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Factors influencing overyielding in young boreal mixedwood stands in western Canada

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ABSTRACT

Mixtures of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) are a prominent component of the boreal forests of western Canada. Overyielding, indicating higher productivity in mixtures than in monocultures, has been observed in mature stands but has not been examined in young stands (< 30 years old) in this region. We used data collected between 2006 and 2015 at 7 locations in Alberta and Saskatchewan for the Western Boreal Growth and Yield Association (WESBOGY) Long Term Study to examine whether overyielding occurs in young mixtures of these species and to identify factors (species composition, stand density, tree size, species proportion, site quality, and climate) that influence overyielding. Our results show that overyielding is occurring in these young boreal mixedwood stands in western Canada. Relative productivity total (RPT), indicating mixing effect (RPT > 1 indicates overyielding), varies from 0.921 to 1.537 among mixedwood treatments, and thinned aspen stands show higher production than unthinned aspen stands. Initial stand density (basal area) and initial aspen size (QMD at the start of the measurement interval) positively influence mixing effect while initial spruce size (QMD) negatively influences mixing effect. The magnitude of overyielding declines with increasing growing season length (DD5) and the relative productivity of aspen decreases with increasing site quality. Species mixtures support higher stocking than pure stands due to differences in growth rate and shade tolerance of the two species. Tree size is also important since productivity will decline when two species compete with each other for space and resources. Consequently, a mixed species stand that has space partitioning and size inequality between species, which reduces competition and favours expression of the functional traits (e.g., shade tolerance) of each species, tends to have better productivity.

1. Introduction

Several studies have demonstrated the benefits of tree species diversity on forest productivity, resilience, wildlife habitat, and aesthetics (Macdonald, 1995; Hoffman and Palmer, 1996; Macdonald et al., 2010; Cavard et al., 2011b; Zhang et al., 2012; Pretzsch et al., 2013b; Liang et al., 2016; Ma and Chen, 2017). Increases in productivity are of interest since this is closely associated with carbon capture and economic values (Ruiz-Benito et al., 2014; Liang et al., 2016). When productivity is higher in mixtures than in associated monocultures, it is termed overyielding (Hector, 1998; Beckage and Gross, 2006; Pretzsch and Schutze, 2009). Overyielding may result from competitive reduction, facilitation or other factors and is often also termed the "mixing effect". In such cases an increase in production results from the mixed environment encouraging species traits to surpass their behaviors in pure stands (Kelty, 2006; Forrester, 2014; Pretzsch, 2014).

Niche partitioning between species can lead to reductions in competition (Man and Lieffers, 1999; Hooper et al., 2005; Kelty, 2006; Pretzsch and Schutze, 2009). For example, shade tolerant species in the understory have a capacity for carbon fixation at low light levels (Givnish, 1988) with shade intolerant species in the overstory needing full light, and with mixtures of understory tolerant and overstory intolerant species resulting in a stand structure that more fully utilizes light over the growing season leading to higher net primary production. In the case of mixtures of coniferous and deciduous species, they can also differ in utilization of light during the growing season due to differences in phenology of leaf development (Constabel and Lieffers, 1996; Man and Lieffers, 1997, 1999). Understory spruce can utilize higher light when overstory aspen does not have leaves in the spring and autumn. For example, young aspen stands (< 20 years old) allowed about 60% of full light at 1.3 m in the spring and autumn but allowed about 20% of full light in the summer (Constabel and Lieffers, 1996). Consequently, spruce can photosynthesize with higher light and accumulate carbon during the spring and autumn (Man and Lieffers, 1997).

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Overyielding in mixtures also results from them supporting potentially higher stocking and canopy stratification (Garber and Maguire, 2004; Condés et al., 2013; Pretzsch and Schütze, 2016). Functional differences (e.g., shade tolerance) and traits (e.g. crown shapes of species) may allow stands to stock more trees in mixtures compared to monocultures (Pretzsch, 2014; Peer et al., 2018; Toïgo et al., 2018). When species occupy different crown layers, there can also be an increase in leaf area index which may contribute to higher productivity of the mixed stand (Man and Lieffers, 1999; Kelty, 2006; Forrester and Albrecht, 2014; Forrester et al., 2018).

Facilitation, which involves certain species improving the environment for other species (Hooper et al., 2005), may also contribute to overyielding (Pretzsch and Schutze, 2009; Forrester, 2014; Mason and Connolly, 2014). Increases in productivity could result from higher humidity in the understory, reductions in frost, insect attacks, and wind exposure (Taylor et al., 1996; Groot and Carlson, 1996; Man and Lieffers, 1999), and/or increases in nutrient availability.

Stand developmental stages can influence the mixing effect because growth rates of each species may differ with age (del Río et al., 2016). Early successional species, such as trembling aspen (*Populus tremuloides* Michx.), typically have rapid initial growth that reaches a maximum over a short period while late successional species, such as white spruce (*Picea glauca* (Moench) Voss), often have slow early growth rates (Cavard et al., 2011a). As a result, the contribution of each species to total production may vary with stand age and influence the magnitude and occurrence of overyielding.

Site quality and climate influence the productivity of mixtures through effects on growth of the component species, nature and intensity of interactions, and potential stocking (Pretzsch et al., 2010; Paquette and Messier, 2011; Prior and Bowman, 2014; Potter and Woodall, 2014; Toïgo et al., 2015; Jucker et al., 2016; Peer et al., 2018; Mina et al., 2018). The stress gradient hypothesis, suggests that interactions among species will tend to be more positive (i.e., interactions leading to increased growth) under poor or stressful conditions whereas under rich or moderate conditions weak positive or negative outcomes are more common (Callaway and Walker, 1997; Paquette and Messier, 2011; Toïgo et al., 2015).

Mixtures of trembling aspen and white spruce are a prominent natural component of the boreal plains and a common forest type in Canada (Man and Lieffers, 1999). As the economic and ecological values of mixed-species stands is recognized, the management of mixedwood stands is being emphasized in contrast to the management of separate pure stands of white spruce and aspen (Macdonald, 1995; Man and Lieffers, 1999; Chen and Popadiouk, 2002; Macdonald et al., 2010). Trembling aspen grows on a broad range of sites with a wide range in soil conditions (Perala, 1990). Aspen regenerates rapidly after stand replacing disturbances such as fire or harvesting and occupies the stand for several decades as a shade intolerant species. White spruce establishes on exposed mineral soil following stand destroying disturbances, and also regenerates on decomposing logs, organic layers, and moss beds under established stands (Nienstaedt and Zasada, 1990; DeLong et al., 1997). In contrast to aspen, white spruce is moderately shade tolerant and can grow under aspen canopies (albeit at slower rate than in the open) until aspen starts declining at age 50–70. At this time it begins to grow into the aspen canopy. In aspen-spruce mixed stands, aspen plays an important role as a nurse tree in protecting young spruce trees from frost damage and winter injury (Filipescu and Comeau, 2011). At the same time, however, shade from aspen does reduce the growth of white spruce (Filipescu and Comeau, 2007).

Higher productivity of these aspen-spruce mixtures has been identified in mature natural forests (Man and Lieffers, 1999; MacPherson et al., 2001) and modelling studies (Comeau et al., 2005; Comeau, 2014) in western Canada, but overyielding has not been examined in young stands in this region. Groot et al. (2014) found no significant effect on production of mixtures in young aspen-spruce stands in eastern Canada, contrary to predictions derived from previous research.

The objectives of the study presented in this paper were to investigate (1) whether or not overyielding occurs in young (< 30 years old) mixed stands, and to examine: (2) effects of species composition, stand density, proportion (i.e., the proportion of basal area of each species), and tree size on overyielding if it occurs; and (3) effects of climate and site quality (Site index) on the magnitude of overyielding in these stands if it occurs.

