Trembling aspen competition and climate effects on white spruce growth in boreal mixtures of Western Canada

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ABSTRACT

We investigated the combined effect of trembling aspen competition and climate on white spruce growth using data from a long term study with matching treatments spread across the boreal mixedwood forests of Alberta and Saskatchewan (Canada). Results indicate that competition (i.e., aspen basal area), initial size of the tree and mean annual temperature can account for 88% of the year to year variation in spruce volume growth for these six locations. Based on the model that we developed, spruce growth, in the absence of competition, is estimated to increase by up to 17% compared with an increase in mean annual temperature from 2 °C to 3.3 °C, while, at high levels of competition (aspen basal area = 27 m² ha⁻¹) spruce growth increases by only 8%. Moreover, effects of aspen on spruce growth increase more than proportionally as temperature increases. This outcome indicates that abundant aspen competition limits the spruce responses to rising temperature, presumably due to competition for light and potentially increased competition for soil resources. Results also show that competition and climate effects vary between locations, indicating that spruce growth is strongly influenced by local factors such as micro-climate, topography, and soil properties.

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1. Introduction

After disturbance by fire or clear-cutting in the western boreal forests, white spruce (*Picea glauca* (Moench) Voss) seedlings are often mixed with abundant trembling aspen (*Populus Tremuloides* Michx.) regeneration (Peterson and Peterson, 1992). For the first six decades aspen tends to dominate the stands while the more shade-tolerant spruce grows slowly under the main canopy layer (Peterson and Peterson, 1992). Spruce growth can be reduced by aspen competition for light, however, an aspen overstory can protect spruce from pests and climate extremes and reduce competition from understory species (Lieffers and Stadt, 1994; Comeau, 1996; Pritchard and Comeau, 2004; Voicu and Comeau, 2006; Man et al. 2008). Some studies have shown that mixedwood stands can be more productive than pure stands (Man and Lieffers, 1999; MacPherson et al., 2001), particularly in the case where an intolerant overstory species such as aspen is growing in combination with a shade tolerant understory species such as white spruce.

Boreal mixedwood stands are often tended to create favorable conditions for both species in an attempt to maximize their productivity. However, our ability to estimate the influence of different tending practices on stand development depends on our understanding of how key factors such as competition and climate influence on tree growth. Competition indices are commonly used to quantify competition in conifer plantations (e.g., Weigelt and Jolliffe, 2003). These indices can be calculated from simple visual estimates of competing vegetation cover or from stand measurements such as basal area which can be collected quickly and consistently in the field (Cortini and Comeau, 2008). Recent studies on the effect of aspen competition on spruce growth have indicated that simple competition indices such as aspen basal area and density can be as effective as more complex indices (e.g., Filipescu and Comeau, 2007a; Stadt et al., 2007). However, Filipescu and Comeau (2007a,b) found that the relationships between aspen competition and spruce growth vary with site location, presumably due to changes in climate (particularly frost) and other factors.

Climate has a strong effect on tree growth and under the current increase in average temperatures, species better suited to warmer climates might become stronger competitors for resources (Spittlehouse, 2008). In northern ecosystems the recent warming is already affecting a wide range of species and ecosystems (e.g., International Panel on Climate Change (IPCC), 2007; with magnitude and type of effect (beneficial or detrimental) being highly depended on the species (e.g., Rehfeldt et al., 1999). Climate is changing faster than the rate of natural selection and seed migration (O'Neill et al., 2008), and this will likely require a change in the current reforestation practices to facilitate assisted migration for those species better suited to grow under future climates (e.g., Gray and Hamann, 2011).

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Recent studies have also shown that climatic variables can be used to improve the predictive ability of growth models (e.g., Woollons et al., 1997; Snowdon et al., 1999). A study in British Columbia (Canada) (Cortini et al., 2011) has indicated that both climate and site preparation treatments influence the growth of white spruce. Results from this study suggest that competition has the potential to exacerbate the influences of warming.

In this study we investigate whether differences in aspen abundance and climate explain year to year and site to site variation in growth of white spruce and we relate these results to options for managing white spruce under climate change in Canada's western boreal forests.

