

Article

The Influence of Stocking and Stand Composition on Productivity of Boreal Trembling Aspen-White Spruce Stands

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Abstract: We analyzed productivity, in terms of periodic annual increment (PAI) in volume, of pure and mixed unmanaged naturally regenerated boreal stands mainly comprised of *Populus tremuloides* Michx. (trembling aspen) and *Picea glauca* (Moench) Voss (white spruce) ranging from 25–260 years old, in Alberta, Canada. Measures of density, site occupancy (Reineke’s stand density index-SDI), height, and site quality were evaluated in non-linear regression models aiming to explain the variation in PAI for the separate component species and for the entire stand. Analyses also included examination of the influence of stand composition. Results indicated a positive effect of both density of deciduous trees and of the percentage of deciduous tree stand basal area on trembling aspen volume PAI. White spruce PAI was positively influenced by spruce and aspen basal area, although effects of aspen were small. Height of both aspen and spruce were the most consistent independent variables in the models tested. Maximum PAI was achieved in mixed stands when site occupancy of both species was at its maximum, indicating the ecological combining ability of these two species. Variation in maximum stocking densities (*i.e.*, stockability) has a strong influence on increment in these forests and is a major factor leading to increased productivity of mixed compared to pure stands.

Keywords: boreal mixedwoods; ecological combining ability; growth rate; periodic annual increment

1. Introduction

Stand density has important effects on growth rates. Understocked stands experience reduced growth rates essentially because trees are not fully occupying the site and hence are unable to fully utilize the site’s resources. In contrast, well stocked stands will achieve their maximum growth potential. As density increases above that required to completely utilize a site, growth is allocated to more and more stems, and results in smaller individual trees. At maximum attainable densities (*i.e.*, maximum stockability), substantial tree mortality induced by competition is experienced. This imposes a constraint beyond which stand growth may not occur [1]. At approximately 60% of maximum density both gross and net stand growth are at their maximum [2], and beyond this point gross growth remains relatively constant while net growth will show a fairly steady decline; a more abrupt decline in net growth will be recorded with 80% of relative density and above [1]. Stand density representing full stocking, in terms of number of trees per unit area, will vary with tree size (particularly crown size), and, consequently, also with age.

As stands increase in age, both net and gross growth will increase to peak values and then decline [3], with net growth falling below gross growth at intermediate densities as tree mortality begins to occur and accumulates [4]. Changes in stand density as a result of tree mortality will also affect individual tree sizes (*i.e.*, stand structure) and growth rate, as well as stand growth, consequently affecting stand yield. With reductions in stand density, temporary decreases in gross total growth at the stand level may occur, and increases in resource availability to the remaining trees are expected, allowing them to increase their growth and accelerate site occupancy, potentially compensating for the density reduction [4,5].

Stand density is widely used in the analysis of forest growth and yield [3,5] in terms of explaining the degree to which the growing space available for tree growth is utilized [3,6]. Density and indicators of relative density, such as Reineke's Stand Density Index (SDI) [7], provide quantitative descriptions of stocking or the degree of crowding expressed by growing space ratios [6]. In mixed species stands and other complex stand types, estimation of site occupancy should consider both total growing space occupancy and how this is allocated among stand components (species, cohorts or canopy strata) [8].

A reliable representation of the relationship between species growth rates and characteristics of the growing stock can be obtained by combining effects of relative density, height, and indicators of site productivity (*i.e.*, site index or a surrogate) [9,10]. Indeed, studies have suggested that Reineke's SDI can be useful as a measure of site utilization and competition between component species in mixed species stands, since it is related to light capture [11], and is independent of species composition [12]. However, SDI has not been widely tested in boreal mixed species stands [13], and hence its potential utility has yet to be determined.

In boreal forests, trembling aspen (*Populus tremuloides* Michx.) is a shade intolerant pioneer species that rapidly occupies sites after major disturbances (*i.e.*, fire, clearcutting), owing to its profuse regeneration from root suckering and fast early height growth [14,15]; meanwhile, white spruce (*Picea glauca* (Moench) Voss) is a shade tolerant species that can survive and grow under an aspen overstory canopy. These mixtures are commonly referred to as boreal mixedwoods and are prominent in boreal forests of western Canada. Competitive and facilitative interactions play important roles in the growth and dynamics of mixtures of these two species [16–19].

Mixed stands are widely thought to be more productive than monocultures when species that differ in key characteristics such as shade tolerance, height growth rate, crown structure, foliar phenology, root depth and phenology are combined resulting in increased capture and/or more efficient use of site resources. This results in greater total stand biomass and higher growth rates than would occur in monocultures of the component species [16,20,21]. Two ecological concepts of species interactions that may help to explain higher stand productivity of mixtures are competitive reduction and facilitative production [16]. Reduced intra-specific competition is suggested when competitive reduction takes place [20–22]. Facilitation could include the positive influence of deciduous species on rates of nutrient cycling [20,23]. Mixtures of species, which have reduced competition or improved growth in one or both species, are considered to have “ecological combining ability” [20], and they can be more productive [16]. Spatial and temporal variability of nutrients and water availability, light absorption/utilization, and interactions among these resources, as well as stand structure (mostly in terms of stand density) could also lead to complementarity or competitive effects in mixtures [24].

It is suggested that some of the mechanisms that could lead to increased productivity of boreal mixedwoods include differences in shade tolerance, physical canopy separation, differences in phenology, changes in availability and utilization of soil and other resources [16,25]. Mixedwoods may also be able to support higher maximum densities (*i.e.*, have higher stockability), owing to the existence of a stratified canopy which is expected to improve light capture and utilization over what is found in mono specific stands [20]. Productivity of mixtures of trembling aspen and white spruce might be higher, in part because aspen will hold nutrients within the stand and may improve nutrient cycling owing to its litter properties [25,26]. Other beneficial effects of aspen on white spruce include

reduction of damage by wind and frost, as well as reduction of competition from grasses and other vegetation [26–31]. Mixedwoods may also be economically more valuable than monocultures, by providing products from both aspen and spruce simultaneously or consecutively, satisfying more diverse requirements, reducing risk (temporal shifts in the end-product demand function), and providing a greater variety of end-products [17]. However, despite the numerous advantages of trembling aspen-white spruce mixtures compared to pure stands of the same species, mixedwood management is a recent silvicultural undertaking within the western Canadian boreal forest, and further study is needed to support its implementation in a context of more demanding markets and societal needs.