2. Material and methods

2.1. WESBOGY long-term study and data selection

Data from the Western Boreal Growth and Yield Association (WESBOGY) Long-Term Study (LTS) collected between 2006 and 2015 were used for these analyses. The WESBOGY LTS uses a randomized block design with 11 agencies and companies, and each agency or company involves one or two installations which differ in site quality (Superior and Median) and contain two replicates of 15 treatment plots. The 15 treatments include five monospecific stands of aspen (1500, 4000 trees/ha, and natural) and white spruce (500 and 1000 trees/ha), as well as mixtures with spruce densities of 500 and 1000 trees per hectare and five aspen densities (200, 500, 1500, 4000 trees/ha, and natural). Spruce was planted at uniform spacing for the two spruce densities and aspen was also fairly uniformly distributed in these stands. At year 5 after planting of spruce and natural regeneration of aspen after harvest, spruce and aspen were thinned to these treatment densities. Each plot is square with 20 m × 20 m (0.04 ha). Diameter at breast height (DBH), tree height (HT), crown width, species age, and tree condition (e.g., dead or alive) for all tagged trees in thinned plots have been measured over time. However, because unthinned aspen plots are so dense, all tagged trees in subplots (e.g., age 1–4: 1 m × 1 m, age 5–19: 2 m × 2 m, and after age 20: 5 m × 5 m) have been measured instead. All tagged trees in each plot were measured at 2 (age 10 through 18) or 3 (age 20 or above) year intervals. Four mixtures (spruce 500 trees/ha with aspen 200 and 500 trees/ha and spruce 1000 trees/ha with aspen 200 and 500 trees/ha) were excluded from this study because of the lack of reference pure aspen stands with these densities (200 and 500 trees/ha).

All study installations are located in the Boreal Plains ecozone (Fig. 1) where mixed stands of trembling aspen and white spruce are naturally common. The Boreal plains ecozone has a mean annual temperature of 0.2 °C and annual precipitation of 472 mm (Price et al., 2013), and it has moderately warm summers with most precipitation occurring during the growing season. Gray Luvisolic soils are prevalent in forested areas in this region (Wiken, 1986; Lavkulich and Arocena, 2011).

This study utilized data from 7 agencies with trees taller than breast height (1.3 m). Alberta-Pacific Forest Industries Inc. (ALP), Daishowa-Marubeni International Ltd. (DMI), Government of Alberta (ESRD), Alberta Plywood (WFR), and Weyerhaeuser Company Ltd. (WGR) are located in Alberta, and Canadian Forest Service (CFS) and Saskatchewan Ministry of Environment (SPA) are from the province of Saskatchewan. In total, 11 installations, 20 replicates, and 220 plots (20 replicates × 11 treatments) were used for the study (Table 1). The number of measurements ranges from 2 to 4 at each location, and years between successive measurements are 2–3 years. In this study, the data from ages (Sw_age and Aw_age) indicated in Table 1 were used for the analysis.

2.2. Mixing effect and potential variables

2.2.1. Calculation of relative productivity total for mixing effect

The dry mass of stems in each stand was calculated based on Canadian national biomass equations (Ung et al., 2008) using diameter at breast height (DBH) and tree height (HT), and the equation is given as:

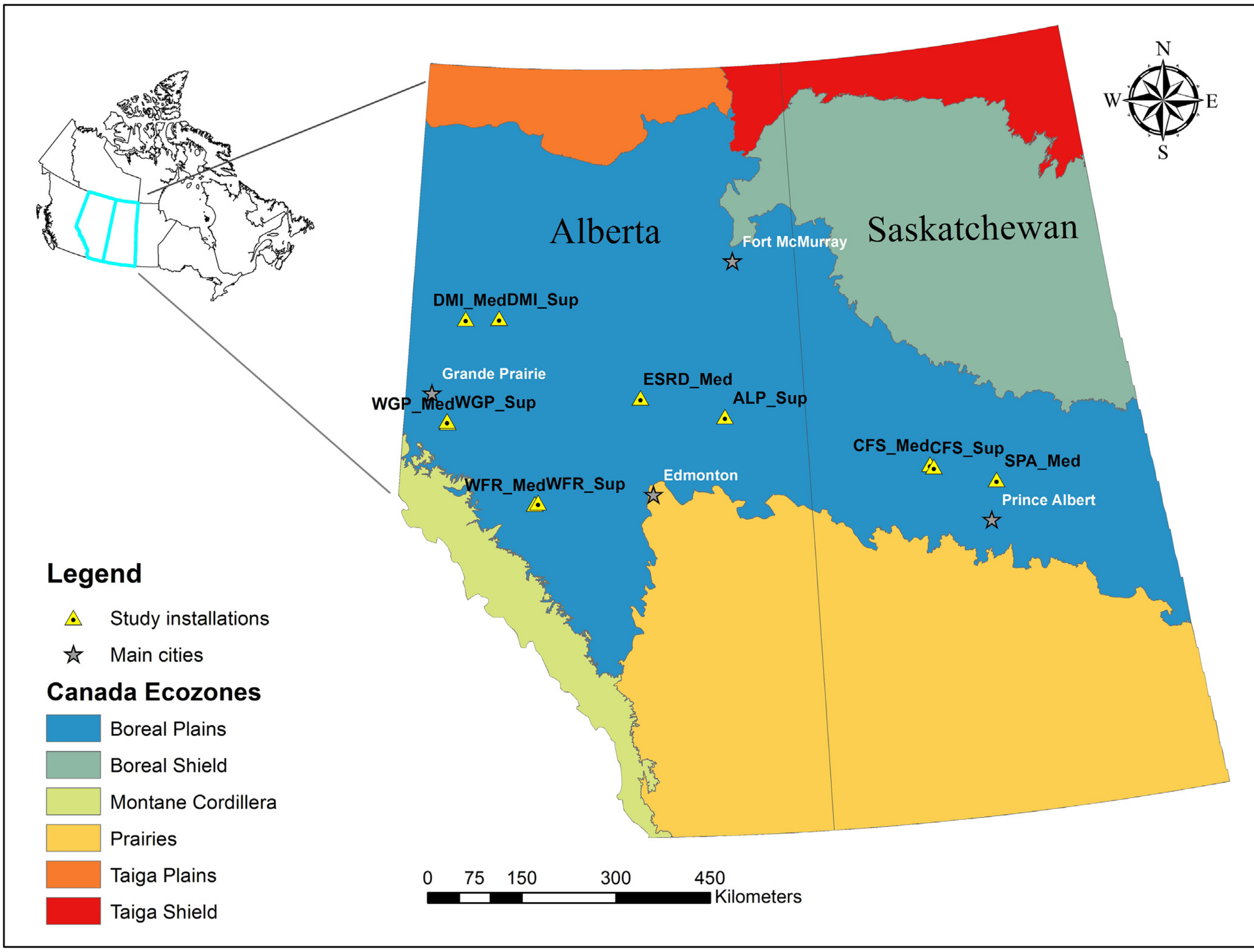

Fig. 1. Ecozones and locations of study sites (7 agencies, 11 installations (ALP, Alberta-Pacific Forest Industries Inc.; CFS, Canadian Forest Service; DMI, Daishowa-Marubeni International Ltd.; ESRD, Government of Alberta; SPA, Saskatchewan Ministry of Environment; WFR, Alberta Plywood; WGP, Weyerhaeuser Company Ltd.; Sup, superior installation; Med, median installation) in total).

$$Biomass_{stem} = \beta_{wood1} DBH^{\beta wood2} HT^{\beta wood3} + \beta_{bark1} DBH^{\beta bark2} HT^{\beta bark3}, \quad (1)$$

where $\beta_{wood1} = 0.0143$, $\beta_{wood2} = 1.9369$, $\beta_{wood3} = 1.0579$, $\beta_{bark1} = 0.0063$, $\beta_{bark2} = 2.0744$, and $\beta_{bark3} = 0.6691$ for trembling aspen, and $\beta_{wood1} = 0.0252$, $\beta_{wood2} = 1.7819$, $\beta_{wood3} = 1.0022$, $\beta_{bark1} = 0.0096$, $\beta_{bark2} = 1.6901$, and $\beta_{bark3} = 0.7393$ for white spruce.