2. Materials and methods

2.1. Study description

Data for this study comes from field installations established by the Western Boreal Growth and Yield Association (WESBOGY) for a long term study of growth and development of tended mixtures of white spruce and trembling aspen (Bokalo et al., 2007). The installations include: the Alberta-Pacific Forest Industries Inc. (ALP) installation located near Boyle, Alberta; the Daishowa-Marubeni (DMI) installations located near Peace River, Alberta; the Weyerhaeuser Saskatchewan Division (SBR and SPA) installations located near Big River and Prince Albert, Saskatchewan; the Alberta Sustainable Resource Development (SRD) installation located near Smith, Alberta; the Westfraser (WFR) installations located near Hinton, Alberta; and the Weyerhaeuser Grande Prairie (WGP) installations located near Grande Prairie, Alberta (Fig. 1).

The WESBOGY long term study uses a randomized block design where each block consists of two installations, one on a superior site and one on a median site and each installation has two replications of a series of 15 plots (WESBOGY, 2007). The data we used were from 20 m square plots (400 m^2) at each installation representing two levels of spruce density (500 and 1000 stems per hectare), and five levels of aspen density (0, 200, 500, 1500, and 4000 stems per hectare).

The WESBOGY long term study also includes natural densities of aspen, and plots with no spruce, however these were not used in the present study due to: (1) the use of very small plots for aspen measurements (2 m × 2 m) in the unthinned natural density plots; and (2) the lack of spruce in the plots without planted spruce. On the selected WESBOGY sites white spruce was planted starting in 1990 and aspen (naturally regenerated) was thinned to treatment densities around age 5. Treatment location, planting year and general climate information are presented in Table 1.

Spruce and aspen have been measured regularly since establishment of the WESBOGY Long Term Study. To avoid confounding results with undocumented competitive effects or initial responses to aspen thinning, we utilized data starting two years after thinning treatments. For this analysis we used data for the period from 1997 to 2006. For ALP, DMI, and SRD there are four current annual increments available; for SBR, SPA, and WFR there are five current annual increments available; and for WGP there are six current annual increments available over this time period. Annual increments for those trees that had form problems resulting from insect injuries, browsing, physical damage or other sources were excluded from the analysis since they will not respond to climate. The overall number of damaged trees excluded was low (i.e., <1%).

Preliminary analysis indicated that the data collected at SPA (medium and superior installation) and SBR (only at the medium installation) had a large number of outliers and were removed from the dataset for analysis: SPA had a dense shrub layer affected the early growth of white spruce and SBR was on a substantially more productive site than all others.

2.2. Data analysis

Spruce stem volume (SV, cm^3) was calculated from stem height (HT, cm) and root collar diameter (RCD, cm) using a modified version of Honer's equation (Honer et al., 1983):

$$SV = \frac{RCD^a}{b + \frac{c}{HT}}$$

where a, b, and c are parameters calculated by Cortini and Comeau (2008) for white spruce plantations in north-western Alberta. The models were fit using tree level data.

The spatial climate model ClimateWNA (Mbogga et al., 2009; Wang et al., 2012) was used to provide climate data for each site based on latitude, longitude and elevation (Wang et al., 2006). For each WESBOGY installation we calculated climate data for each growth year for a selected number of annual variables including Mean Annual Temperature (MAT), Mean Annual Precipitation (MAP), Mean Summer Precipitation (MSP), and growing degree days above 0° (DD > 0), Annual Heat:Moisture index (AH:M; (Mean Annual Temperature + 10)/(Mean Annual Precipitation/1000)); Summer Heat:Moisture index (SH:M; (Mean Warmest Month Temperature)/(MSP/1000)); Hargreaves Climatic Moisture Deficit (CMD; Hargreaves and Samani, 1985).

Relationships between spruce volume increment (VI) and climate were examined using non-linear regression. Initial spruce stem volume (IV), was selected as a predictor based on results from other studies (Filipescu and Comeau, 2007a,b). Agency was added to the models using indicator variables (e.g., $Z_n * d_n$; where d_n is the indicator variable 1 if agency = ALP, 0 otherwise, and Z_n is the agency parameter), similar to Peng et al. (2001). Aspen basal area per hectare (AwBA) measured at the plot level was also used in the models as an estimate of competition.