In this study, we examine the individual and combined productivity (periodic annual increment in volume per unit area) of white spruce (Sw) and trembling aspen (Aw) when growing in pure and mixed stands, in mid-rotation and mature boreal unmanaged forests in Alberta, Canada. We concentrate our analyses on stands comprised primarily of trembling aspen and white spruce in different proportions and developmental stages. Based upon the principle that growth of forest stands is primarily a function of site occupancy, site quality, and tree size [32], the objectives of this research were: (1) to evaluate the usefulness of selected stand attributes such as tree density, total stand basal area, basal area of deciduous species (mainly trembling aspen), and basal area of white spruce, in explaining white spruce, trembling aspen, and total stand periodic annual increment in volume (PAIV); (2) to examine the effects of stand composition (percent of basal area in deciduous species and percent of basal area of white spruce); and (3) to examine the influence of species site occupancy (represented by -SDI by component species and for the entire stand) [7], on PAIV. We also evaluate the hypothesis that the presence of a coniferous and deciduous component positively influences total stand growth rates, which would be consistent with observations that the presence of understory spruce does not negatively influence the productivity of trembling aspen [25].

2. Materials and Methods

2.1. Study Sites and Data

This research was conducted using data from long-term permanent sample plots (PSP), established in pure aspen, pure white spruce, and mixed stands of both species in the Boreal Forest Natural Region of Alberta, Canada. This region varies in altitude from 150 m in the Northern Mixedwood Natural Subregion to above 1100 m in the Upper Boreal Highlands Natural Subregion, and is characterized by the presence of plains, high elevation plateaus, and dune fields [33]. The region is also characterized by long, cold, and dry winters, short and relatively moist summers, with 50–100 frost-free days, average annual precipitation lower than 500 mm, and a mean average temperature of approximately $-0.2\text{ }^{\circ}\text{C}$ [33,34]. PSPs located in the Central, the Dry, and the Northern Mixedwood ecological sub-regions were included in this study [33,34]. Although varying in size, the majority of these PSPs are 0.10 ha in size, with all trees larger than 2.5 cm in diameter at breast height (1.3 m) tagged and measured at periodic time intervals ranging from three to ten years in length (average of eight years). Data were compiled to calculate several stand characteristics, which are summarized in Table 1. In order for a plot to be included for analysis, the following criteria were applied:

- (1) The plot was primarily comprised of trembling aspen and/or white spruce.
- (2) No more than 10% of the total stand basal area was comprised of species other than trembling aspen and/or white spruce.
- (3) If other deciduous species were present in the plot, they were grouped with aspen, as long as they accounted for less than 10% of the total basal area.

Individual tree height was not directly measured in the field for all trees but for a sub-sample inside each plot. Consequently, height was estimated for all remaining trees (*i.e.*, those for which

height was not measured) using equations previously generated for Alberta’s tree species [35]. We also calculated average tree height by species for each plot included in the analysis. Site index (top height at 50 years of breast height age) was also available for each species in each plot. An average combined site index for white spruce and aspen was calculated and tested in the models developed for mixed plots, whereas the dominant species site index was used in pure species plots. Subjective assessments of site quality were also used in model development and they included soil moisture (M_{or}) and soil nutrient regimes (N_{ur}). Both are indicators of site quality, representing the availability of moisture and the amount of nutrients essential for plant growth on a site [33]. There were five levels for M_{or} and four levels for N_{ur} in our dataset. A description of their determination and characteristics are provided in [33]. A total of 163 PSPs were available for this study distributed as follows: 24 pure spruce plots, 40 pure aspen, and 99 mixed plots.

Table 1. Summary of the mensurational characteristics of the selected boreal pure and mixed stands used in this study.

Variable	Mean (SD)			Maximum			Minimum		
	Aw	Sw	Mix	Aw	Sw	Mix	Aw	Sw	Mix
Deciduous density (trees·ha ⁻¹) = TPH _{dec}	932 (782)	70 (90)	380 (409)	5350	326	2863	222	0	25
White spruce density (trees·ha ⁻¹) = TPH _{sw}	28 (33)	1190 (850)	737 (782)	130	4593	4890	0	361	55
Total density (trees·ha ⁻¹) = TPH _{tot}	962 (781)	1270 (825)	1125 (989)	5350	4617	7038	237	381	200
Total stand age (years)	90 (23)	147 (41)	120 (25.1)	132	264	195	40	78	46
Spruce periodic annual increment in volume (m ³ ·ha ⁻¹ ·year ⁻¹) = PAIV _{sw}	0.179 (0.28)	6.61 (2.11)	4.11 (2.3)	0.98	10.3	12.7	0.01	2.3	0.001
Aspen periodic annual increment in volume (m ³ ·ha ⁻¹ ·year ⁻¹) = PAIV _{aw}	6.67 (2.5)	0.17 (0.18)	2.86 (2.8)	12.8	0.66	21.7	3.24	-0.15	-0.21
Total stand periodic annual increment in volume (m ³ ·ha ⁻¹ ·year ⁻¹) = PAIV _{tot}	6.85 (2.57)	6.62 (2.11)	7.03 (3.02)	13.41	10.7	24.6	3.28	2.68	1.58
Percentage of basal area of white spruce = PBA _{sw}	1.90 (2.6)	95.7 (3.76)	55.6 (22.3)	9.5	100	89	0.1	89.5	11.1
Percentage of basal area of deciduous = PBA _{dec}	97.8 (2.6)	3.89 (3.69)	43.3 (22.2)	100	10.8	89	90.5	0.1	11
Deciduous basal area per hectare (m ² ·ha ⁻¹) = BAH _{dec}	37.4 (8.8)	1.92 (1.85)	17.9 (9.4)	57.9	6.32	50.3	12.6	0.1	2.34
White spruce basal area per hectare (m ² ·ha ⁻¹) = BAH _{sw}	0.74 (0.89)	50.16 (10.91)	26.7 (14.1)	3.72	72.3	58	0.01	34.3	4.7
Total stand basal area per hectare (m ² ·ha ⁻¹) = BAH _{tot}	38.22 (8.82)	52.35 (10.36)	45 (10.8)	57.9	74.6	73.9	12.8	38.7	21.3
Average white spruce height (m) = HT _{sw}	7.7 (7.5)	20.1 (3.17)	19 (4.3)	28.6	25.3	27	0.1	11.4	8
Average trembling aspen height (m) = HT _{aw}	22.3 (3.8)	5.93 (10.3)	21 (7.1)	30.5	26	32	10.9	0.5	0.5
Dynamic SDI deciduous = SDI _{dyd}	734 (174)	34 (32)	351 (184)	1137	114	990	254	0	46
Dynamic SDI white spruce = SDI _{dysw}	14 (19)	909 (190)	487 (246)	66	1340	1029	0	604	55
Total stand dynamic SDI = SDI _{dysw}	690 (184)	906 (222)	650 (206)	1090	1305	1130	320	580	214
Site index (m) = SI	20 (2.0)	16 (3.0)	18 (2.3)	25	20	23	16	8	9
Nutrient regime = N _{ur}	3	3	3	5	4	5	2	3	2
Moisture regime = M _{or}	5	5	5	8	7	8	4	4	4

