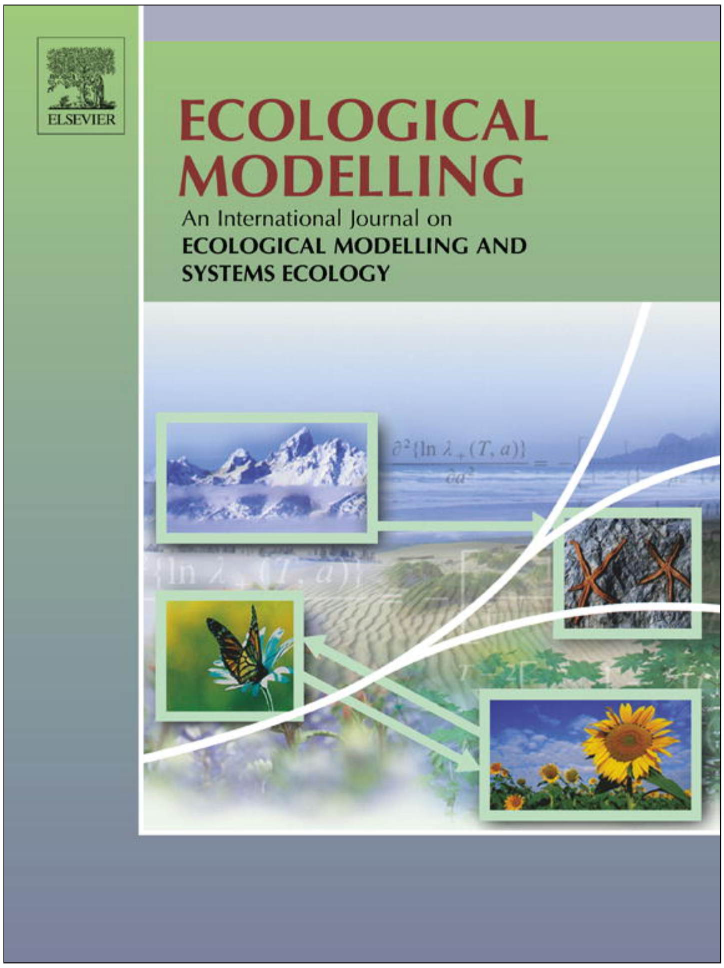
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Using height growth to model local and regional response of trembling aspen (*Populus tremuloides* Michx.) to climate within the boreal forest of western Québec

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ABSTRACT

Studies relating site index to climatic variables basically assume that the sensitivity of a species to climate remains stable across the geographic range of their study area. Yet, provenance trials speak to the contrary and show that populations are adapted to their local climatic conditions and tend to respond differently to climate. Spatial and temporal complexity of forest productivity and climate-relationships has been globally reported and recent studies have emphasized the necessity for regional studies on forest growth dynamics of current and future populations. The objective of this study was to determine whether the main climatic and non-climatic drivers of trembling aspen (*Populus tremuloides* Michx.) growth in Québec should be treated as regional (the study area reacts as a unique population) or local factors (the area is composed of different populations) when modeling the spatio-temporal variability of aspen productivity as measured with site index. Stem analysis data was collected from 124 trees (32 stands) that span a north-south (latitude 46–51°N) transect in western boreal Québec. Most stands were dense with cover density above 60%, even-aged, 50–90 years old, and very often mixed. The northernmost regions (latitude 48–51°N) are characterized by either organic or clay deposits, while in the south (latitude 46–48°N) till or clay deposits predominate. Climate variables that met selection criteria as major regional or local factors that influence aspen productivity were selected. A mixed modeling approach was subsequently employed to identify the categorization unit that could be defined as a population. We then predicted variation in the random error with prior information obtained at stand level. Our results show that aspen height growth is mainly driven by annual sums of degree days and stand age. Surface deposit type, which is an indicator of soil nutritive status and moisture potential, was found to have modulated climate influence. Finally, aspen productivity is better explained with a model that assumes that specific populations have a different response function to climate and are adapted to their local climatic conditions. This has implications when predicting the response to climatic change for forest growth models that assume that conspecifics respond to climate similarly.

1. Introduction

The productive potential of a site is a function of climate, soil organic matter, soil nutrient status and water availability (Landsberg and Sands, 2011). Several methods exist to estimate forest site productivity (Weiskittel et al., 2011, for a recent review) but site index defined as the mean height of dominant trees at a reference age is commonly used, especially in North America (Hagglund, 1981). On more productive sites, higher dominant height-age trajectories are observed compared to poorer sites (Garcia, 2004). Dominant height growth is largely independent of stand stocking (Skovsgard and Vanclay, 2007), making it a useful measure of productivity.