To account for the auto-correlation related to the repeated measurements of each tree, several combinations of predictors were tested as random factors (with tree ID as the subject) (Hall and Bailey, 2001). The models with the best fit include one random effect (b_2) added to initial spruce stand volume (β_2). Mixed effect models with more than one random factor either failed to converge or resulted in non-significant estimates. This outcome is likely because the number of measurements per tree was small and prevented models with more than one random parameter from converging.

The goodness-of-fit of the models was compared using the coefficient of determination (R^2), the root mean squared error (RMSE), and the Akaike information criterion (AIC, Burnham and Anderson, 1998). The models tested were:

$$VI_{ij} = \beta_1 \times IV_{ij}^{(\beta_2)} + \varepsilon_{ij} \tag{1}$$

$$VI_{ij} = (\beta_1 + Z_n \cdot d_n) \times IV_{ij}^{(\beta_2)} + \varepsilon_{ij} \tag{2}$$

$$VI_{ij} = (\beta_1 + Z_n \cdot d_n) \times IV_{ij}^{(\beta_2)} \times AwBA^{(\beta_3)} + \varepsilon_{ij} \tag{3}$$

$$VI_{ij} = (\beta_1 + Z_n \cdot d_n) \times IV_{ij}^{(\beta_2)} \times AwBA^{(\beta_3)} \times Climate^{(\beta_4)} + \varepsilon_{ij} \tag{4}$$

$$VI_{ij} = (\beta_1 + Z_n \cdot d_n) \times AwBA^{(\beta_3)} \times Climate^{(\beta_4)} + \varepsilon_{ij} \tag{5}$$

$$VI_{ij} = (\beta_1 + Z_n \cdot d_n) \times IV_{ij}^{(\beta_2 + b_{2i})} \times AwBA^{(\beta_3)} \times Climate^{(\beta_4)} + \varepsilon_{ij} \tag{6}$$

where β_1, β_2, β_3 and β_4 are fixed effects parameters, and b_{2i} represents the random effect (normally distributed with mean zero and an unknown variance component) associated with the ith tree. The index j represents the multiple measurements recorded per tree. The ε_{ij} term represents the unexplained error, also assumed
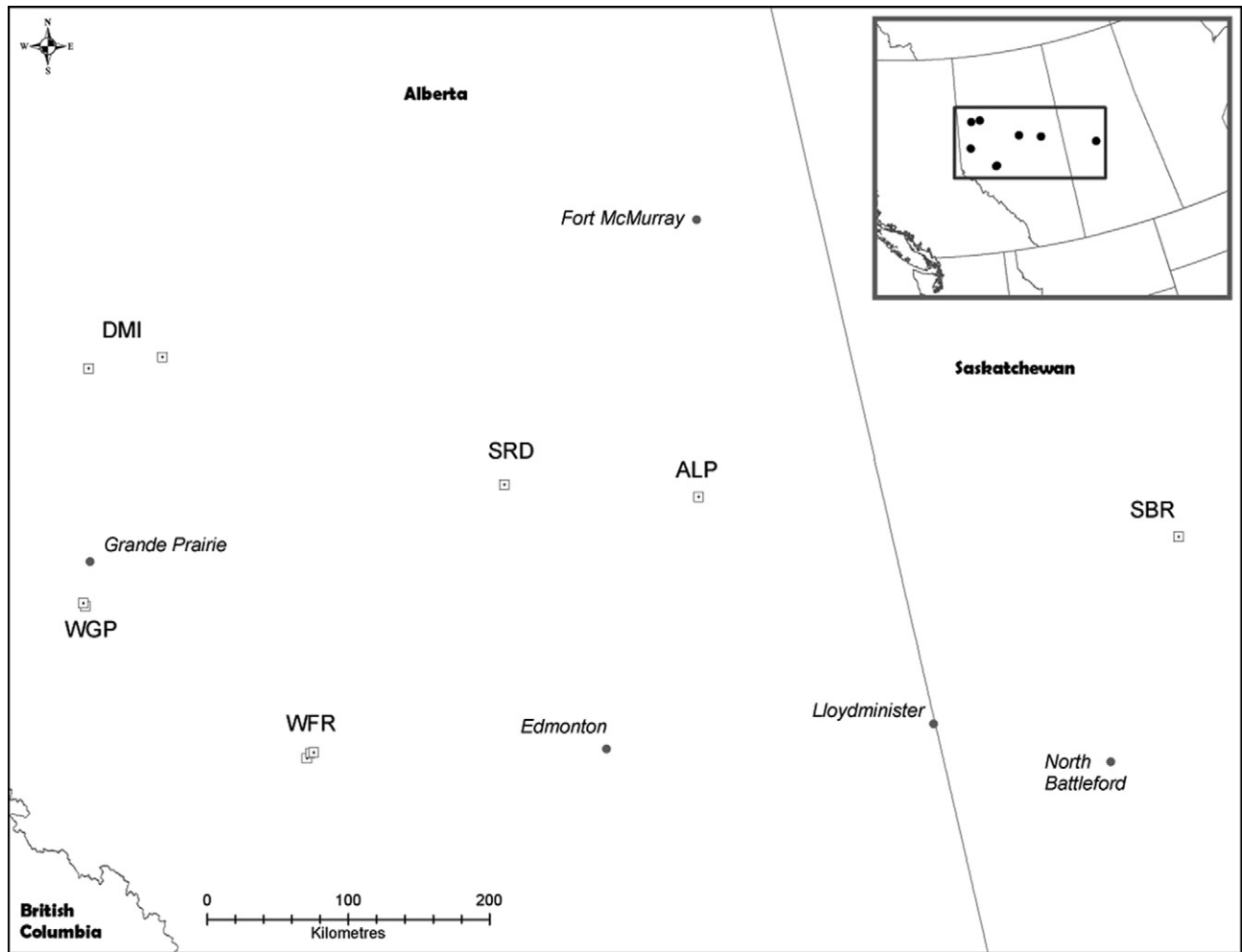
Fig. 1. Location of each selected agency and installation of the WESBOGY long-term study.