Columns subheadings: “Aw” refers to trembling aspen dominated plots; “Sw” refers to white spruce dominated plots; “mixed” refers to mixed plots; N (number of plots): Aw = 40, Sw = 24, Mixed = 99; Total = 163; SD = standard deviation.

Individual tree gross stem volume (m^3) was estimated using species-specific tree volume equations developed for Alberta's tree species [36]. Individual periodic annual increment in volume for spruce (PAIV_{sw}), for trembling aspen (PAIV_{aw}), and for all species combined in the plot (PAIV_{tot}), expressed as $\text{m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$, was calculated by obtaining the difference in net volume values (including ingrowth but excluding mortality) estimated at the beginning and at the end of the measurement period divided by years between measurements. Total periodic annual increment by species and for the plot, as previously indicated, was then calculated by summing individual PAIV for all trees in the plot, and scaled up to a per hectare basis. We used only the most recent growth interval in the statistical analyses in order to avoid problems with serial autocorrelation that would result from using repeated measures, to avoid effects of major differences in climate that occur over time, and since recent measurements provide the largest number of samples.

2.2. Data Analysis

We based our analysis upon the principle that growth is primarily influenced by a combination of site quality, site occupancy, stand composition, and age [9,10,32]. Under this premise, and due to the fact that a reliable estimation of age of the stands under examination was not available (*i.e.*, it is only an approximate value given in the original datasets, and not a direct measurement based on any sampling method), periodic annual increment in volume of white spruce, trembling aspen, and the total stand was regressed against a number of stand attributes that represent density, site occupancy, site quality, and a surrogate of stand age or developmental stage (average height by species). Site occupancy can be characterized by a combination of stand density and tree size [10]. We used number of trees per hectare, basal area per hectare, and a modified version of Reineke's SDI [7] as measures of stand density and site occupancy.

Reineke's SDI was calculated separately for each species, based on maximum size-density relationships previously obtained for these forests (and based on analysis of dynamic thinning lines) [37]. The traditional calculation of Reineke's SDI includes the use of quadratic mean diameter of the stand to compute a single SDI value. In this case, a modification in the calculation of SDI was performed and the summation method [38,39]) was used, as follows:

$$\text{SDI}_{\text{sum}} = \sum [\text{TPH}_i \times (\text{D}_i/25)^r] \quad (1)$$

where D_i is the diameter at breast height of the i_{th} tree in the plot, TPH_i is the number of trees per hectare⁻¹ characterized by the i_{th} tree, and r is the logarithmic slope of the maximum size-density relationship ($r = -1.74$).

In this paper, SDI_{dyt} , SDI_{dysw} , and SDI_{dyd} refer to total stand dynamic SDI, white spruce dynamic SDI, and deciduous dynamic SDI. Although SDI_{dyd} is mainly composed by trembling aspen, other deciduous species were also included, namely balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh.), but these accounted for less than 5% of the total stand basal area in the stands in which they occur. Dynamic SDI (total stand dynamic SDI) in the sampled plots ranged from 214–1305 (Table 1).

The general model for the analysis of the relationship between white spruce, trembling aspen, and total stand volume PAI (*i.e.*, growth rates), with selected stand attributes (*i.e.*, growing stock characteristics) including stand composition, was specified as follows:

$$\text{PAIV} = f(\text{Density, HT, site quality, PBA}_{\text{dec}}, \text{PBA}_{\text{sw}}) \quad (2)$$

where: PAIV is periodic annual increment in volume for spruce, aspen, or total stand ($\text{m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$) calculated using the two most recent measurements for each plot, as previously indicated; density is represented either by number of trees per hectare, basal area, or SDI. HT is the average white spruce (HT_{sw}) or trembling aspen (HT_{aw}) height in meters; site quality is nutrient regime (N_{ur}), moisture regime (M_{or}), or average site index (SI_{p}); PBA_{dec} is the percentage of basal area in deciduous species; and PBA_{sw} the percentage of basal area for white spruce. All of the independent

variables that were used in model development were obtained from the stand conditions at the beginning of the last remeasurement (*i.e.*, they are initial values).

We used three density measures (trees per hectare, basal area, and SDI), which were evaluated either as a total value per stand, or separately for deciduous and for spruce components. Hence, for basal area ($\text{m}^2 \cdot \text{ha}^{-1}$), BAH_{dec} is basal area per hectare for deciduous, BAH_{sw} is basal area per hectare for white spruce, and BAH_{tot} is total stand basal area. Similarly, for density ($\text{trees} \cdot \text{ha}^{-1}$), TPH_{tot} , TPH_{aw} , and TPH_{sw} are stand total, trembling aspen, and white spruce densities; SDI remains as explained in the previous paragraph.