The concept of site index fundamentally assumes that site capacity to produce timber volume is approximately constant over a stand rotation (Monserud, 1984a). Per definition, site index is determined at a reference age and therefore includes an implicit temporal inertia of site capacity equivalent to the reference age.

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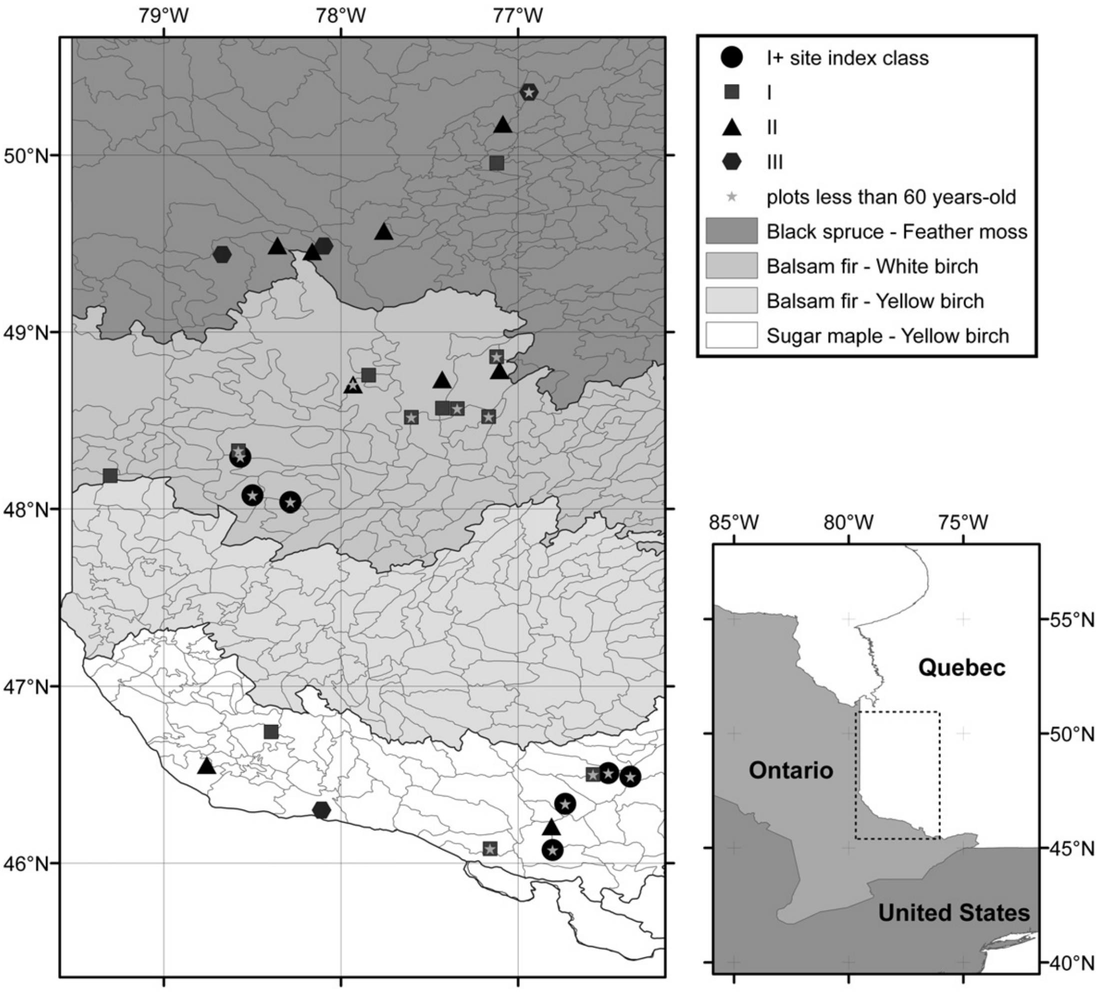

Fig. 1. Plot distribution. Black-spruce – Feather moss, Balsam fir – White birch, Balsam fir – Yellow birch and Sugar maple – Yellow birch correspond to ecological sub-regions. The gray lines delineate one ecological district from another.