Table 1
Information relating the selected WESBOGY sites and climate normals for the period 1987–2006 (MAT = mean annual temperature (°C), MAP = mean annual precipitation (mm), MSP = mean summer precipitation (mm), and DD > 0 = growing degree days above 0°; source: ClimateWNA).

Agency	Installation	Blocks	Lat.	Long.	Elevation	Year Spruce Planted	MAT	MAP	MSP	DD > 0
ALP	Superior	1,2	55.00	−112.00	567	1994	1.7	418	306	1665
DMI	Medium	1,2	56.39	−118.59	781	1992	1.3	409	264	1674
DMI	Superior	1,2	56.41	−117.73	728	1992	1.1	399	261	1726
SBR	Superior	1,2	54.05	−106.98	515	1992	1.1	434	289	2870
SRD	Medium	1,2	55.30	−114.10	640	1992	1.6	459	322	1902
WFR	Medium	1,2	53.77	−116.69	1056	1993	2.9	557	411	1906
WFR	Superior	1	53.80	−116.64	1106	1993	2.9	570	418	2012
WFR	Superior	2	53.80	−116.61	1085	1994	2.9	565	415	1946
WGP	Medium	1	54.89	−118.90	701	1991	2.6	493	329	1643
WGP	Superior	1,2	54.91	−118.92	709	1991	2.6	486	324	1066

normally distributed with mean zero and an unknown variance component.

F-ratio tests (as described by: Ott, 1997; Draper and Smith, 1981) were then used: (1) to investigate if data from the medium and superior installations could be pooled and modeled together at the agency level; and (2) to compare Eqs. (1)–(6) to determine if the increasing complexity of the models significantly ($\alpha = 0.05$) improved model fit.

Parameter estimation for both fixed-effects and mixed-effects models was completed using the NLMIXED procedure in the SAS statistical package (version 9.2) (SAS Institute Inc., Cary, NC).