Based on calculated stem biomass for each stand, periodic annual increment (PAI) of stem biomass was computed for use as the response variable in examining overyielding. The equation is:

$$PAI_{total} = \frac{BM_{t2} - BM_{t1}}{t2 - t1}, \quad (2)$$

where PAI_{total} is the total periodic annual increment of two species between two measurements at time t_1 and t_2 for a plot, and BM is the total stem biomass of two species. Specific PAI_{sw} and PAI_{aw} were also computed as response variables.

Relative Productivity Total (RPT) used in this study (Eq. (3)) is equal to the Land Equivalent Ratio (LER) and is useful in evaluating the

Table 1
Locations and information on available data.

Location	INST	REPL	PLOT	N	Latitude and longitude	Elev. (m)	Measurement	Sw_age	Aw_age
ALP	Sup	R1, R2	22	4	55°00′N, 112°00′W	568	2008–2014	16–22	15–21
CFS	Sup	R1, R2	22	2	54°03′N, 106°58′W	505	2008–2010	17–19	16–18
	Med	R1, R2	22	2	54°05′N, 107°03′W	515	2008–2010	17–19	16–18
DMI	Sup	R1, R2	22	4	56°24′N, 117°43′W	728	2006–2012	15–21	15–21
	Med	R1, R2	22	4	56°23′N, 118°35′W	788	2006–2012	15–21	15–21
ESRD	Med	R1, R2	22	4	55°18′N, 114°06′W	643	2006–2014	15–23	15–23
SPA	Med	R1, R2	22	3	53°45′N, 105°30′W	548	2006–2010	16–20	16–20
WFR	Sup	R2	11	4	53°47′N, 116°36′W	1085	2007–2013	13–20	18–25
	Med	R1, R2	22	4	53°47′N, 116°41′W	1050	2007–2013	15–22	17–24
WGP	Sup	R1, R2	22	3	54°55′N, 118°53′W	906	2010–2015	20–25	23–28
	Med	R1	11	3	54°53′N, 118°53′W	926	2010–2015	20–25	23–28

INST, installation; REPL, replicate; PLOT, number of plots (11 treatments × number of replicates at each installation); N, number of measurements; Elev., elevation; Measurement, measurement periods; Sw_age, age of white spruce at last indicated measurement; Aw_age, age of trembling aspen at last indicated measurement.

Table 2
Characteristics of variables used in the analysis.

Var.	QMD (cm)		HT (m)		BA (m^2/ha)		SDI		TPH (trees/ha)		RD		Prop.
	Sw	Aw	Sw	Aw	Sw	Aw	Sw	Aw	Sw	Aw	Sw	Aw	
Mean	4.07	7.08	3.7	8.23	1.00	11.21	39.00	376.65	649.61	3291.48	3.36	32.38	0.08
SD	1.58	1.98	1.05	1.96	0.88	4.49	29.23	134.18	274.02	1652.38	2.51	11.52	0.07
Max.	9.69	12.09	6.33	14.26	4.26	27.62	142.07	824.10	1175.00	9250.00	12.21	70.74	0.34
Min.	0.00	2.59	0.87	3.80	0.00	4.38	0.00	195.12	0.00	1075.00	0.00	16.77	0.00
Var.	Biomass (t/ha)		PAI (t/ha*year)		SI	MAT	DD5	MAP	AHM	MSP	SHM	FFP	CMI
	Sw	Aw	Sw	Aw		(°C)		(mm)		(mm)			(cm)
Mean	2.20	33.30	0.42	4.01	21.07	1.71	1304.14	498.38	23.80	336.66	49.85	107.10	5.20
SD	2.06	18.18	0.39	2.16	2.64	0.81	98.72	51.90	2.26	46.28	7.43	6.73	6.00
Max.	10.82	122.38	2.29	11.79	27.13	3.10	1511.00	607.67	28.30	426.67	63.80	121.00	17.44
Min.	0.00	9.54	0.00	0.08	14.30	−0.05	1096.67	388.00	19.35	262.00	34.15	93.50	−4.43

Sw, white spruce; Aw, trembling aspen; QMD, initial quadratic mean diameter; HT, initial mean tree height; BA, initial basal area; SDI, initial stand density index; TPH, initial trees per hectare; RD, initial relative density; Prop., initial spruce proportion; Biomass, stem biomass; PAI, periodic annual increment; SI, site index; MAT, mean annual temperature; DD5, growing degree days above 5 °C; MAP, mean annual precipitation; AHM, annual heat moisture index (MAT + 10)/(MAP/1000); MSP, mean summer precipitation; SHM, summer heat moisture index (MWMT)/(MSP/1000); FFP, frost free period; CMI, climate moisture index.

effect of species mixing without considering the mixing proportions of species in mixture (Willey and Osiru, 1972; Forrester and Pretzsch, 2015; Pretzsch et al., 2017). RPT means the required land area of the pure stand to produce the same yield as a mixture and is applicable to additive experimental designs where total densities and species proportions differ between treatments. Additive effects of two species in mixture were examined using relative productivity (e.g., RP = productivity of spruce or aspen in mixture/productivity of spruce or aspen in monoculture), and relative productivity total was calculated by summing up relative productivities of two species (i.e., RP_{sw} and RP_{aw}) at equivalent densities for each species. Relative productivity was calculated using PAI of each species. The equation is:

$$RPT_{sw,aw} = RPsw\left(\frac{PAI_{sw(aw)}}{PAI_{sw}}\right) + RPaw\left(\frac{PAI_{aw(sw)}}{PAI_{aw}}\right), \tag{3}$$

where PAI_{sw} and PAI_{aw} are periodic annual increment of each pure spruce or aspen stand, and $PAI_{sw(aw)}$ is the periodic annual increment of spruce in the mixed stand and $PAI_{aw(sw)}$ is the periodic annual increment of aspen in the mixed stand. A relative productivity total higher than 1, indicates an advantage of species mixing. The pure spruce plots (500 and 1000 trees/ha) and the pure aspen plots (1500, 4000 trees/ha, and unthinned natural plot) in each replicate were used as reference pure stands for each density combination.

2.2.2. Potential predictor variables

Stand density represents site occupancy by trees and is closely related to resources and growing space used by trees in a stand (del Río et al., 2016). Stem number, basal area, and stand density index per unit area are commonly used as measures of site occupancy, and this study also used these variables to quantify species-specific site occupancy of pure and mixed stands. Species proportion is often used as an indicator of composition of a mixed stand (del Río et al., 2016). In this study, basal area of aspen or spruce was divided by total basal area to calculate species proportion.

Canopy stratification can influence the productivity of mixtures because it can reduce competition among species and increase light interception due to increasing leaf area index and better filling of canopy space (Seidel et al., 2013; del Río et al., 2016; Pretzsch and Schütze, 2016). Young aspen-spruce mixtures generally consist of two canopy layers because of differences in growth rates and shade tolerance. Thus, the difference of tree height between two species was used as a proxy variable for canopy stratification. Since tree size is associated with stand structure in mixtures, quadratic mean diameter (QMD) and mean tree height (HT) were also included as covariates.

Environmental factors can influence species interactions in mixtures and the interactions lead to changes in stand structure (Forrester et al., 2013; Huber et al., 2014; Toïgo et al., 2015), consequently we also tested the effects of climate and site quality. Climate data was obtained from ClimateWNA (climate data for western North America) (Hamann et al., 2013) and climate averages for intervals between two measurement years were used in this analysis. As representative climate variables, mean annual temperature (MAT), annual heat moisture index (AHM), degree days above 5 °C (DD5), mean annual precipitation (MAP), mean summer precipitation (MSP), summer heat moisture index (SHM), frost free period (FFP), and climate moisture index (CMI) were utilized. Climate moisture index was calculated using monthly temperature, annual precipitation, and elevation for each location (Hogg, 1997). In the study only one climate variable was used in each model to avoid potential problems with collinearity of climate variables. As a result, multiple models were tested using various combinations of variables. To examine the effect of site quality on mixing effect, aspen site index was calculated using tree heights measured in pure aspen plots (Husch et al., 2003; Huang et al., 2009) for each installation.

