aw*	4	0.2806	0.3660	***0.0378***	0.9885	0.5769	0.7230
*I*Sw*	1	0.6438	0.5725	0.9944	***0.0481***	0.7764	0.8584
*I*Aw*Sw*	4	0.9797	0.8861	0.9960	07607	0.8483	0.9437
Residual Error	178	-	-	-	-	-	-
Total	217	-	-	-	-	-	-

Deciduous culmination ages ranged between 37 and 65 years, with the unthinned having the shortest culmination age and with increases in spruce density causing decreases in aspen culmination age at least for aspen densities of 1500 or higher (Table 15). Stand culmination ages, reflecting when total stand MAI reached maximum values, ranged between 40 and 102 years. Stand culmination ages declined with increasing aspen density but increased with the addition of spruce at either 500 or 1000 stems$\cdot$ha^{-1}.

Deciduous MAI at conifer culmination age was largest for the 4000 stems$\cdot$ha^{-1} treatment with values being significantly larger for the 4000 stems$\cdot$ha^{-1} than unthinned for all spruce densities combined and for the 1000 stems$\cdot$ha^{-1} spruce, but not for the 500 spruce stems$\cdot$ha^{-1}. At deciduous culmination ages, deciduous MAI increases with increasing aspen density and declines slightly with increasing spruce density, with values being slightly, but not significantly, larger for the 4000 aspen stems$\cdot$ha^{-1} than the unthinned. Stand MAI at stand culmination age are significantly higher in the 4000 and unthinned aspen densities than other treatments and decline with increasing spruce density.

At conifer culmination age, conifer MAI ranged between 0.62 and 2.38 m$^3\cdot$ha^{-1}y^{-1}, was highest in the absence of aspen and declined with increasing aspen density but increased with increasing spruce density. While 200 aspen ha^{-1} did not differ significantly from 0 aspen for the 1000 stems$\cdot$ha^{-1} spruce density, higher aspen densities were associated with significant reductions in spruce MAI. The significance of the Aw*Sw interaction term (Table 14) reflects small differences in the trends for aspen density between the two spruce densities. Conifer MAI was much lower at deciduous and stand culmination ages than was the case for conifer culmination ages, due to the shorter rotations for all but the 0 aspen density. Stand MAI values reflect effects of culmination age on yields of both species and were lowest for the pure spruce stands and highest for the 4000 aspen stems$\cdot$ha^{-1} and unthinned treatment.

Since aspen stands are typically planned for harvest at age 60 and spruce stands at age 90, the effects of harvesting of these stands on DBH, gross total volume and MAI were also examined and are summarized in table 16. At age 60, spruce DBH ranged from 14.5 to 19.3 cm and declined with increases in both aspen and spruce density. Aspen DBH at age 60 ranged between 18.2 and 29.5 cm and declined with increasing aspen density but was not significantly affected by spruce density (p=0.1377). At age 90, spruce DBH varied between 19.5 and 26.0 cm, and declined with increases in both aspen and spruce density. While at age 90 aspen DBH ranged from 24.2 to 38.7 cm, and declined with increasing aspen density but was not significantly affected by spruce density (p=0.1443).

Effects of aspen and spruce densities on volume and MAI were generally similar at both ages (Table 16), however actual values change with age. Aspen and spruce volumes and spruce MAI were higher at age 90 than 60 while aspen MAI was higher at age 60. Aspen volume increased with increasing aspen density up to 4000 stems$\cdot$ha^{-1}, with no significant difference between the 4000 and U treatments and decreased with increasing spruce density ($p<0.001$). At age 90, stand volume and stand MAI were largest in stands with aspen densities of 1500 stems$\cdot$ha^{-1} or higher and with an initial spruce density of 1000 stems$\cdot$ha^{-1}, with these stands providing aspen with diameters ranging between 24.5 and 30.1 cm, spruce diameters between 19.5 and 21.3 cm, spruce volume between 103.5 and 133.4 m$^{3}\cdot$ha^{-1}, aspen volume between 237.8 and 286.1 m^{3}ha^{-1}, and stand volume between 372.8 and 397.3 m$^{3}\cdot$ha^{-1}. MAI at age 90 ranged between 4.14 and 4.16 m$^{3}\cdot$ha^{-1}y^{-1} for these mixed stands with 1000 planted spruce and 1500 or more aspen.