Statistical analyses were completed using non-linear regression with PROC NLIN of SAS[®] version 9.2 for windows (SAS Institute, Cary, NC, USA) [40]. Model goodness-of-fit was assessed using adjusted R^2 values and residual sum of squares. We also tested the parameters estimated for their significance. However, since the standard error of the estimate, the t-value, and its significance levels are only approximate for non-linear models [40,41], we also used the standardized Hougaard's measure of skewness [41] to assess the "close-to-linear" behavior of each parameter, and decide whether or not to include a parameter in the final models. The "close-to-linear" behavior of a parameter in a non-linear regression model essentially indicates that the parameter has properties similar to those of a linear regression model, that is, that they are unbiased, normally distributed, and have minimum variance [41]. Skewness below 0.1 in absolute value indicates close-to-linear behavior, values between 0.1 and 0.5 indicate a reasonably close-to-linear behavior, and values above 1.5 indicate that the close-to-linear behavior is questionable. If a parameter exhibited skewness below 1.5, then its standard errors and confidence intervals could be safely used for inferences, and they were included in the final models. Independent variables that had parameter values with skewness above these levels were excluded from the model under evaluation, although they were still considered for evaluation in other models. The standardized Hougaard's measure of skewness was estimated with the option HOUGAARD in PROC NLIN of SAS[®]. We also graphically examined Studentized residuals against predicted PAI in volume for each of the models tested. When the distribution of residuals suggested non-homogenous variances, we tested transformed variables in the models. However, transformations provided no improvement in the distribution of residuals, and we present only results for untransformed variables.

Due to the characteristics of the variables that were used in model testing, we were concerned with potential collinearity that could be problematic and bias the results. In an attempt to reduce the risk of collinearity, we avoided the inclusion of highly correlated variables in the same model ($r > 0.5$, $p < 0.01$). The variance inflation factor (VIF) was also calculated for all the variables included in the same model. Values of $\text{VIF} > 10.0$ were considered as an indicator of considerable levels of collinearity, and the less significant variable was removed from the model.

3. Results

3.1. Trembling Aspen PAI in Volume

Trembling aspen periodic annual increment ranges from <0.1 – $12.8 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$, with an average of $3.3 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$. Combinations of selected independent variables explained up to 80% of the variation in trembling aspen periodic annual increment in volume. Fit statistics for the best and for the second best models are presented in Table 2. Average heights of deciduous and spruce were among the most consistently significant variables in the models evaluated. While the final set of selected models shows similar goodness-of-fit and performance metrics, the most parsimonious model was obtained when the number of trees of deciduous species was utilized in combination with the average height of both spruce and aspen. This model explains 80% of the variation in aspen PAI and had the lowest residual sum of squares ($\text{SS}_{\text{res}} = 261.7$) among the competing models.

Similar adjusted R^2 values were obtained when deciduous dynamic SDI and deciduous basal area per hectare were used in combination with average height of both deciduous and white spruce

(Adjusted $R^2 = 0.76$ in both cases). Only the model that includes effects of deciduous dynamic SDI is presented. Spruce Dynamic SDI (SDI_{dysw}) and percentage of deciduous species were also significant, but the incorporation of these variables did not contribute significantly to improvements in model performance.

Table 2. Fit statistics and parameter estimates for the best and second best models for trembling aspen, white spruce, and total stand periodic annual increment in volume ($PAIV_{aw}$, $PAIV_{sw}$, and $PAIV_{tot}$, respectively).

Model	SS _{res}	Parameter					Adj R^2	
		β_0	β_1	β_2	β_3	β_4		β_5
$PAIV_{aw} = \beta_0 \times TPH_{dec}^{\beta_1} \times HT_{sw}^{\beta_2} \times HT_{aw}^{\beta_3}$	261.7	4.2E-7 (5.5E-7) {3.0}	1.02 (0.07) {0.08}	0.20 (0.11) {0.07}	2.96 (0.26) {0.05}			0.80
$PAIV_{aw} = \beta_0 \times SDI_{dyd}^{\beta_1} \times SDI_{dysw}^{\beta_2} \times HT_{sw}^{\beta_3} \times HT_{aw}^{\beta_4}$	296.1	0.0002 (0.0002) {3.5}	1.24 (0.12) {0.11}	0.03 (0.03) {0.05}	0.17 (0.14) {-0.06}	0.65 (0.27) {0.08}		0.75
$PAIV_{sw} = \beta_0 \times SDI_{dyd}^{\beta_1} \times SDI_{dysw}^{\beta_2} \times HT_{sw}^{\beta_3} \times HT_{aw}^{\beta_4}$	187.7	0.001 (0.001) {2.1}	0.99 (0.09) {0.11}	0.06 (0.04) {0.15}	0.32 (0.18) {-0.05}	0.15 (0.23) {0.16}		0.84
$PAIV_{sw} = \beta_0 \times BAH_{dec}^{\beta_1} \times BAH_{sw}^{\beta_2} \times HT_{sw}^{\beta_3} \times HT_{aw}^{\beta_4}$	194.6	0.02 (0.17) {2.0}	0.06 (0.04) {0.17}	0.94 (0.09) {0.14}	0.61 (0.18) {-0.03}	0.04 ** (0.21) {0.15}		0.83
$PAIV_{tot} = \beta_0 \times SDI_{dysw}^{\beta_1} \times SDI_{dyd}^{\beta_2} \times HT_{sw}^{\beta_3} \times HT_{aw}^{\beta_4} \times PBA_{dec}^{\beta_5}$	540.0	0.222 (0.16) {1.08}	-0.03 (0.03) {0.07}	0.99 (0.17) {0.06}	0.11 (0.14) {-0.05}	0.31 (0.21) {0.11}	-0.93 (0.17) {-0.06}	0.31
$PAIV_{tot} = \beta_0 \times BAH_{dec}^{\beta_1} \times BAH_{sw}^{\beta_2} \times HT_{sw}^{\beta_3} \times HT_{aw}^{\beta_4} \times PBA_{dec}^{\beta_5}$	545.7	4.0 (2.5) {1.4}	0.95 (0.16) {0.06}	-0.09 (0.03) {0.06}	0.04 ** (0.14) {-0.04}	0.32 (0.21) {0.11}	-0.88 (0.17) {-0.07}	0.30