2.3. Data analysis

2.3.1. Comparison of aspen-spruce combinations

Stand characteristics (e.g., tree size, stand density, and productivity) among 11 treatments including pure stands were compared to investigate the responses of two species according to aspen-spruce combinations and to determine reasons for differences in mixing effect.

Effects of treatments (combination of spruce and aspen density) on relative productivity total (RPT) were tested using a linear mixed effects model to control for regional variation. Treatment was used as a fixed effect and replicate nested in installation nested in agency was used as a random effect. Because repeated measurements can be correlated over time, autocorrelation functions were tested and the order 1 autocorrelation function was selected. After developing the linear mixed effects model, Tukey's HSD (honestly significant difference) test was conducted to determine which treatments were different from others using the function lsmeans (Russell, 2016). The equation of a linear mixed effects model is:

$$Y = \mu + r + T + \varepsilon, \tag{4}$$

where Y is relative productivity total, μ is the overall mean, r is the random intercept of replicate nested in installation nested in agency, T is a fixed effect of aspen-spruce treatment, and ε is the error term.

Density effects can be confounded with the effect of species mixing when under stocked stands are included in the data. In particular, under stocked aspen stands can allow understory spruce to grow better than in well stocked aspen stands in this study. To control for density effects, we investigated effects of stocking using both relative density (Curtis,

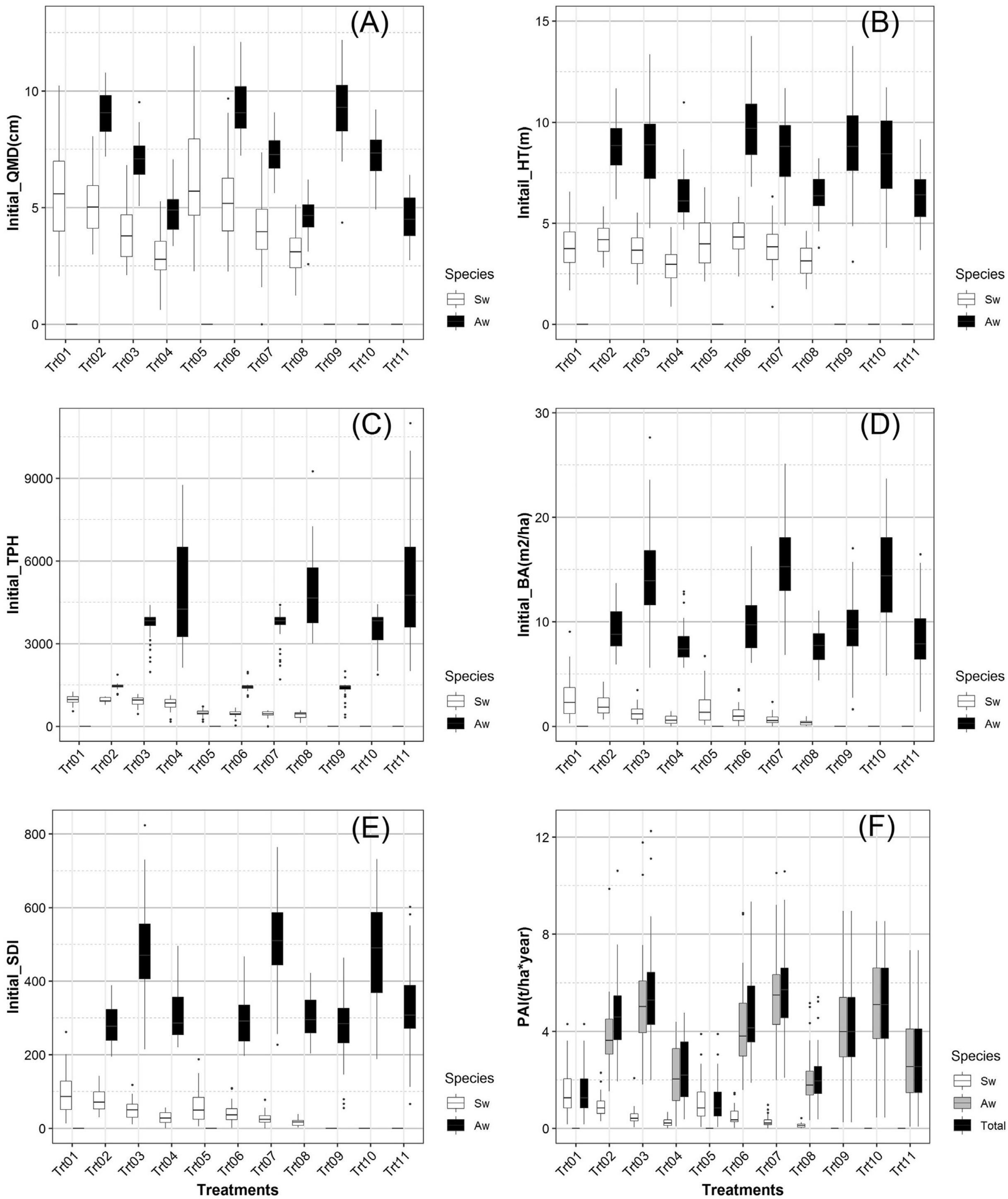

Fig. 2. Comparisons of tree size, stand density, and productivity among treatments (Sw, white spruce; Aw, trembling aspen; Total, Sw + Aw; Initial_QMD, initial quadratic mean diameter; Initial_HT, initial mean tree height; Initial_TPH, initial trees per hectare; Initial_BA, initial basal area; Initial_SDI, initial stand density index; PAI, periodic annual increment; Trt01, Sw1000; Trt02, Sw1000/Aw1500; Trt03, Sw1000/Aw4000; Trt04, Sw1000/AwNatural; Trt05, Sw500; Trt06, Sw500/Aw1500; Trt07, Sw500/Aw4000; Trt08, Sw500/AwNatural; Trt 09, Aw1500; Trt10, Aw4000; Trt11, AwNatural). For the analysis, 193 experimental units were used.

1982) and relative stand density index (SDI of aspen in mixture divided by maximum SDI of unthinned aspen stand). Relative density or relative stand density index of unthinned aspen stands experiencing self-thinning was higher than relative density = 15 or relative SDI = 0.3 respectively. Based on these values of aspen stocking, 32 plots considered to be under stocked and 22 plots having negative PAI values due to self-thinning were removed. In addition, 35 outliers (15.4% of 228 plots) which were outside of the range of 2.5–97.5 standard normal quantiles were removed to achieve equal variance and normal distribution of residuals for all models developed in this analysis. Relative productivity total and periodic annual increment total used in the analysis are from the sum of aspen and spruce values (e.g., relative productivity or periodic annual increment of two species), so the errors of aspen and spruce values can cause increases in variation for coefficients in models with the total response variables. In addition, since the relative values (e.g., relative productivity = biomass of a species in a mixture/biomass

Table 3
The least square means of relative productivity total (RPT) among treatments.

Treatment (level)	lsmean	SE	df	lower.CL	upper.CL	T-test with μ = 1	Overyielding rate
Sw1000/Aw1500 (a)	1.537	0.084	6	1.331	1.743	*P*-value = 0.001*	96.5% (28/29)
Sw1000/Aw4000 (a)	1.349	0.078	6	1.160	1.539	*P*-value = 0.004*	86.5% (32/37)
Sw1000/AwNat (b)	1.083	0.089	6	0.866	1.300	*P*-value = 0.386	54.2% (13/24)
Sw500/Aw1500 (a)	1.483	0.083	6	1.280	1.685	*P*-value = 0.002*	93.5% (29/31)
Sw500/Aw4000 (a)	1.420	0.076	6	1.235	1.606	*P*-value = 0.001*	82.5% (33/40)
Sw500/AwNat (b)	0.921	0.081	6	0.722	1.120	*P*-value = 0.370	31.3% (10/32)

* Significantly different from relative productivity total = 1 (using likelihood ratio test α = 0.05); Sw1000 or Sw500, 1000 spruce or 500 spruce trees per hectare; Aw1500 or Aw4000, 1500 aspen or 4000 aspen trees per hectare; AwNat, unthinned aspen stand; Overyielding rate, number of overyielding plots/number of available plots.

of a species in a monoculture) were used in the analysis, the relative value can become extreme when tree mortality results in the biomass of a species in a monoculture being low relative to its biomass in a mixture. In particular, unthinned aspen stands showed wide variations of these response variables because self-thinning is active in these stands compared to thinned aspen stands. Log or Box-Cox transformation of data was also tested, but this did not resolve issues with extreme values.