The chosen reference age needs to be shorter than a rotation, but needs to be long enough to identify "with any confidence" the site quality (Assmann, 1970, p. 159). One way to deal with this conceptual inertia when modeling site index sensitivity to climate is to use climate normals that are estimated on a more comparable time frame (e.g. Ung et al., 2001; Beaulieu et al., 2011). Another way could be to model a growth index at a finer temporal scale (e.g. height growth at the yearly time scale) and to sum this index up to the time frame of site index, as chosen by the reference age.

Climate–productivity studies basically assume that over time and varying spatial scales, the nature of these relationships remains constant, which in dendrochronology is referred to as the uniformitarian principle (Speer, 2010). Some studies have reported however that growth sensitivities and responses differ from one spatial scale to another (Chen et al., 2002; Wilmking et al., 2004; Lapointe-Garant et al., 2010) and also through time (Andreu et al., 2007). Spatio-temporal differences in growth sensitivity thus potentially complicate the modeling of site productivity. One way to deal with heterogeneous sensitivities is to explore climate–productivity relationships along complex environmental gradients (e.g. Hofgaard et al., 1999; Huang et al., 2009).

We used the height growth data of trembling aspen (*Populus tremuloides* Michx.) to explore a climate–productivity relationship along climate/latitudinal, age and site gradients within the boreal forest of Québec. Aspen is an abundant deciduous species distributed across wide latitudinal and longitudinal gradients in North America (Perala, 1990). Its growth and distribution has been influenced directly by climatic conditions (Chen et al., 1998; Huang et al., 2009) as well as indirectly through climate influences on disturbance regimes that create peculiar environmental conditions (Bergeron et al., 2004). Aspen distribution and growth is also limited by soil physical and chemical properties. It grows better on clay deposits (Paré et al., 2001) and is influenced by varying soil moisture (Hogg et al., 2002) and nutrient regimes (Chen et al., 2002; Pinno and Bélanger, 2011). As noted by Chen et al. (1998) and Hamel et al. (2004), however, climate was expected to be much more important than any other factor in explaining aspen productivity over a wide latitudinal gradient (Lapointe-Garant et al., 2010). In this study we (a) parameterized a climate sensitive model of height growth in order to understand the relationship between climate and aspen productivity and (b) analyzed the temporal and spatial variability of aspen productivity.

2. Materials and methods

2.1. Study area

The study region spans from latitude 46°N to 51°N and longitude 76°W to 79°W (Fig. 1). Plots are located south of James Bay with a generally flat or slightly hilly topography. The northernmost regions (latitude 48°N to 51°N) are characterized by either organic or clay deposits, while in the south (latitude 46°N to 48°N) till or clay deposits predominate. The study area covers one temperate and three boreal bioclimatic domains (Fig. 1), where the mean annual temperature ranges from −2 °C to 4 °C for the northernmost and southernmost domains, respectively. Length of the growing season (number of days with a mean daily temperature above 5 °C) and degree-days above 5 °C vary similarly (115–165 days per year, 950–1650 degree-days). Total annual precipitation ranges from 700 mm to 1000 mm but there is no evident spatial trend associated to this variability (Robitaille and Saucier, 1998).

2.2. Data description

Data for the study was obtained from the Ministère des Ressources naturelles et de la Faune du Québec (MRNFQ) as part of a bigger project across the province of Québec in which 1197 trees of nine species were felled during autumn from 1998 to 2006 (Grondin et al., 2000; Saucier et al., 2007). From this pool, 124 dominant and co-dominant trembling aspen trees, felled from 32 stands (Fig. 1) located within our study region, were obtained for this study. Most stands were dense (cover density above 60%), even-aged, 50–90 years old, and very often mixed. Frequent companion species such as red and sugar maple species (*Acer rubrum* L. and *A. saccharum* Marsh.), balsam fir (*Abies balsamea* (L.) Mill.) and black spruce (*Picea mariana* (Mill.) B.S.P.), changed according to the bioclimatic domain. Trembling aspen was the dominant species in 20 stands (62%). Three stands found in the sugar maple – yellow birch bioclimatic domain were uneven-aged. Stem discs were extracted from heights of 15 cm, 60 cm, 1.3 m and then every 2 m after. Ring measurements were conducted on four axes for stem discs at breast height (1.3 m) and below and along two radii for stem discs above 1.3 m with Windendro (Régent Instruments, Québec City, Canada). The number of rings was counted at each cross-sectioned point, and then converted to age above stump height (15 cm). Height growth was assumed to be constant between two discs (Carmean, 1972) and mean height increment was estimated by dividing the height difference of two stem discs by their age difference.