$n = 163$; $PAIV_{aw}$, $PAIV_{sw}$, and $PAIV_{tot}$ = trembling aspen, white spruce, and total stand periodic annual increment in volume ($m^3 \cdot ha^{-1} \cdot year^{-1}$); TPH_{dec} = deciduous density ($trees \cdot ha^{-1}$); HT_{sw} and HT_{aw} = Average white spruce and average aspen height height (m); SDI_{dyd} = dynamic SDI for deciduous species; SDI_{dysw} = dynamic SDI for white spruce; BAH_{dec} = deciduous basal area ($m^2 \cdot ha^{-1}$); BAH_{sw} = spruce basal area ($m^2 \cdot ha^{-1}$); PBA_{dec} = percentage of basal area in deciduous; SS_{res} = Residual sum of squares; β_0 – β_5 = parameters estimated; All parameters shown are significant ($\alpha < 0.10$), except **; Adj R^2 = adjusted R squared; standard errors are shown in parentheses; Hougaard’s Skewness estimates are shown in braces.

Although other models with different combinations of independent variables were also obtained, selection of the best model for explaining aspen PAI was based on the significance of the model, residual sum of squares, adjusted R^2 values, significance of model parameters and their skewness, and the distribution of residuals. Figure 1 shows the distribution of studentized residuals for the best model. While one point had a studentized residual of approximately -5 , we found that removing this one point had no effect on the model, and consequently decided to retain it in the model. Figure 2 shows the performance of aspen volume increment as a function of dynamic deciduous SDI and dynamic spruce SDI; this model is presented since it is useful in understanding the effects of site occupancy on aspen volume PAI, and it is consistent with models obtained for white spruce and for the entire stand.

3.2. White Spruce PAI in Volume

White spruce $PAIV$ ranges up to $12.7 m^3 \cdot ha^{-1} \cdot year^{-1}$ with an average of $3.5 m^3 \cdot ha^{-1} \cdot year^{-1}$. SDI and basal area of the component species were also among the most significant and consistent independent variables in the models evaluated (Table 2). The best model explained 84% of the total variation in spruce volume increment (Table 2), while alternative models (only the second best model is shown) explained between 80%–83% of the total variation in $PAIV_{sw}$.

The percentage of basal area in deciduous (PBA_{dec}) also had a significant effect on white spruce volume increment. However, its contribution to model performance was rather small, and it demonstrated conflicting behavior with other independent variables. Basal area and SDI performed similarly in the models evaluated (Table 2). However, the model that includes SDI and average height

for the component species shows the smallest residual sum of squares. This model explains 84% of the total variation in spruce volume increment. Fit statistics for the best and for the second best model for spruce are presented in Table 2. Figure 3 shows the distribution of studentized residuals for the best model. The performance of spruce volume PAI as a function of deciduous dynamic and spruce dynamic SDI is shown in Figure 4.

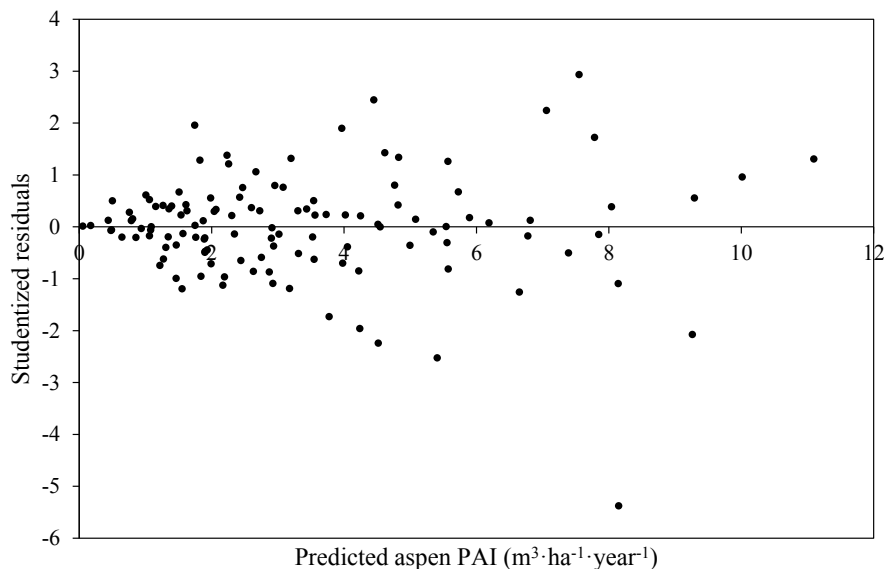


Figure 1. Residuals for the best model for trembling aspen PAI: $PAIV_{aw} = \beta_0 \times TPH_{dec}^{\beta_1} \times HT_{sw}^{\beta_2} \times HT_{aw}^{\beta_3}$.

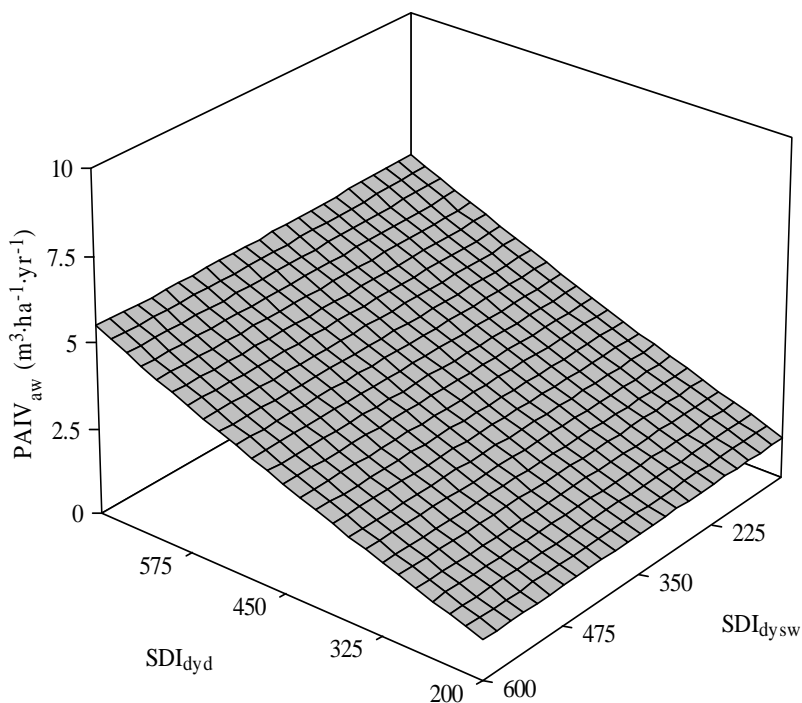


Figure 2. Trembling aspen volume PAIV as a function of deciduous (SDI_{dyd}) and spruce dynamic SDI (SDI_{dysw}) (HT_{sw} and HT_{aw} held constant). Model: $PAIV_{aw} = 0.0002 \times SDI_{dyd}^{1.24} \times SDI_{dysw}^{0.03} \times HT_{sw}^{0.17} \times HT_{aw}^{0.65}$.