2.3.2. Relationships between mixing effects and stand variables

To determine which factors influence relative productivity total (RPT), a linear mixed effects model was fit to the data. Fixed effects (species proportion, basal area, stand density index, tree size, age, canopy stratification, climate, and site index) and random effects (Agency, installation, and replicate) were used for the analysis. Correlations between fixed effects variables included in each model were examined and were found to be non-significant. Variables which were strongly collinear (e.g., Basal area and SDI) were not included together in any models. To better account for relationships between relative productivity and predictor variables, we examined how predictor variables influence PAI total and PAI for each of the two species in mixtures. The equation for a linear mixed effects model is:

$$Y = \mu + r + \beta_1 \times x_1 + \beta_2 \times x_2 + \dots + \beta_i \times x_i + \varepsilon, \quad (5)$$

where Y is the response variable (e.g., relative productivity total, aspen or spruce, PAI total, PAI aspen, or PAI spruce), μ is the overall mean, r is the random intercept of replicate nested in installation nested in agency, β_1, β_2, …, β_i are coefficients of stand factors (e.g., tree size, basal area or SDI, climate, and site index), and ε is the error term.

In addition, we selected four agencies (i.e., ALP, DMI, ESRD, and WGP) which had at least 3 measurements to examine the effect of stocking (e.g., SDI and species proportion) on mixing effect over time. The analysis was conducted at the treatment plot level (6 subsets) instead of the replicate level because each treatment plot had different ranges and variation in stocking. Relative productivity total was used as the response variable and stand density index total and spruce proportion were used as predictor variables.

A first order autocorrelation function was included to control for correlation among repeated measurements (2–4 measurements for 3–9 years). Variance inflation factors (VIF) were tested to examine potential multicollinearity among predictor variables and models with VIF greater than 4 were excluded because higher VIF (e.g., VIF > 5) often causes increases in variance for coefficients and decreases in the statistical power of the analysis (Mason et al., 2003; Sheather, 2009). The maximum likelihood method was used to compare models, and the best model was selected based on lowest AIC (Akaike Information Criterion) and the likelihood ratio test. All parameters were estimated using the nlme package (Pinheiro and Bates, 2000; Pinheiro et al., 2015) of R software, version 3.0.3 (R Core Team, 2017).

3. Results

3.1. Comparisons of stand characteristics between mixtures and monocultures

Tree size (e.g. quadratic mean diameter and mean tree height), stand density (e.g. trees per hectare (tph), basal area, and stand density index), and periodic annual increment of stem biomass were compared among treatments including pure spruce and aspen treatments (Fig. 2). The mean diameter of pure spruce stands (e.g., 500 or 1000 spruce tph without aspen) is largest compared to mean spruce diameter of other treatments. Among mixtures the combinations of either 500 or 1000 spruce tph with 1500 aspen tph have the largest mean aspen diameter and mean aspen diameter decreases as stem number increases. For mean tree height, however, the combinations of either 500 or 1000 spruce tph with either 1500 or 4000 aspen tph have similar heights. Mean tree height is substantially smaller at both spruce densities in the natural (unthinned) aspen densities. With regard to stand density, unthinned aspen treatments have higher numbers of trees and larger variation in the number of trees due to self-thinning, while thinned aspen treatments have narrower variation in the number of trees. For basal area, unthinned aspen treatments are lower than other treatments although stem numbers are higher than for other treatments. Stand density index is highest in the 4000 aspen tph treatments, and 1500 aspen tph treatments have a similar range of SDI to unthinned aspen treatments. Unthinned aspen treatments have lower PAI total than other treatments and 4000 aspen tph treatments with both spruce densities have the highest PAI total.

3.2. Evidence of overyielding in young mixedwood stands

Overall, 145 out of 193 (75.1%) plots had relative productivity total higher than one. The combination of 1000 spruce and 1500 aspen trees per hectare (tph) had the highest overyielding rate (96.5%, overyielding plots to stocked plots), whereas the combination of 500 spruce tph and unthinned aspen had the lowest overyielding rate (31.3%, overyielding plots to stocked plots) (Table 3). According to Tukey's test, thinned aspen stands with 1000 spruce and 500 spruce tph did not differ significantly, but were significantly different from the combinations of unthinned aspen stands with either 1000 spruce or 500 spruce tph (Table 3).

Relative productivity total varied from 0.921 to 1.537 among mixedwood treatments. The combination of 1000 spruce tph and 1500 aspen tph had 53.7% higher productivity compared to pure stands. In addition, except for the combinations of unthinned aspen stands with 1000 spruce and 500 spruce tph, mixtures had significantly higher relative productivity totals than pure stands (RPT = 1).

Fig. 3 shows the contribution of each species to relative productivity total. Relative productivity of aspen was only different from relative productivity = 1 for the combination of 500 spruce tph and unthinned aspen while all relative productivities of spruce were significantly lower than relative productivity = 1. This result indicates that productivity of

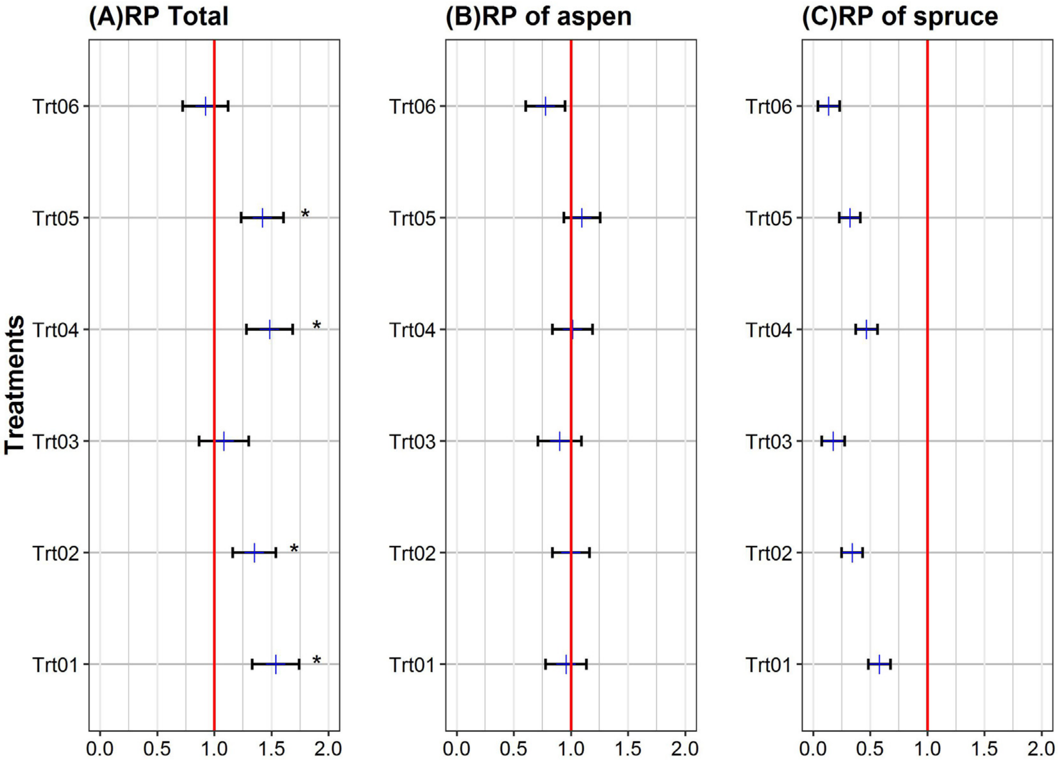

Fig. 3. Comparisons of relative productivities among treatments (Trt01, Sw1000/Aw1500; Trt02, Sw1000/Aw4000; Trt03, Sw1000/AwNatural; Trt04, Sw500/Aw1500; Trt05, Sw500/Aw4000; Trt06, Sw500/AwNatural). (A) Relative productivity total (sum of relative productivities of two species, Eq. (3)), (B) Relative productivity of aspen, and (C) Relative productivity of spruce. The red solid-vertical line represents that overyielding rate is equal to 1 (i.e. non-mixing effect) and star (*) represents significant overyielding. For the analysis, 193 experimental units were used.

aspen in mixtures does not differ from that of pure aspen stands. PAI of spruce in the mixture has a lower value than PAI of spruce in the monoculture because of suppression by the overtopping aspen canopy, with the degree of suppression being influenced by aspen density.