3. Results

Table 2 provides basic statistical information (e.g., mean and standard deviation) by agency for a number of representative variables such as spruce volume increment (VI), initial volume (IV), aspen basal area (AwBA), and climate. Our analysis indicated that mean annual temperature (MAT) explained the largest amount of variation in growth among the seven climate variables investigated (e.g., lowest AIC value), and consequently it was included in the final models.

F-tests investigating the hierarchical structure of the data for those agencies with installations for both medium and superior

Table 2
Basic statistical information of individual tree, competition variables and mean annual temperature (MAT of each year observed) for each agency. For each Agency the number of observations and growth year range (GY) are also provided.

Agency	Variable	Minimum	Mean	Maximum	Standard deviation
ALP	VI	1.60	162.3	1519.4	170.0
Observations:	IV	2.48	231.2	2041.6	219.6
2702	AwBA	0	2.87	15.16	3.37
GY:2002–2005	MAT	0.7	1.3	2.6	0.7
DMI	VI	7.72	253.5	1801.0	220.1
Observations:	IV	12.1	326.0	2343.5	295.0
4501	AwBA	0	2.50	11.91	2.77
GY:1999–2002	MAT	0.7	1.2	1.8	0.4
SBR	VI	1.07	144.2	3714.1	318.4
Observations:	IV	0.68	181.4	3938.8	405.0
1629	AwBA	0	2.86	26.84	3.54
GY:1998–2006	MAT	0.7	2.0	2.6	0.7
SRD	VI	4.14	168.5	2587.7	232.6
Observations:	IV	4.54	293.2	3504.7	407.9
2101	AwBA	0	4.37	22.66	4.75
GY:1999–2004	MAT	0.9	1.6	2.3	0.6
WFR	VI	1.57	110.7	2327.2	136.6
Observations:	IV	1.27	146.1	22.73.9	190.9
5341	AwBA	0	1.12	9.10	1.57
GY:1998–2002	MAT	2.2	2.9	3.3	0.4
WGP	VI	1.61	62.1	1255.6	88.7
Observations:	IV	1.87	93.6	1336.5	121.2
3740	AwBA	0	2.55	16.49	3.21
GY:1997–2004	MAT	1.9	2.6	2.9	0.3

VI = Volume increment (cm^3); IV = Initial volume (cm^3); AwBA = Aspen basal area ($m^2\ ha^{-1}$); MAT = Mean Annual Temperature (°C).

quality sites (i.e., DMI, WFR, and WGP) showed non-significant ($\alpha = 0.05$) differences between sites. For this reason data were pooled by agency and the analysis using indicator variables was carried at the agency level.

The results (Tables 3 and 4) indicated that the models developed (i.e., Eqs. (1)–(6)) were significant and all the parameter values were significantly different from zero ($\alpha = 0.05$). Goodness-of-fit values (Table 4) and the pairwise F-tests indicate that the models progressively improve when adding: indicator variables (2), aspen competition (3), mean annual temperature (4), and tree ID as random factor (6). Fig. 2 shows the relationship between observed and predicted spruce volume increment according to Eq. (6). The distribution of the data points around the 1:1 line suggests that the models are providing unbiased and consistent estimates of observed values.

Predicted values for Eq. (6) were calculated using an average value of the six indicator variables (783.1), and average initial volume (206.7 cm^3). The results were then presented as percent change in volume increment relative to the average volume increment (149.5 cm^3) (Fig. 3). The change in volume growth was calculated for three levels of aspen competition (i.e., zero, average, and high) and plotted against mean annual temperature. The scenario with zero aspen competition (AwBA = 0) shows that an increase in volume increment of 16.9% should occur with a rise in MAT from 2 °C to 3.3 °C. In contrast, the average competition level (i.e., AwBA = 2.4 $m^2\ ha^{-1}$) shows an increase of 10.3%, and the scenario with highest competition level (i.e., AwBA = 26.8 $m^2\ ha^{-1}$) indicates an increase of 8.4%. At the minimum value of mean annual temperature (0.8 °C), the scenario with zero aspen competition shows a decrease of 0.9% in predicted volume increment compared to increment at 2 °C (the average value); the average competition level shows a decrease of 6.5%, and the scenario with highest competition level shows a decrease of 8.1%. The comparison between scenarios with zero aspen and high aspen competition levels for the maximum and minimum temperature values shows that the differential at minimum temperature is 7.3% while the difference at maximum mean annual temperature is 8.6%.