Table 15. Effects of aspen and spruce densities on culmination ages and associated deciduous (D_), conifer (C_), and stand (Stand_) MAI (least-squares means). (in all cases effects of aspen density had *p<0.01*). Values within each row with different letters were found to be significantly (α=0.05) different using Tukey's test.

Culmination	Sw density (stems·ha^{-1})	Culmination Age						D_MAI@culmination age						C_MAI@culmination age						Stand_MAI@culmination age					
		Aspen Density (stems·ha^{-1})						Aspen Density (stems·ha^{-1})						Aspen Density (stems·ha^{-1})						Aspen Density (stems·ha^{-1})					
		0	200	500	1500	4000	U	0	200	500	1500	4000	U	0	200	500	1500	4000	U	0	200	500	1500	4000	U
Con	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	500	102ab	104a	104a	104a	98b	102ab	0.04e	0.69d	1.35c	2.38b	3.23a	2.93a	1.52a	1.34b	1.19c	0.91d	0.69ef	0.62f	1.56e	2.03d	2.54c	3.29b	3.91a	3.55ab
	1000	99ab	99a	98ab	93bc	89c	95abc	0.05f	0.72e	1.47d	2.72bc	3.37a	3.02b	2.38a	2.14ab	1.90b	1.51c	1.23cd	1.16d	2.43d	2.87c	3.37b	4.22a	4.60a	4.18a
	All	101a	101a	101a	99a	94b	98a	0.05f	0.71e	1.41d	2.55c	3.30a	2.97b	1.95a	1.74b	1.54c	1.21d	0.96ef	0.89f	2.00e	2.45d	2.96c	3.76b	4.26a	3.87b
Dec	0	-	-	-	54a	47b	41c	-	-	-	3.84b	5.12a	4.22a	-	-	-	-	-	-	-	-	-	3.85b	5.12a	5.24a
	500	-	65a	59b	53c	43d	40d	-	1.05d	2.09c	3.59b	4.99a	4.86a	-	1.13a	0.97b	0.69c	0.44d	0.30d	-	2.17d	3.04c	4.27b	5.42a	5.15a
	1000	-	65a	60b	51c	43d	37e	-	1.02d	1.95c	3.55b	4.69a	4.81a	-	1.88a	1.61b	1.16c	0.81d	0.56e	-	2.89d	3.56c	4.71b	5.49a	5.37a
	All	-	65a	60b	53c	44d	39e	-	1.02d	2.01c	3.67b	4.94a	4.95a	-	1.51a	1.29a	0.62b	0.42c	0.29c	-	2.52d	3.29c	4.28b	5.35a	5.23a
Stand	0	-	-	-	54a	47b	40c	-	-	-	3.85b	5.12a	5.22a	-	-	-	-	-	-	-	-	-	3.85b	5.12a	5.24a
	500	102a	82b	72c	62d	48e	47e	0.04e	1.01d	2.04c	3.55b	4.95a	4.70a	1.52a	1.28b	1.10c	0.79d	0.50e	0.41e	1.56e	2.28d	3.13c	4.33b	5.45a	5.10a
	1000	99a	83b	75c	62d	52e	49e	0.02e	0.97d	1.90c	3.49b	4.59a	4.57a	2.38a	2.09ab	1.82b	1.38c	1.05d	0.87d	2.42e	3.06d	3.73c	4.88b	5.64a	5.45a
	All	101a	83b	73c	59d	49e	46e	0.03e	0.98d	1.97c	3.63b	4.89a	4.80a	1.96a	1.69ab	1.46b	0.72c	0.52cd	0.44d	1.98e	2.67d	3.43c	4.36b	5.41a	5.24a

Table 16. Effects of aspen and spruce densities on aspen and spruce DBH, volume and MAI at ages 60 and 90 estimated using MGM21.