3.3. Factors influencing overyielding of mixtures among treatments

As shown in Table 4, tree size (QMD), stand density (Basal area), site quality (site index), and climate (one climate variable used for each model) significantly influence relative productivity. In general, initial stand density and tree size influenced relative productivity in spruce-aspen mixtures, and addition of site index and climate (e.g., DD5, degree days above 5 °C) led to a slight improvement in the goodness of fit of models. For relative productivity total (RPT), initial tree size (QMD) of two species and DD5 provided the best model. Initial aspen size (QMD) positively influenced RPT while initial spruce size (QMD) and DD5 negatively influenced RPT (Figs. 4 and 5). For relative productivity of aspen (RPA), the effect of tree size was the same as for the model of RPT, with RPA decreasing with increasing aspen site index (Fig. 5). However, relative productivity of spruce (RPS) increased as initial

Table 4
Models developed with potential variables across treatments. Model 1 is the best with relative productivity total (RP_total), model 3 is the best with relative productivity of aspen (RP_Aspen), and model 3 is the best with relative productivity of spruce (RP_Spruce).

Models	AIC
1. RP_Total = 2.2112 - 0.0676 ×Init_SwQMD + 0.1303×Init_AwQMD - 0.0012×DD5	175*
(0.5357) (0.0237) (0.0170) (0.0004)	
2. RP_Total = 3.0733 + 0.0913×Init_SwBA + 0.0228×Init_AwBA - 0.0016×DD5	214
(0.6449) (0.0360) (0.0070) (0.0005)	
3. RP_Aspen = 1.5623 - 0.1083×Init_SwQMD + 0.0924×Init_AwQMD - 0.0396×SI	125*
(0.2719) (0.0193) (0.0150) (0.0128)	
4. RP_Aspen = 1.5683 - 0.0713×Init_SwBA + 0.0279×Init_AwBA - 0.0408×SI	137
(0.2668) (0.0282) (0.0057) (0.0129)	
5. RP_Spruce = - 0.1457 + 0.0582×Init_SwQMD + 0.0367×Init_AwQMD	-134*
(0.0507) (0.0109) (0.0079)	
6. RP_Spruce = 1.0984 + 0.0871×Init_SwBA - 0.0117×Init_AwBA + 0.0649×Init_SwHT + 0.0234×Init_AwHT – 0.0009×DD5	-120
(0.3921) (0.0208) (0.0031) (0.0209) (0.0104) (0.0003)	

All estimates are significant at α = 0.05 level and standard errors are shown in parentheses of estimates; RP_Total, relative productivity total; RP_Aspen, relative productivity aspen; RP_Spruce, relative productivity spruce; star (*) indicates the best model for each response variable; Init_SwQMD, initial quadratic mean diameter of spruce; Init_AwQMD, initial quadratic mean diameter of aspen; Init_SwBA, initial basal area of spruce; Init_AwBA, initial basal area of aspen; Init_SwHT, initial mean tree height of spruce; Init_AwHT, initial mean tree height of aspen; DD5, growing degree days above 5 °C; SI, site index; AIC, Akaike's information criterion.

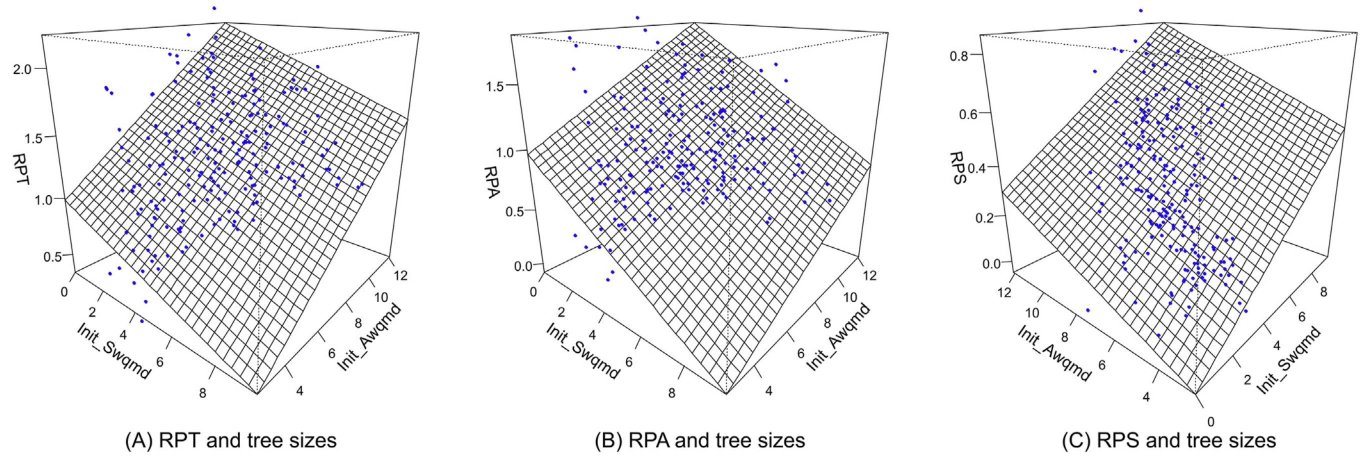

Fig. 4. Relationships between relative productivities and tree sizes for two species (i.e., Init_Swqmd, initial quadratic mean diameter of spruce; Init_Awqmd, initial quadratic mean diameter of aspen). (A) Relative productivity total (RPT) and tree sizes from model 1, (B) Relative productivity of aspen (RPA) and tree sizes from model 3, and (C) Relative productivity of spruce (RPS) and tree sizes from model 5. For DD5 and site index, average values were used in the model (Table 2) and 193 experimental units were used in the analysis. See Table 4 for parameter estimates.

spruce size (QMD) increased (Fig. 4).

3.4. Relationships between productivity and stand factors (predictor variables) in mixtures

Table 5 shows relationships between PAI total, PAI aspen, and PAI spruce and predictor variables. Increases in stand density (e.g., Basal area and stand density index) and tree size (e.g., tree height) were associated with increases in total and aspen periodic annual increment. However, as stand density of aspen increased, spruce PAI decreased. Increases in climate moisture index (CMI) were associated with an increase in PAI while increases in annual heat moisture index (AHM) were associated with a decrease in PAI.

3.5. Relationships between mixing effect and stand stocking over time

Figs. 6 and 7 show the relationships between mixing effect and stand density index total or spruce proportion. As either SDI total or spruce proportion increased, relative productivity total tended to decrease. For SDI total, 4000 aspen tph treatments with both spruce densities and the natural aspen treatment with 500 spruce tph (Fig. 6b, e, and f) showed significant trends in relative productivity total. In particular, Fig. 6f (Sw 500 tph and Aw Natural) had a steeper declining slope than other treatments and a likelihood ratio test ($\alpha = 0.05$ level) indicated that the intercept of Fig. 6f was higher than Fig. 6b and c.

All thinned aspen treatments (with both spruce densities) and the natural aspen treatment with 500 spruce tph showed significant declining trends as spruce proportion increased. According to the likelihood ratio test ($\alpha = 0.05$ level), Fig. 7b and f had steeper slopes than Fig. 7c, and Fig. 7a had a larger intercept than Fig. 7c and d.