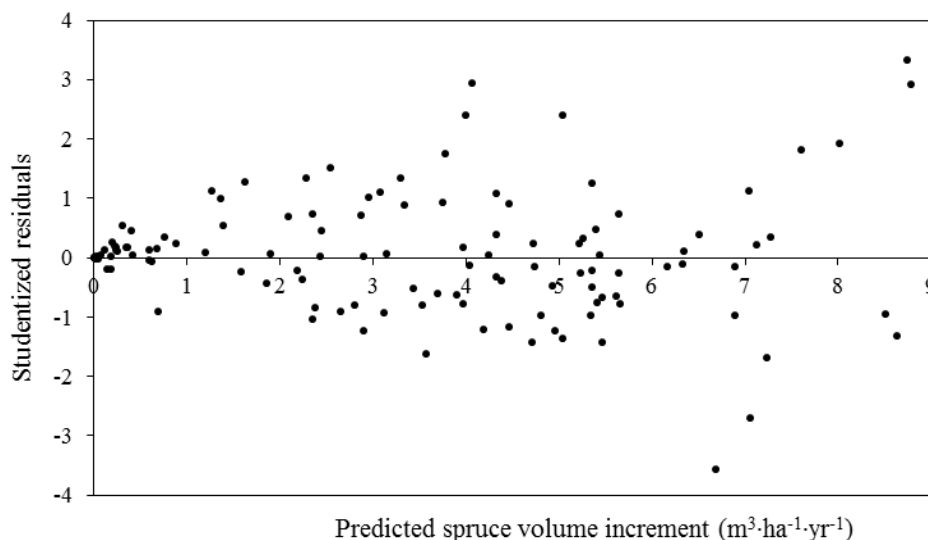


Figure 3. Residuals for the best model of spruce volume periodic annual increment. $PAIV_{sw} = \beta_0 \times SDI_{dysw}^{\beta_1} \times SDI_{dyd}^{\beta_2} \times HT_{sw}^{\beta_3} \times HT_{aw}^{\beta_4}$.

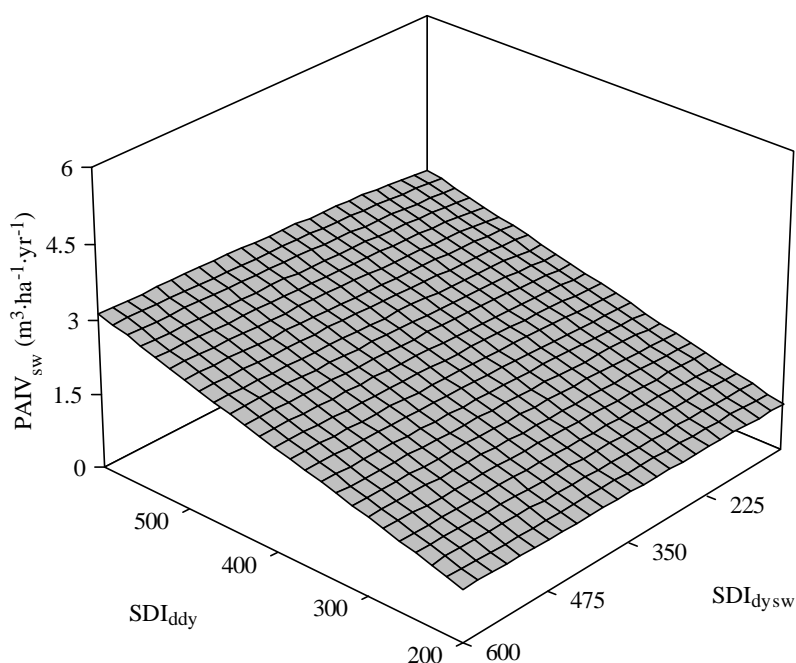


Figure 4. White spruce PAIV as a function of spruce SDI (SDI_{dysw}) and deciduous SDI (SDI_{dyd}); (HT_{sw} and HT_{aw} held constant). Model: $PAIV_{sw} = 0.001 \times SDI_{dyd}^{0.99} \times SDI_{dysw}^{0.06} \times HT_{sw}^{0.32} \times HT_{aw}^{0.15}$.

3.3. Total Stand PAI in Volume

Total stand periodic annual increment in volume ranges from 0.01–14.7 $m^3 \cdot ha^{-1} \cdot year^{-1}$, with an average of 6.8 $m^3 \cdot ha^{-1} \cdot year^{-1}$. Since this data set characterizes a wide range of species composition and proportions of both white spruce and trembling aspen, the effects of stand composition on total stand volume increment (*i.e.*, growth rates) was evaluated. Different sets of independent variables were able to explain only between 30% and 31% of the total variation in stand volume PAI. However, dynamic SDI for each species, basal area per hectare for each species, average height of component species, and percentage of basal area of deciduous were among variables that were consistently significant in the models evaluated (Table 2).

Better model performance is achieved when the effects of SDI of deciduous and spruce are used in the same model, separately but in combination with the average height of both components and the percentage of basal area of deciduous, explaining up to 31% of the variation in total PAI. A marginal decrease in residual sums of squares of the model is achieved when SI_p is included in the model, but there is no improvement in adjusted R^2 ($R^2_{adj} = 0.30$, $SS_{res} = 535.9$, results not shown).