Age	Species	Sw density (stems·ha^{-1})	DBH (cm)						Volume (m^3 ha^{-1})						MAI (m^3 ha^{-1} y^{-1})					
			Aspen Density (stems·ha^{-1})						Aspen Density (stems·ha^{-1})						Aspen Density (stems·ha^{-1})					
			0	**200**	**500**	**1500**	**4000**	**U**	**0**	**200**	**500**	**1500**	**4000**	**U**	**0**	**200**	**500**	**1500**	**4000**	**U**
60	**Spruce**	**0**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		500	19.3a	18.8ab	18.3b	17.1c	15.6d	15.0d	72.2a	63.9ab	57.8b	45.4c	34.7d	30.8d	1.20a	1.06ab	0.96b	0.76c	0.58d	0.52d
		1000	18.1a	17.8ab	17.3b	16.3c	15.0d	14.5d	117.8a	108.0ab	97.5b	80.1c	66.0cd	60.8d	1.96a	1.80ab	1.63b	1.34c	1.10cd	1.01d
		All	18.8a	18.3a	17.8b	16.7c	15.3d	14.8e	95.0a	85.9ab	77.7b	62.8c	50.3cd	45.8d	1.58a	1.43ab	1.30b	1.05c	0.84cd	0.76d
	Aspen	**0**	-	-	-	24.0a	20.8b	18.4c	-	-	-	224.1a	284.7b	281.0b	-	-	-	3.74b	4.74a	4.68a
		500	-	29.5a	27.2b	23.4c	20.5d	18.2e	2.3e	62.0d	123.2c	207.4b	272.9a	251.6a	0.04e	1.03d	2.05c	3.46b	4.55a	4.19a
		1000	-	28.8a	26.7b	23.4c	20.0d	18.5d	1.7e	60.2d	116.1c	205.2b	246.5a	240.4a	0.03e	1.00d	1.94c	3.42b	4.27a	4.01a
		All	-	29.2	27.0	23.6	20.4	18.4	1.7e	60.8d	119.3c	212.6b	271.7a	256.1a	0.03e	1.01d	1.99c	3.54b	4.53a	4.27a
	Stand	**0**										224.3b	285.0a	282.5a	-	-	-	3.74b	4.75a	4.71a
		500							74.1e	125.4d	180.6c	252.4b	307.2a	282.1ab	1.24e	2.09d	3.01c	4.21b	5.12a	4.70ab
		1000							119.5e	168.1d	213.6c	285.4b	322.4a	301.2ab	1.99e	2.80d	3.56c	4.76b	5.37a	5.02a
		All							96.6e	146.6d	196.9c	254.1b	305.0a	287.0a	1.61e	2.44d	3.28c	4.23b	5.08a	4.78a
90	**Spruce**	**0**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		500	26.0a	25.2a	24.4b	22.7c	20.8d	20.1d	132.4a	117.0b	103.8c	79.5d	60.6e	54.9f	1.47a	1.30b	1.15b	0.88c	0.67d	0.61d
		1000	24.0a	23.5ab	22.8b	21.3c	19.7d	19.5d	208.8a	188.2ab	167.0b	133.4c	109.6cd	103.5d	2.32a	2.09ab	1.86b	1.48c	1.22cd	1.15d
		All	25.0a	24.4a	23.6b	22.0c	20.2d	19.8d	170.6a	152.6ab	135.4b	106.5c	85.1d	79.2d	1.90a	1.70ab	1.50b	1.18c	0.95d	0.88d
	Aspen	**0**	-	-	-	30.9a	27.0b	24.6c	-	-	-	266.0b	325.1a	320.5a	-	-	-	2.96b	3.61a	3.56a
		500	-	38.7a	35.1b	30.2c	26.5d	24.2e	1.9e	72.7d	145.1c	242.2b	303.6a	285.2a	0.02e	0.81d	1.61c	2.69b	3.37a	3.17a
		1000	-	37.7a	34.7b	30.1c	26.1d	24.5d	1.3e	69.4d	141.5c	237.8b	286.1a	269.6ab	0.01e	0.77d	1.57c	2.64b	3.18a	3.00ab
		All	-	38.2a	34.9b	30.4c	26.6d	24.4e	1.2e	70.7d	142.9c	249.1b	305.3a	290.2a	0.01e	0.79d	1.59c	2.77b	3.39a	3.22a
	Stand	**0**							-	-	-	266.2b	325.6a	322.1a	-	-	-	2.96b	3.62a	3.58a
		500							134.5e	189.9d	249.1c	321.9b	364.4a	340.4ab	1.49e	2.11d	2.77c	3.58b	4.05a	3.78ab
		1000							211.6d	259.2c	310.0b	372.8a	397.3a	374.6a	2.35d	2.88c	3.44b	4.14a	4.41a	4.16a
		All							172.7e	224.2d	279.2c	320.5b	362.6a	344.4a	1.91e	2.49d	3.10c	3.56b	4.03a	3.83a