4. Discussion

Relative productivity was used to determine the mixing effect (i.e. overyielding) in mixtures and factors influencing overyielding were examined. Overyielding was evident in these young boreal mixedwood stands and species interactions varied with species composition and stand density. Adding spruce into thinned aspen stands was generally associated with maintaining aspen PAI in mixtures similar to that in pure aspen stands and adding extra spruce PAI, while treatments combining spruce with unthinned aspen had lower PAI for both species and less frequency of overyielding (Table 3 and Fig. 3). This trend reflects shade tolerance of white spruce, effects of increasing understory light levels on growth of white spruce by thinning aspen, and the effects of reducing intraspecific competition for aspen. This is consistent with results from other studies showing that light levels and growth of understory spruce decline with increasing aspen density (Comeau, 2001; Comeau et al., 2006; Filipescu and Comeau, 2007; Prévost and Gauthier, 2012). 14 m^2/ha of aspen basal area (transmittance = 40%) can reduce the radial growth of spruce up to 51%, and spruce mortality rapidly increases when aspen densities exceed 20 m^2/ha of basal area (Comeau, 2001). Spruce survival is low at 8% transmitted light or lower (Lieffers and Stadt, 1994; Comeau, 2001) but increases dramatically with increases in light levels. Spruce height growth shows an

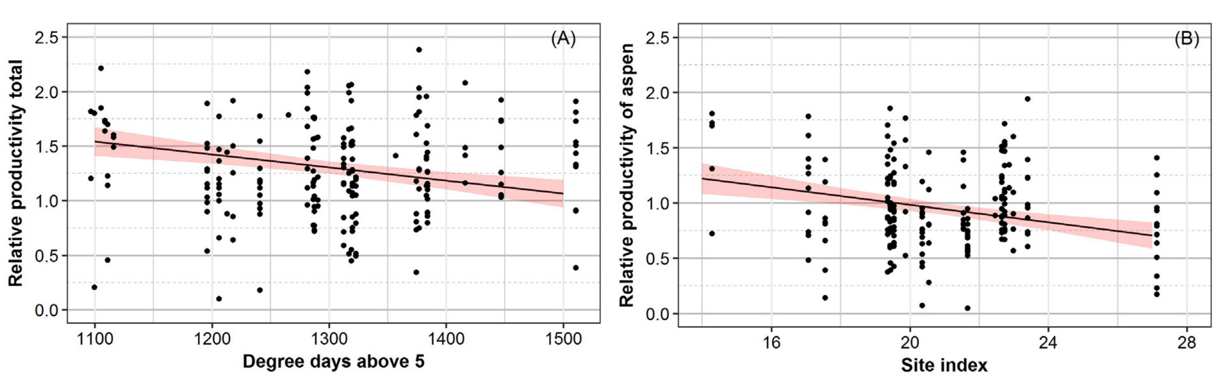

Fig. 5. Effects of climate and Aspen site index on relative productivity. (A) Relative productivity total and degree days above 5 °C from model 1 (Table 4) and (B) Relative productivity of aspen and site index from model 3 (Table 4). For initial spruce QMD and aspen QMD, average values were used in the models (Table 2) and 193 experimental units were used in the analysis.

Table 5
Relationships between periodic annual increment total and two species and predictor variables in mixtures.

Models	AIC
PAI_Total = 3.6730 + 0.4625×Init_SwBA + 0.2452×Init_AwBA + 0.3110×Init_SwHT + 0.2699×Init_AwHT - 0.2564×AHM	719*
(1.4502) (0.1794) (0.0238) (0.1370) (0.0736) (0.0625)	
PAI_Total = -4.2831 + 0.0129×Init_SwSDI + 0.0067×Init_AwSDI + 0.3425×Init_SwHT + 0.4347×Init_AwHT + 0.1024×CMI	731
(0.5907) (0.0050) (0.0007) (0.1371) (0.0678) (0.0261)	
PAI_Aspen = 3.2250 + 0.3163×Init_SwBA + 0.2547×Init_AwBA + 0.2926×Init_AwHT - 0.2136×AHM	709*
(1.3927) (0.1439) (0.0233) (0.0700) (0.0595)	
PAI_Aspen = -4.3000 + 0.0071×Init_AwSDI + 0.3920×Init_SwHT + 0.4166×Init_AwHT + 0.0963×CMI	714
(0.556) (0.0006) (0.1117) (0.0641) (0.0254)	
PAI_Spruce = 0.3678 + 0.0104×Init_SwSDI - 0.0004×Init_AwSDI + 0.0170×Init_AwHT - 0.0153×AHM	-279*
(0.1067) (0.0004) (0.0001) (0.0062) (0.0045)	
PAI_Spruce = 0.3971 + 0.3756×Init_SwBA - 0.0099×Init_AwBA + 0.0161×Init_AwHT - 0.0160×AHM	-277
(0.1054) (0.0149) (0.0027) (0.0072) (0.0045)	

All estimates are significant at $\alpha = 0.05$ level and standard errors are shown in parentheses of estimates; PAI_Total, periodic annual increment total in stem biomass; PAI_Aspen, period annual increment of aspen in stem biomass; PAI_Spruce, periodic annual increment of spruce in stem biomass; star (*) indicates the best model for each response variable; Init_SwBA, initial basal area of spruce; Init_AwBA, initial basal area of aspen; Init_SwSDI, initial stand density index of spruce; Init_AwSDI, initial stand density index of aspen; Init_SwHT, initial mean tree height of spruce; Init_AwHT, initial mean tree height of aspen; AHM, annual heat moisture index; CMI, climate moisture index; AIC, Akaike's information criterion.

asymptotic trend and reaches a maximum at about 40% transmitted light (or BA of aspen below 14 m^2/ha).

Our results indicate that tree size (e.g., diameter and height) and stand density (e.g., basal area and stand density index) were the main factors determining the yield of young trembling aspen-white spruce mixtures (Tables 4 and 5). In general, tree size is an important factor influencing productivity of a mixture since productivity will decline when two species compete. Consequently, a mixed species stand that has space partitioning and size inequality between species leads to competitive reduction and favours differences in functional traits (e.g. shade tolerance) between the component species (Pretzsch and Schütze, 2016; Toïgo et al., 2018; Forrester et al., 2018). In our study, interspecific competition between two species is less severe than observed in mature mixed stands because most spruce trees are still substantially shorter than the aspen. The shade tolerance of spruce enables spruce to survive under the aspen canopy and allows mixtures of aspen and spruce to maintain higher stocking (Man and Lieffers, 1999; Peer et al., 2018). In addition, model 1 from Table 4 indicates that the relationship between initial tree size and relative productivity total is also associated with intraspecific competition amongst aspen. Treatments with higher relative productivity total have bigger differences in tree size between two species and less intraspecific competition (Fig. 4). Thus, thinned plots with larger aspen lead to higher basal area than unthinned plots and spruce are receiving higher light levels due to their larger tree height (Fig. 2). In contrast, mixing effect decreases when sizes of the two species are similar.

Species mixtures often support higher stocking than pure stands (Condés et al., 2013; Pretzsch and Biber, 2016; Pretzsch and Schütze, 2016) leading to increases in productivity. This is consistent with our results indicating that PAI total in mixtures increases as both spruce and aspen basal area increase (Table 5). Canopy stratification resulting from differences in species growth rates and increases in stocking in mixtures lead to increases in light capture and biomass production (Forrester et al., 2018). However, when aspen densities are high, understory light levels and spruce growth are low and lead to little or no overyielding. In our study, the combinations of spruce with unthinned aspen stands have relatively small tree sizes compared to the others (Fig. 2a and b) and mixing effect is also lower than others (Table 3). This also indicates the importance of tree size to the productivity of aspen-spruce mixtures.