4. Discussion

Results from our analysis indicate that an estimate of competition, initial size of the tree, and mean annual temperature (MAT) modeled with a random effect for initial spruce volume can account for 88% of the variation in annual spruce volume increment at the individual sampled sites. Other studies have shown that the predictive ability of growth models improves when climate is taken into account (e.g., Snowdon, 2001). In light of the current warming in global temperatures (IPCC, 2007), there is also an increasing demand for projections of tree productivity based on future climate.

The inclusion of initial size has a strong influence on the amount of variation explained by the models. The "initial size advantage" hypothesis states that trees with a larger initial size are more competitive than their smaller cohorts and therefore growth analyses (e.g., response to competition) enhance their predictive ability by taking into account the initial size of the trees (e.g., Ford, 1984; Larocque, 1998). On an annual basis, climate and competition explain about 11% of the variation in spruce growth; and initial size, which is related to both tree leaf area and social position, explains a larger portion of the variation in annual growth rates. Nevertheless, climate and competition are both significant in the models and remain important factors in modeling spruce growth.

This study also indicated that as MAT increases the growth of pure white spruce stands will potentially increase up-to 16.9% compared to average growth, and in mixed stands with high levels of aspen competition the growth increase would be only 8.4%. Some studies investigating the effect of climate warming on boreal forests have indicated that the main reason for the general increase in productivity with raising mean temperatures is related to the increased length of the growing season (e.g., Eggers et al., 2008). This is reflected at least partially in the effect of mean annual temperature in our study. Johnston and Williamson, 2005 show increases in productivity of pure spruce stands ranging from 40% to 60% in the absence of drought, in the presence of drought, productivity increases were reduced to 20% or lower.

Table 3
Parameters estimates (reported with standard errors) and standard deviation of the random factor (σ_{b2}^2) for spruce volume increment modeled as a function of initial volume increment, aspen basal area per hectare, and climate (MAT), according to Eqs. (1)–(6), as described in Section 2.2. The number of observations is 20,014.

Eq.	β_1	β_2	β_3	β_4	Z_1 ALP	Z_2 DMI	Z_3 SBR	Z_4 SRD	Z_5 WFR	Z_6 WGP	σ_{b2}^2
1	2.1396 (0.0561)	0.818 (0.0041)	–	–	–	–	–	–	–	–	–
2	−687.25 (0.1028)	0.8030 (0.0045)	–	–	689.54 (0.088)	689.80 (0.088)	689.87 (0.093)	689.30 (0.087)	689.57 (0.087)	689.11 (0.091)	–
3	−675.66 (0.1022)	0.8013 (0.0045)	−0.01293 (0.0009)	–	677.94 (0.087)	678.19 (0.087)	678.31 (0.093)	677.72 (0.087)	677.94 (0.087)	677.53 (0.091)	–
4	−680.20 (0.1062)	0.8049 (0.0045)	−0.01271 (0.0010)	0.1171 (0.0125)	682.31 (0.093)	682.67 (0.094)	682.56 (0.097)	682.16 (0.093)	682.19 (0.094)	681.84 (0.096)	–
5	−663.78 (1.7035)	–	−0.01661 (0.0024)	−0.1432 (0.0213)	820.14 (3.694)	919.96 (2.724)	813.87 (4.380)	844.80 (3.929)	788.46 (3.263)	733.41 (3.225)	–
6	−781.43 (0.0405)	0.8411 (0.0048)	−0.00747 (0.0018)	0.1168 (0.0089)	783.02 (0.023)	783.37 (0.027)	783.60 (0.044)	782.77 (0.023)	782.90 (0.021)	782.71 (0.024)	0.003269 (0.0001)

When comparing the relative differences between scenarios with 'no competition' and 'high competition' levels for the minimum and maximum MAT values, the results show that the gap between the two scenarios increases more than proportionally as temperatures increase. This outcome suggests that the competitive effect of aspen increases as MAT increases, implying that under the current global warming trend, aspen canopy could have: (1) a moderating effect on white spruce growth (Filipescu and Comeau, 2011), limiting response of spruce to temperature increases (due to light limitations), and/or (2) it may be competing more aggressively for water and light compared to past climates. Another study based on future climate scenarios in northeastern British Columbia has indicated potential growth decreases for white spruce growing under high levels of competition as a result of increasing levels of drought stress and shading (Cortini et al., 2011).