Discussion

Trembling aspen responses

Results to date from the long-term study indicate only small decreases in density of unthinned aspen stands between ages 10 and 28, with aspen density averaging 16,490 $stems{\cdot}ha^{-1}$ at age 28. This contrasts with other reports of dramatic early declines in aspen density during the first 10 to 15 years (Bokalo et al. 2007; Comeau 2021a) but is consistent with reports of small decreases in aspen density after age 10 (Kabzems et al. 2016; Bjelanovic et al. 2021).

Repeated measures analysis suggested that only age and not aspen density had significant effects on the height of the 200 largest diameter aspen while analysis completed separately for each of 3 selected ages (10, 20 and 28) indicated effects of aspen density on height of the 200 largest diameter aspen, with height tending to be larger (by 1.08 m) in the 4000 $stems{\cdot}ha^{-1}$ treatment than in the 200 $stems{\cdot}ha^{-1}$ treatment at age 28. Overall, however, results are consistent with those from other studies that indicate little effect of thinning on the height of dominant aspen (Penner et al. 2001; Bokalo et al. 2007; Kabzems et al. 2016; Comeau 2021a) while Bella and Yang (1991) found that thinning increased average height of aspen in three out of seven stands that they studied.

Age and aspen density had significant effects on DBH, slenderness, HTLC (height to crown base), and CW (crown width) of the 200 largest diameter aspen. DBH, CW and HTLC increased with age while slenderness decreased with age for all treatments. Except for DBH at age 10, where aspen DBH was slightly (but not significantly) smaller for the 200 than the 500 $stems{\cdot}ha^{-1}$ treatment, DBH and CW decreased with increasing aspen density while slenderness and HTLC increased with increasing aspen density. Reductions in DBH with increasing aspen density and increases in DBH following thinning are consistent with results from many other studies (Bickerstaff 1946; Steneker 1976; Perala 1978; Rice et al 2001; Bokalo et al. 2007; Prevost and Gauthier 2012; Diacanu et al 2015; Kabzems et al. 2016; Bjelanovic et al. 2021; Comeau 2021a; Comeau et al. 2023).

Increases in aspen density are generally observed to result in increases in slenderness (Opio et al. 2000; Bokalo et al. 2007; Kabzems et al. 2016; Comeau 2021a) while environmental (climate and soil) factors may interact with competition and result in further adjustments to slenderness

(Wang et al. 2023). Decreases in aspen slenderness with age are small and consistent with an observed decrease in slenderness with age reported for Chinese fir (Zhang et al. 2020).

Decreases in CW and increases in HTLC (which is linked to a decrease in live crown ratio) with increase in aspen density were also reported by Groot and Schneider (2011), Kabzems et al. (2016) and Comeau (2021a, b).

White spruce responses

As observed in this study, other studies also demonstrate increases in spruce height and DBH following reductions in aspen density (Bokalo et al. 2007; Kabzems et al. 2016; Bjelanovic et al. 2021; Comeau 2021a; Kabzems et al 2022; Comeau et al. 2023). However, increases in height growth may be delayed for a few years following thinning. Bokalo et. al. (2007) observed no effect of thinning on spruce height growth 3 to 4 years after treatment and Bjelanovic et al. (2021) observed a reduction in spruce height growth for about 3 years after complete removal of aspen. In the 8th year following aspen removal, Bjelanovic et al. (2021) found that spruce in this treatment had the largest height growth. Analysis of the LTS data indicates significant differences between unthinned and thinned plots at age 10, with differences amongst aspen densities becoming larger and increasingly significant with age.

Competition has an immediate effect on diameter growth of conifers, while impacts on height growth may not 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) or height to DBH (slenderness) increases in response to increases in intensity of competition (Opio et al. 2000). 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). Climate is also likely to influence both HDR and slenderness and interact with other factors (Wang et al. 2023).