Mixing effect is influenced by site quality and environmental

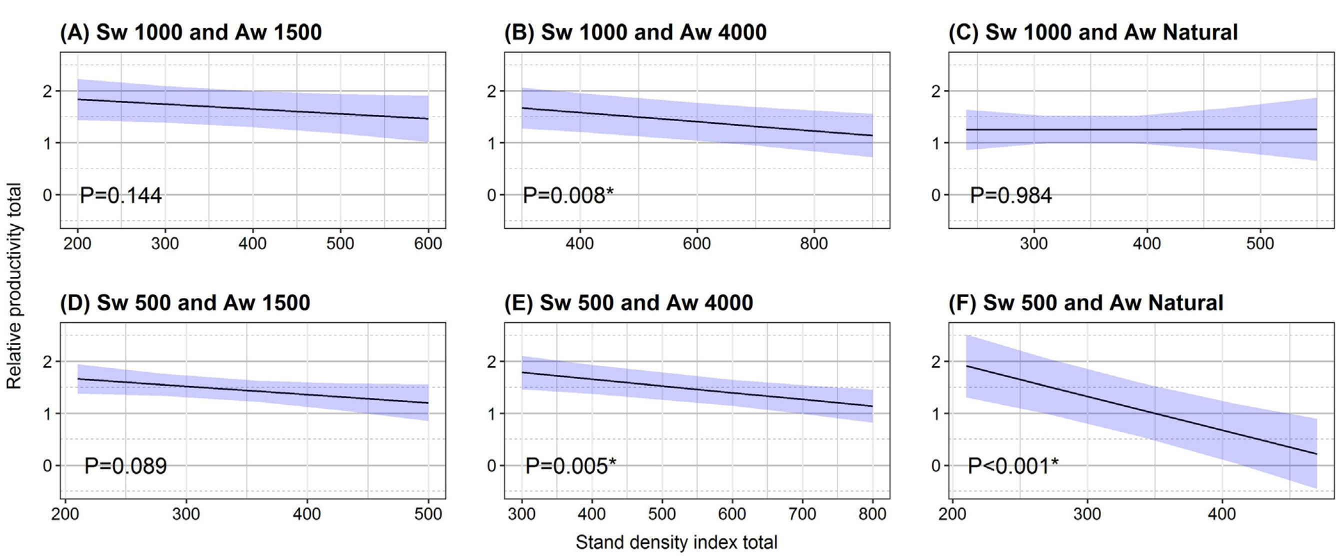

Fig. 6. Relationships between stand density index and relative productivity total at each treatment. Star (*) indicates the significance of slope at each treatment and *p*-values were shown in each panel.

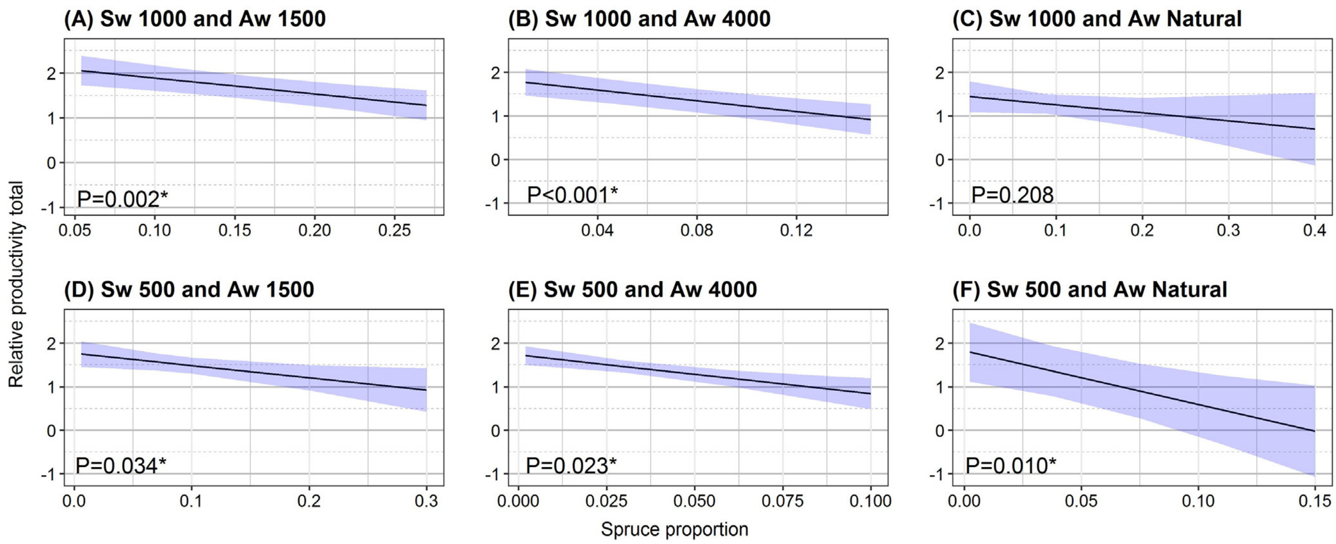

Fig. 7. Relationships between spruce proportion and relative productivity total at each treatment. Star (*) indicates the significance of slope at each treatment and *p*-values were shown in each panel.

conditions. Fig. 5 indicates that relative productivity in mixtures declines as site index and DD5 increase. This is consistent with other studies (Pretzsch et al., 2010, 2013a; Toïgo et al., 2015) which have shown that overyielding occurs more commonly on poor sites than good sites. Pretzsch et al. (2013a) state that species interactions change from facilitation to competition along a gradient of increasing site quality, and the result is supported by the stress gradient hypothesis that facilitation among species is more common under stressful conditions (Bertness and Callaway, 1994). As expected for a harsh boreal environment, stand mixing effect is negatively influenced by increasing growing season length (DD5), which appears to be primarily associated with increases in competition in our study (Table 4). For the relative productivity of aspen, as site index increases, intraspecific competition may lead to decreasing aspen PAI and also increase interspecific competition, especially in unthinned aspen plots.

With regard to changes in mixing effects over time, it is expected that mixing effect will decrease as stand stocking (e.g., stand density index and spruce proportion) increases (Figs. 6 and 7). Increasing total stocking is expected to lead to increased resource utilization and increasing intraspecific competition among aspen trees, leading to reduced productivity of aspen. In addition, increasing aspen stocking can suppress the growth of understory spruce. For these reasons, treatments with higher stocking (i.e., 4000 aspen tph plots) might show significant declines than treatments with lower stocking (Fig. 6). However, in unthinned aspen treatments, relative productivity was irregular and variable (Figs. 6 and 7) due to self-thinning (Fig. 2c). Continued measurement of this study will be useful in evaluating trends over a longer period, beyond age 28.

In addition to these reasons for the positive mixing effect, faster nutrient cycling, low mortality rate of spruce, and differences in phenology between two species are expected to lead to increases in productivity in boreal mixedwood stands (Groot and Carlson, 1996; Taylor et al., 1996; Constabel and Lieffers, 1996; Man and Lieffers, 1997, 1999; Macisaac and Krygier, 2009). Spruce roots are primarily located near the surface while aspen roots are most abundant between 15 cm and 40 cm (Strong and La Roi, 1983; Man and Lieffers, 1999; Lawrence et al., 2012). This difference in the distribution of root systems is likely to contribute to niche separation between aspen and spruce and increases in total productivity. Further research is needed to evaluate contributions of these and other factors to overyielding and to increase our understanding of mixing effects.

5. Conclusions

Our study focuses on productivity of mixtures and illustrates the occurrence of overyielding in young (13 to 28 year old) boreal mixedwood stands in western Canada. Our results show that overyielding varies depending on species composition. Thinned aspen stands show higher production than unthinned aspen stands and also contain larger trees than unthinned stands. Overyielding ranges up to 1.537 in the stands studied and is greatest in mixtures with 1500 aspen tph and 1000 spruce tph at approximately 20 years of age. Initial stand densities (basal area) of two species and initial aspen size (QMD) positively influence mixing effect while initial spruce size (QMD) negatively influences mixing effect. In other words, a mixed species stand that has space partitioning and size inequality between species, which reduces competition and favours expression of the functional traits (e.g., shade tolerance) of each species, tends to have higher productivity. The magnitude of overyielding declines with increasing growing season length (DD5) and the relative productivity of aspen decreases with increasing site quality. Overyielding may decrease as these stands age and spruce become larger, indicating a need for ongoing measurement and monitoring of the WESBOGY LTS installations, and other related studies.

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