Other combinations of independent variables (not shown) were able to explain only between 10% and 20% of the total variation in PAIV. Including these other variables did not improve adjusted R^2 values of the models. Fit statistics for the best and for the second best model for explaining total stand PAIV are presented in Table 2. The distribution of studentized residuals for the best model is shown in Figure 5. Figure 6 shows the performance of the best model for explaining total PAIV as a function of deciduous dynamic and spruce dynamic SDI.

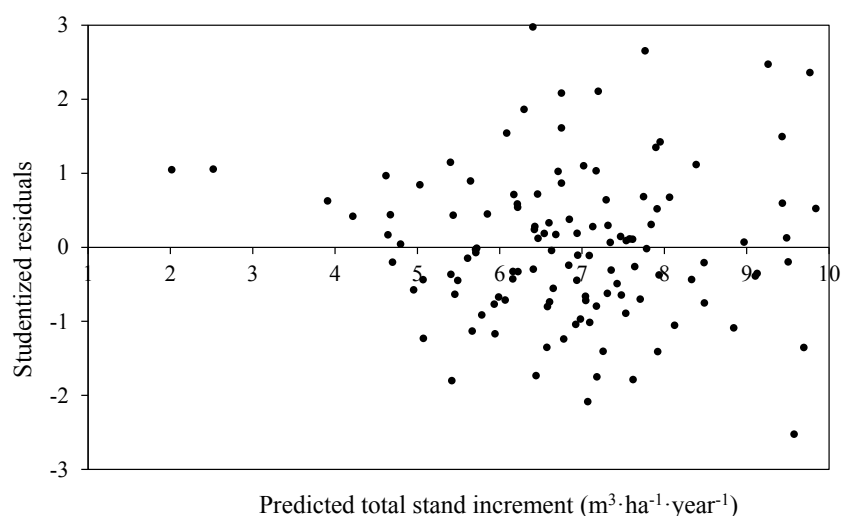


Figure 5. Residuals for the best model for total periodic annual increment in volume ($PAIV_{tot}$)
 $PAIV_{tot} = \beta_0 \times SDI_{dysw}^{\beta_1} \times SDI_{dyd}^{\beta_2} \times HT_{sw}^{\beta_3} \times HT_{aw}^{\beta_4} \times PBA_{dec}^{\beta_5}$.

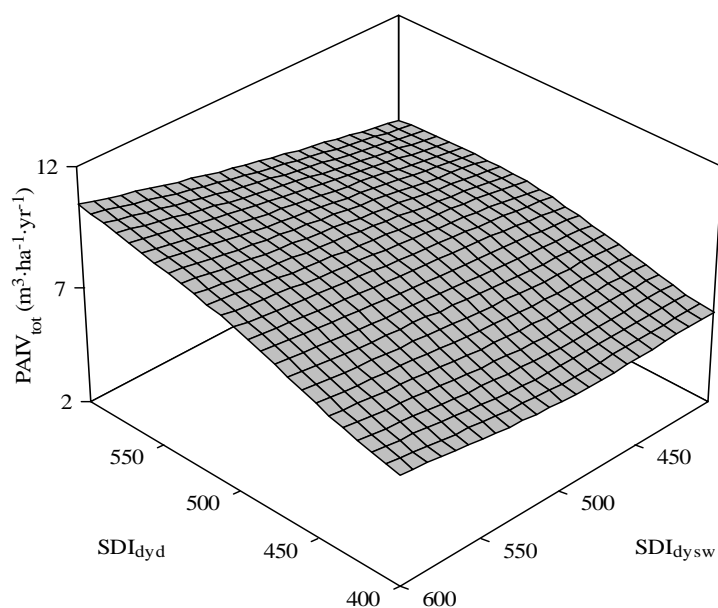


Figure 6. Total volume PAI as a function of deciduous (SDI_{dyd}) and spruce (SDI_{dysw}) dynamic SDI; (HT_{sw} and HT_{aw} held constant and PBA_{dec} varying with changes in SDI_{dyd} . Model: $PAIV_{tot} = 0.222 \times SDI_{dysw}^{-0.03} \times SDI_{dyd}^{0.99} \times HT_{sw}^{0.11} \times HT_{aw}^{0.31} \times PBA_{dec}^{-0.93}$.

4. Discussion

Average periodic annual increment for trembling aspen in boreal mixedwoods, over the 48–105 years of age at breast height, ranges from $9.2 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ to roughly $11.5 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ [25]; for white spruce growing in mixed stands and with ages ranging from 4 to 64 years at breast height, reported average biomass periodic annual increment values are around $1.5 \text{ Mg} \cdot \text{ha}^{-1}$ [25] (approximately $3.3 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$). Other reports for natural mixed unmanaged stands indicate stem volume periodic increment values of about $2.5 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ for white spruce, and an average of $4.8 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ for white spruce growing in stands that have been previously released from deciduous competition, ranging from 15 to 60 years of age [42]. The volume increment values that we obtained for trembling aspen, white spruce, and for the whole stand appear to be largely within the range of variation for volume/biomass increment previously reported for this type of forests.

None of the indicators of site productivity that were available for this study (*i.e.*, average site index, moisture regime, and nutrient regime) showed a significant effect on either white spruce or trembling aspen volume increment in the models evaluated. In the case of total stand volume PAI, average site index showed significance in one of the models, although its effects were small and did not contribute to better model performance. The lack of site index effects is likely due to the fact that most plots included in this analysis come from circum-mesic sites with Clay-Loam and Silty Clay Loam soils which are moderately-well to imperfectly drained and therefore encompass only a narrow range of site conditions. Nonetheless, we believe that the general relationships proposed for both species (Equations 3 for aspen and 4 for white spruce) and for the stand as a whole (Equation 5), effectively characterize the relationship between volume increment and growing stock for these boreal mixedwood stands.

Results for trembling aspen suggest a positive effect of deciduous density and relative site occupancy on aspen volume increment (Figure 2). The significance of aspen density indicates that the number of trees per hectare may be a good predictor of aspen PAIV in unmanaged forests, if a variable describing site and age is incorporated into the same model (*i.e.*, average height as in this case). While the presence of understory spruce in boreal mixedwoods does not seem to have a negative impact on aspen productivity [25], spruce occupancy in later stages of stand development appears to be negatively influencing trembling aspen volume increment, as suggested by the negative effect of SDI_{dysw} on aspen PAI (Table 2). This negative effect of spruce on aspen volume increment appears to be rather small.