While spruce CW was not significantly affected by aspen density at age 10, significant decreases with increasing aspen density were evident at ages 20 and 28. Decreases in crown width with increases in aspen density are also reported by Groot and Schneider (2011), Kabzems et al. (2016) and Comeau (2021a, b).

At both ages 20 and 28, spruce HTLC was only influenced by aspen density with 1000 spruce while HTLC was not affected by aspen density for the 500 spruce. Consistent with results presented by Groot and Schneider (2011), Kabzems et al. (2016) and Comeau (2021a, b) HTLC at age 20 increased with increasing aspen density. At age 28, differences appear inconsistent due to rapid growth of spruce in the lower aspen densities leading to crown closure and intraspecific competition, and a reversal of the more direct effects of aspen densities which resulted in HTLC in the 0 aspen not differing from that in the unthinned.

Effects of aspen and spruce densities on growth and yield

Figure 13 illustrates effects of aspen and spruce densities on aspen and spruce volumes predicted by MGM at age 90 expressed as a % of volumes in the unthinned. Aspen volume and MAI increased with aspen density and reaches a maximum of 101 to 106% of unthinned values at 4000 stems$\cdot$ha^{-1}. Spruce volume and MAI declined with increasing aspen density with volume of pure spruce stands being about double that of stands where aspen was unthinned in agreement with other previous studies (Kabzems et al. 2016, Bjelanovic et al. 2021, Comeau 2021a). In addition, stand volume and MAI at age 90 is largest with 4000 aspen and 1000 spruce stems$\cdot$ha^{-1}.

Contributions of spruce and aspen to stand volume and MAI are highlighted in Figure 14. Spruce volume and spruce MAI at age 90 increased with increasing initial spruce density and reductions in aspen density (Table 15, Fig. 14) while aspen volume and MAI at age 90 and stand volume and MAI increase with aspen density up to 4000 stems$\cdot$ha^{-1}. Thinning aspen to 4000 stems$\cdot$ha^{-1} at an early age maintained nearly full stocking of aspen, but released retained trees and resulted in a sustained increase in growth and survival. Lower aspen volume in the unthinned is likely resulting from loss of volume to self-thinning. It is also notable that thinning to 1500 stems$\cdot$ha^{-1} resulted in a small reduction in aspen volume and MAI compared to the unthinned, but resulted in increased spruce volume and MAI and a similar stand volume and stand MAI. For stands with the 3 highest aspen densities MAI exceeded 4.14 m^{3}ha^{-1}y^{-1}.