Many forest managers recognize the need to include climate considerations in their strategic and operational plans in order to maximize forest sustainability and productivity (e.g., Ogden and Innes, 2007). While it is widely believed that growing mixed species forests is a potentially useful strategy for improving forest resilience in the face of climate change (Bolte et al., 2009), our results indicate that this may involve some cost in terms of reduced growth of white spruce. However, this cost must be balanced against the reduction in risk due to fire, insect and disease associated with having two species growing on site, reduced risk of frost and winter injury to young white spruce, increased total stand productivity and yield, enhancement in nutrient cycling, biodiversity, and other benefits (Comeau 1996; MacPherson et al. 2001; Ogden and Innes 2007; Pretzsch and Schütze 2009). Consequently, mixedwood management, on appropriate sites in the boreal forest, and particularly where it is being used to avoid reductions in biodiversity, remains as a viable and useful strategy. Spruce growth reductions, and perhaps even mortality, would be expected to be most severe under conditions where temperature has increased to the point where there is substantial risk to spruce survival even in the absence of aspen. Having aspen established on such high risk sites will help to ensure maintenance of a forest ecosystem that may be well adapted to the site.

The F-tests exploring the hierarchical structure of the data indicated that there are significant differences between the six agencies. This outcome suggests that competition and climate effects on spruce growth vary between locations as reported by Filipescu and Comeau (2007a). However, we expect that important factors such as frost injury and winter injury, soil temperature, and soil moisture will also have a strong influence on white spruce growth in boreal forests (e.g., Stathers and Spittlehouse, 1990; Krasowski et al., 1993) and which do not seem to be explained by the climate data used in this study.

Table 4
Goodness-of-fit for spruce volume increment modeled as a function of initial volume increment, aspen basal area per hectare, and climate (MAT), according to Eqs. (1)–(6), as described in Section 2.2. The number of observations is 20014.

Eq.	(pseudo)R^2	RMSE	AIC
(1)	0.683	111.8	245,610
(2)	0.695	109.8	244,894
(3)	0.697	109.4	244,729
(4)	0.699	109.1	244,643
(5)	0.113	187.2	266,239
(6)	0.885	67.3	234,303

$$(pseudo)R^2 = 1 - \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{\sum_{i=1}^{n}(y_i - \bar{y})^2}; \quad RMSE = \sqrt{\frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{n-k}}; \quad AIC = -2\ln(L) + 2k;$$

where y_i – observed values; $\hat{y}_i$ - predicted values; $\bar{y}$ average; n – sample size; k – number of mode parameters; ln (L) – logarithm of the likelihood function.
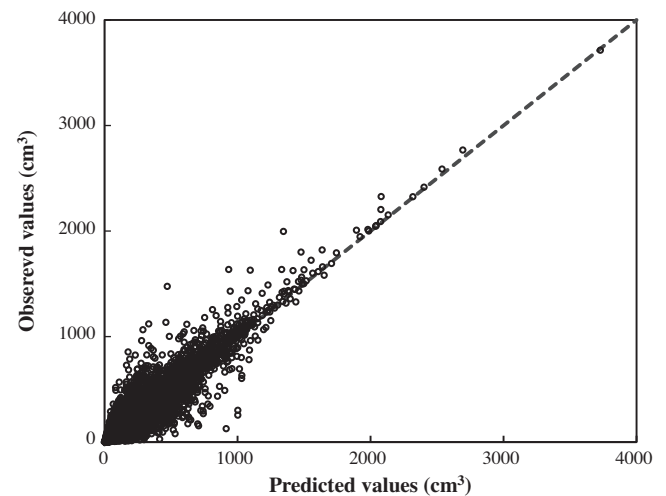

Fig. 2. Relationship between observed and predicted values of spruce volume increment (cm³). Predicted values are calculated from Eq. (6) and the parameter values are provided in Table 3. The line 1:1 is indicated.