Results for spruce indicate a significant positive relationship between white spruce volume increment and basal area of spruce (BAH_{sw}) and trembling aspen (BAH_{dec}) (Table 2), with the effect of aspen being small. These results also suggest that the presence of aspen in boreal mixed stands enhances the productivity of white spruce in mid-rotation and mature forests, which also agrees with previous observations for similar forests in the same region [16,25]. The positive sign of the parameters relating to deciduous dynamic SDI and deciduous basal area in the models shown (Table 2) suggest that the presence of a deciduous component has a significant positive effect on white spruce volume increment (Figure 4). These results are consistent with the findings of Legaré *et al.* [43], who found that 5%–15% of trembling aspen basal area in mixture with black spruce was beneficial to black spruce volume growth. Our models indicate that increases in spruce volume increment are largest when spruce basal area is above $20 \text{ m}^2 \cdot \text{ha}^{-1}$.

Average aspen height appears to be positively affecting spruce growth (Table 2), which is consistent among the models presented. The positive exponent for spruce height agrees with other studies indicating that tree growth typically increases with size [18,44]. Changes in white spruce volume increment show a positive effect of both spruce SDI and deciduous SDI on spruce PAIV (Figure 4), although the effect of spruce is smaller than the effect of trembling aspen.

A fairly low proportion of the variation in total stand volume increment could be explained by the model that showed the best performance ($R^2_{\text{adj}} = 0.31$). The complexity of the interactions between spruce and aspen, the fact that interactions may change with age and associated changes

in stand structure, and the contributions of other factors such as position in the canopy of each component species, may be limiting the ability of these simple models to explain larger amounts of variation in growth [19,44]. In general, this model suggests a beneficial effect of trembling aspen and a negative but small effect of white spruce on total stand volume growth rates, as suggested by the signs of their respective parameter estimates (negative for white spruce dynamic SDI and positive for deciduous dynamic SDI). Average height of both species has a positive effect on stand volume increment (Figure 6). It is important to note that the value of total SDI_{sum} in Figure 6 (*i.e.*, the sum of deciduous SDI and white spruce SDI), has been constrained to a maximum of 1200. This guarantees that it does not go above the range of our data for mixed stands. The nearly planar nature of the surface shown in Figure 6 indicates that SDI_{dyd} and SDI_{dysw} are the predominant factors influencing stand volume increment. Although earlier studies suggest that maximum stockability is invariant for tree species, [7,45], several more recent studies (*e.g.*, [46,47]) have indicated that climate, site, and other factors can cause variation in the position of maximum density-size lines and lead to variation in maximum stockability. Variation in attainable maximum stockability among stands has been proposed as one of the main mechanisms that could significantly impact productivity of forests [48,49]. Recent studies for boreal mixedwoods suggest that both the slope and the intercept of the maximum size-density relationship vary with changes in stand composition and site characteristics [37], and that a decline in maximum densities (*i.e.*, maximum stockability) as the proportion of aspen in the stand decreases could be expected for these boreal mixed stands.

According to our results, decreases in SDI of either the deciduous species or of the spruce component are associated with a decrease in total stand volume increment (Figure 6). This also indicates that total volume increment is highest when SDI_{sum} of both species combined is at its maximum, suggesting important ecological combining ability. An admixture of white spruce and aspen with a combined total dynamic SDI_{sum} of 1200 ($SDI_{dysw} \sim 600$ and $SDI_{dyd} \sim 600$) would be close to full site occupancy, and would achieve maximum total PAI (approximately $12 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$) for the ranges of SDI_{sum} of the stands under consideration.

Differences in maximum stockability are a result of complex interactions between environmental conditions, stand history, crown architecture, species autoecology, and physiological differences among species [48–51]. High stockabilities for a given species have also been attributed to complex crown-class structures that allow for more efficient site occupancy with more active leaf area [49]. It has also been documented that leaf structure and photosynthetic capacity are sensitive to the light environment [52]. Therefore, leaf and crown differences and differences in species tolerances could allow penetration of sunlight deep into the canopy and increases in the efficiency of light utilization [50]. Also, a relatively low incidence of pests, a long growing season, improved soil conditions (temperature, nutrient supply, and moisture), and appropriate air temperature could enhance component species growth rates among different sites [49], and lead to variability in their maximum stockabilities.

5. Conclusions

Effects of competition and facilitation are difficult to separate even in very well established experiments [53] and especially in unmanaged stands of trees, due to variation in sizes, developmental stages, and other factors. Although the data sets that we used in this study include a wide range of variation in sizes, species composition, and developmental stages, the lack of information relating to environmental conditions and availability of resources at the local level may limit our ability to interpret the results, as temporal and spatial variability in resources availability and their interactions, can also cause complementarity (or competition) [24]. Effects of mixtures are indeed further complicated with changes in stand developmental stage, type of mixture, and site conditions [54], which is also the case for boreal mixedwoods [19]. However, results presented here

clearly indicate a link between increased stocking and productivity of either spruce or aspen, or both, at the stand level.

Our results, which suggest increases in volume increment in these stands with increasing stocking of either of the two main species, appear to contradict some classic works in forestry literature that suggest a decline in forest productivity under intense competition (Langsaeter hypothesis) [55]. However, there is evidence in this study and other studies [48–50] indicating that increases in maximum stockability can lead to an increase in productivity in forest stands.

The mixed species stands include a range of distribution patterns of the component species and two-species mixtures and, consequently, spatial distribution patterns for the component species, and changes in these patterns over time might also affect growth rates, as this will influence the occurrence and timing of interactions among the species [24,56] and the productivity of the stand. For example, in a two-species mixture, mixtures of single trees inside patches or groups are expected to experience greater competition than trees that are aggregated in groups or clusters of the two species within the stand [57]. Further analysis of the effects of species segregation and spatial distribution of trees, light capture and utilization, and resource availability and utilization in mixed stands, and their influence on growth of component species in mixed and pure boreal stands would be useful in explaining our findings.

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