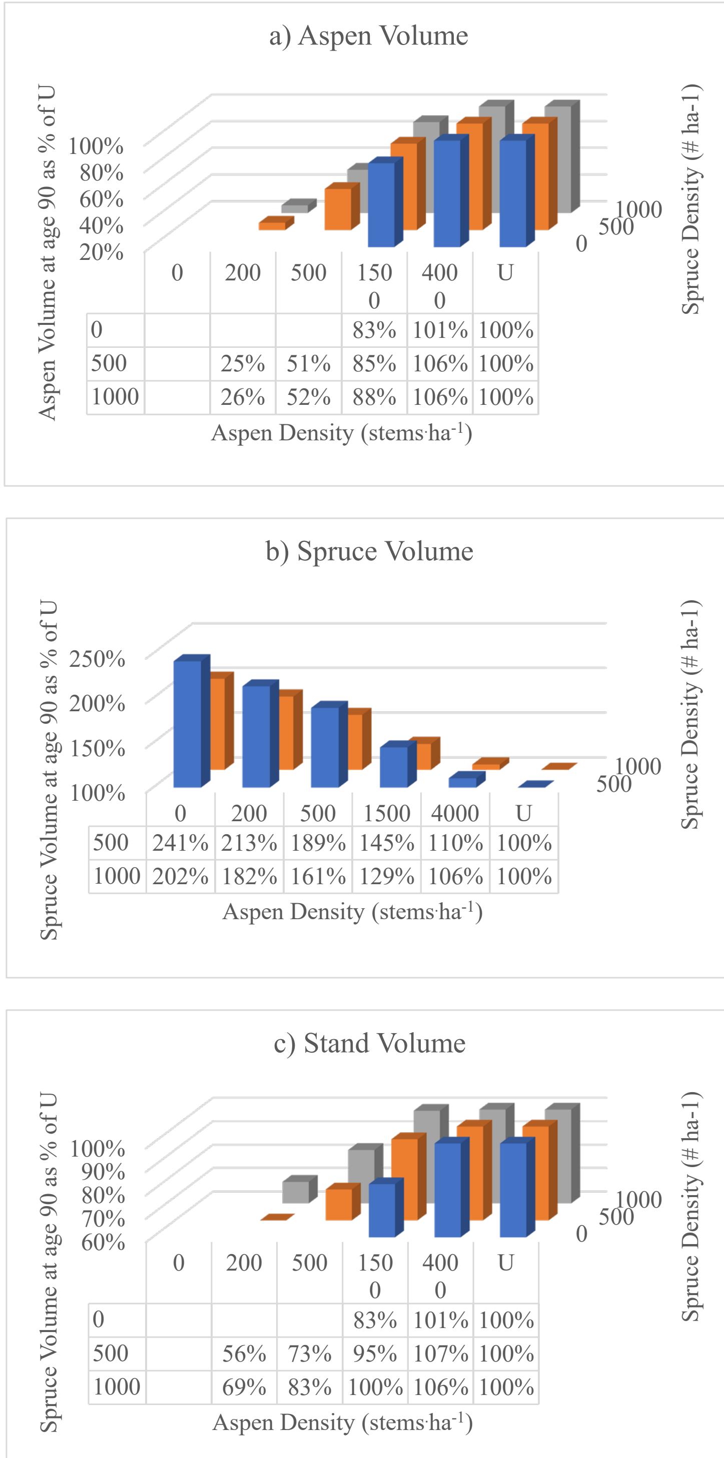


Figure 13. Effects of aspen and spruce densities on a) aspen, b) spruce, and c) stand volumes at age 90 expressed as a % of volume in the unthinned.

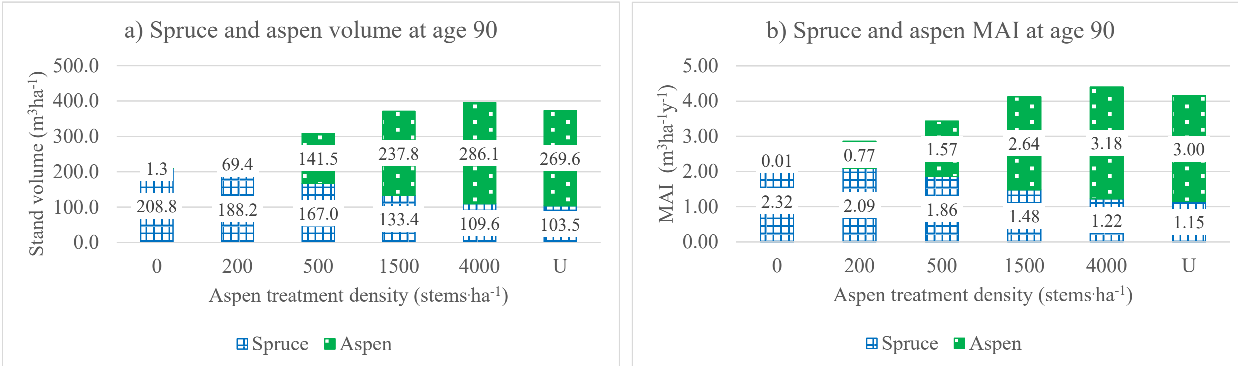


Figure 14. Treatment effects on spruce and aspen volume and MAI at age 90 for initial spruce densities of 1000 stems·ha^{-1}.