Gray and Hamann (2011) indicated that climate change may result in substantial reduction in the range of white spruce in Alberta, suggesting that ecosystems in the Dry Mixedwood and Parkland natural subregions may no longer be suitable for white spruce. In contrast, the model developed in this study, and based partially on sites in the Dry Mixedwood natural subregions (i.e., ALP and DMI), indicated a potential growth increase as mean temperatures increase. These conflicting results highlight the need for collection of on-site climate data to account for influences of local factors
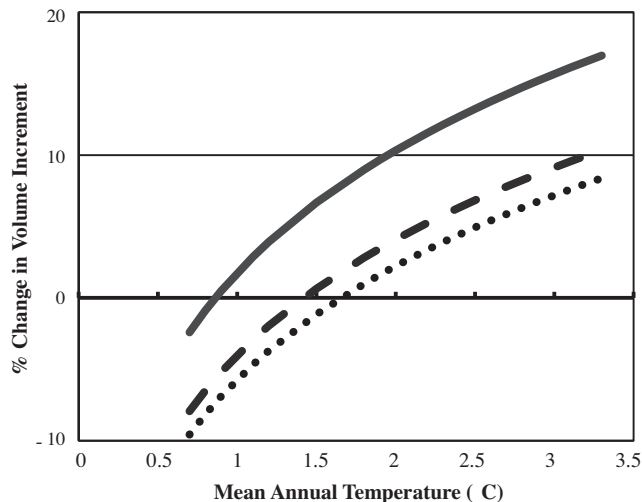
Fig. 3. Percent change in predicted volume increment compared to the average value (149.5 cm^3) calculated using Eq. (6) (Table 3). Average values for the indicator variables (783.1) and for the initial volume (206.7 cm^3) were used for this calculation. The solid curve represents the 'no aspen' scenario (AwBA = 0), the dashed curve represents the 'average competition' scenario (AwBA = 2.4 m^2 ha^{-1}), and the dotted curve represent the 'high competition' scenario (AwBA = 26.8 m^2 ha^{-1}).

such as aspect, topography, topographic position, adjacent stands, and soil properties on climatic factors controlling growth. The differences between these two models may also be attributed to the fact that the sites used in our study may have higher available soil moisture than other sites in this subregion.

Each agency involved in this study used local seed sources to grow the white spruce seedlings that were planted. This resulted in genetic differences across the WESBOGY long term study and an inability to account for provenance effects in these models. Studies have shown a relationship between the temperature sum needed for certain phenological events and the total length of the growing season of the original growing site of different tree provenances (e.g., Sarvas, 1967). Moreover, spring temperatures, which are related to the risk of spring frost damage, have been linked to the differences in the timing of bud burst for trees from different areas (e.g., Burley, 1966). These factors should be explored further using approaches such as those outlined by Wang et al. (2010) in order to account for the genetic (provenance) effect on white spruce growth.

Estimates of competition and initial size of the tree can account for significant portions of the variation in annual spruce volume growth, and model fit improved when mean annual temperature was included in the model. This study also indicated that as mean annual temperature increases the growth of pure white spruce stands will potentially increase by twice that observed in mixed stands with high levels of aspen competition. The comparison between scenarios with 'no competition' and 'high competition' for extreme values of mean annual temperature indicated that the net competitive effect of aspen can increase more than proportionally suggesting that aspen is suppressing either temperature increases or the temperature response of white spruce or it is competing more aggressively for water and light under warmer temperatures. This study also showed that competition and climate effects on white spruce growth vary between locations, indicating a strong influence of local factors such as micro-climate, topography and soil properties. The influences of these factors should be explored further and used to improve the predictive ability of growth models through incorporating climate.

Our study has not addressed potential impacts of insect, disease and extreme climatic events (e.g., ice storms, heavy wet snow) on white spruce which may also be related to climate change (e.g., Gillett et al., 2004; Woods et al., 2005; van Mantgem et al., 2009). These, and other factors need to be considered for a complete assessment of potential responses.

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