Effects of aspen and spruce densities on stemwood biomass and carbon

The potential for carbon sequestration is being increasingly recognized as an important ecological service provided by forests. Mixed stands of aspen and spruce with apsen densities of 1500 or more aspen stems·ha^{-1} carry the largest total stand volume (Fig. 14) and contain the most carbon at age 90 (Table 16, Fig. 15). While 4000 aspen stems·ha^{-1} has higher stemwood carbon, values do not differ significantly between 1500, 4000 and unthinned. These results contrast with Laganiere et al. (2015) who found higher aboveground carbon in aspen than in mixtures of aspen and jack pine or aspen and black spruce and likely reflect the higher productivity of white spruce and the fact that many factors influence overyielding (Kweon and Comeau 2019). While our results indicate that mixed stands have the potential to sequester more carbon than pure spruce stands, implications to the global carbon budget also depend on utilization and conversion of both aspen and spruce to wood products and require further study. Differences between carbon storage in harvested wood products for these two species will depend on how much of the harvested carbon is placed in long-term storage in construction materials (eg. lumber, panelboard) as opposed to short-lived products such as paper (Zhao et al. 2022). In addition, examination of treatment effects on soil carbon storage would provide a more complete picture.

Table 16. Effects of aspen and spruce densities on aspen and spruce stemwood biomass and stemwood carbon at age 90 estimated using MGM21. (note that values represent total aboveground stemwood biomass and do not include bark). Calculation of carbon from biomass was based on a conversion from biomass to carbon using values of 0.4709 and 0.5039 for trembling aspen and white spruce, respectively, from Lamlon and Savidge (2003).

Species	Sw density (stems·ha^{-1})	Stemwood Biomass (tonnes ha^{-1}) Aspen Density (stems·ha^{-1})						Stemwood Carbon (tonnes ha^{-1}) Aspen Density (stems·ha^{-1})					
		0	**200**	**500**	**1500**	**4000**	**U**	**0**	**200**	**500**	**1500**	**4000**	**U**
Spruce	**0**	-	-	-	-	-	-	-	-	-	-	-	-
	500	40.5a	36.0bc	32.1c	24.5d	18.6e	16.9e	20.4a	18.1bc	16.2c	12.3d	9.4e	8.5e
	1000	63.6a	57.5ab	51.1b	40.9c	33.5cd	32.2d	32.0a	29.0ab	25.8b	20.6c	16.9cd	16.2d
Aspen	**0**	-	-	-	100.6b	122.1a	118.0a	-	-	-	47.4b	57.5a	55.6a
	500	0.8e	30.1d	57.3c	91.9b	114.1a	103.9ab	0.4e	14.2d	27.0c	43.3b	53.7a	48.9ab
	1000	0.6e	28.6d	56.0c	90.1b	106.3a	98.7ab	0.3e	13.5d	26.4c	42.4b	50.1a	46.5ab
Stand Total	**0**	-	-	-	100.7b	122.2a	118.5a	-	-	-	47.4b	57.6a	55.8a
	500	41.4e	66.2d	89.5c	116.4b	132.8a	120.8ab	20.8e	32.4d	43.2c	55.6b	63.2a	57.5b
	1000	64.6d	86.6c	107.6b	131.5a	140.4a	131.4a	32.5d	42.7c	52.4b	63.3a	67.2a	63.0a

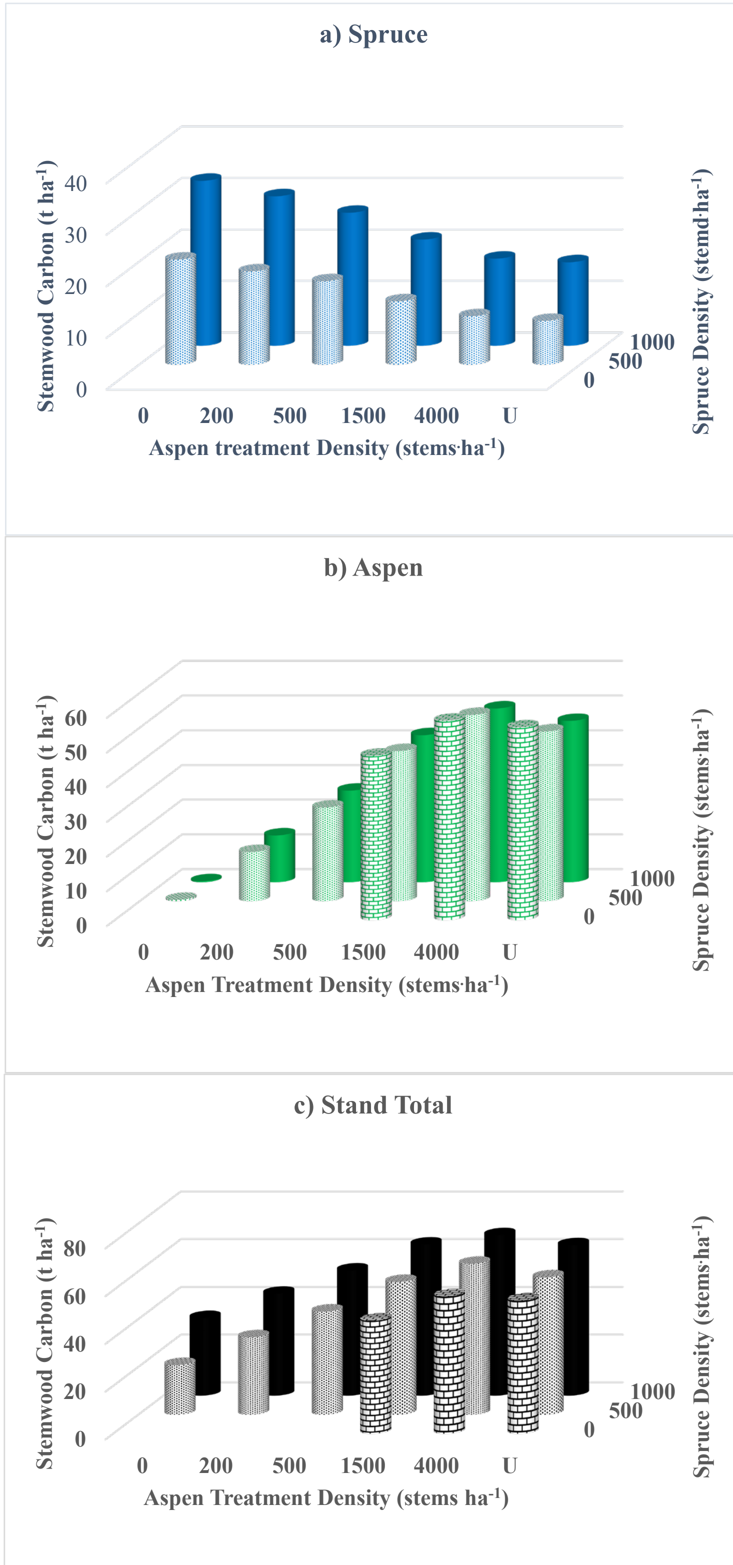


Figure 15. Effects of aspen and spruce densities on stemwood carbon at age 90.

Conclusions

Thirty-one years after the establishment of the Long-Term Study by the Western Boreal Growth and Yield Association we continue to discover interesting outcomes. Thinning of aspen resulted in increases in aspen diameter and increases in height and diameter of white spruce.

At age 20 and 28 spruce were largest with no aspen with both spruce height and diameter declining with increasing aspen density. Between treatment differences for spruce height and diameter continue to increase to age 28. As reported by other studies, thinning resulted in significant increases in aspen DBH and crown size, with DBH and CW declining with increasing aspen density while slenderness and HTLC increased with increasing aspen density. Thinning had only small and variable effects on the height of the 200 largest aspen stems$\cdot$ha^{-1}. Ongoing periodic remeasurements would be useful in determining whether differences between treatments will continue to increase and to provide quantification of long-term outcomes.

Yield predictions based on simulations with the Mixedwood Growth Model (MGM21) indicate that spruce yields at age 90 will be largest in pure spruce stands, while aspen yields and mixed stand yields will be largest in stands with aspen densities of 1500 stems$\cdot$ha^{-1} or higher. While thinning results in some increase in both aspen and stand culmination ages, where the objective is to grow both spruce and aspen to a single harvest age then it is necessary to extend the rotation to age 80 or 90 in order to achieve acceptable merchantable volumes of white spruce. Results also indicate that carbon storage in stemwood at age 90 is likely to be higher in mixed stands with more than 1500 aspen ha^{-1} than in pure spruce stands, with this occurring in addition to the benefits of mixed stands in terms of mitigating early competition, frost and insect issues, and risks and increased resistance and resilience of stands to climate change.

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