2.3. Estimation of a periodic growth index

To relate height growth to site index, we modified Plonski's site index model for trembling aspen (Payandeh, 1977). Plonski's model was calibrated from stem analysis data which Payandeh (1977) refitted for major timber species of Ontario:

$$H = b_1 S^{b_2} (1 - \boldsymbol{e}^{b_3 A})^{b_4 S^{b_5}} + \varepsilon \tag{1}$$

where H is total height in meters of dominant and co-dominant trees at age A (years). S is site index (height at age 50 years) and b_1, b_2, b_3, b_4 and b_5 are species specific parameters of the model. $\boldsymbol{e}$ is base of natural logarithm and ε is model error (Payandeh, 1977). Taking the first derivative of Eq. (1) with respect to time and replacing expressions that are a function of age with expressions that are a function of height with Eq. (1), dominant height growth and height are related by:

$$i_H = \frac{\partial H}{\partial A} = -b_3 b_4 S^{b_5} H \left(\left(\frac{H}{b_1 S^{b_2}} \right)^{(-S^{-b_5}/b_4)} - 1 \right) \tag{2}$$

One assumption of Eq. (2) is that height increment is measured on an annual time scale. With stem analysis data, however, only the mean height increment between two stem disks can be estimated. A second modification was therefore done to adapt Eq. (2) to the nature of stem analysis data by estimating the mean height increment between two heights:

$$\bar{i}_H = \frac{\int_{H_2}^{H_1} aH[(H/b)^c - 1]dH}{[H_2 - H_1]} = \frac{[aH^2(H^c/b^c(a+2)) - 0.5]_{H_2}^{H_1}}{[H_2 - H_1]} \tag{3}$$

where $a = b_3 b_4 S^{b_5}$, $b = b_1 S^{b_2}$, and $c = (-S^{-b_5}/b_4)$.

Site index can be estimated with Eq. (3) from a pair of height observations by an iterative procedure such as nonlinear ordinary least squares or binary search. Site index is then the only parameter to estimate, while the other parameters b_1–b_5 are held constant and equal to those estimated by Payandeh (1977). An estimation of site index derived from Eq. (3) will hereafter be called the periodic growth index (S_{iH}), in order to differentiate it from the usual estimation with dominant height and age (S_H).

2.4. Removing early growth suppression

Tree growth can be suppressed for several years especially for naturally regenerated stands (Groot and Hökkä, 2000) with the consequence of underestimating site potential (Monserud, 1984a). Some studies (e.g. Carmean, 1972; Chen et al., 2002; Simard et al., 2007) proposed careful selection of candidate trees for site index estimation such that only trees that have grown freely without any suppression are selected. But it has been demonstrated that even if a tree is dominant at the time of selection, it might have been suppressed previously. For instance, Mailly et al. (2009) observed for trembling aspen with permanent sample plots in Québec that between 12 and 18% of the dominant cohort die every ten years. Some previous studies proposed the elimination of height growth below specific heights in site index estimation (e.g. 1 m by Boucher et al., 2006; 1.3 m by Monserud, 1984a and Pothier and Savard, 1998), but this approach is quite subjective as some trees are released several years after reaching breast height.

Groot and Hökkä (2000) identified three phases for trees released from past suppression: a suppression phase, a phase of acclimation following release and a phase of normal growth. These three phases are difficult to pick in either the height versus age curve, or the height growth versus height curve, because of the complexity of these relationships. However, site index, as estimated by the periodic growth index with Eq. (3), should remain approximately constant during the phase of normal growth and could also be expected to remain very low and constant during the suppression phase. Therefore, the adjustment of a three segmented linear function should permit the identification of the "free-to-grow" phase. For each tree, we estimated the parameters of three segmented linear models using the NLIN procedure in SAS version 9.0 (SAS Corporation, Cary, NC, USA) by: (1) assuming all three phases were present, (2) assuming only the acclimation and normal phases were present and (3) assuming there was only one normal growth phase. For each tree, the best of these three models was chosen with the minimum residual error. Only the "free-to-grow" phase was considered thereafter.

2.5. Climate data acquisition

Mean monthly climate data spanning 1900–2000 were generated from the BioSIM model (Régnière and Saint-Amant, 2008) with the Canadian Daily Climate Data (Environment Canada, 2010). Ninety-six weather stations were geographically located within the study region; their location was non-uniformly distributed across space and time. Hence, we inquired if the distances of a sample plot to the nearest weather stations and the number of stations used could influence the quality of climate data generated for the sample plots. Ten weather stations with the longest series of climate data were selected from the database and disabled one at a time from the weather database. The climate data for that station (monthly value of degree days above 5 °C and precipitation) was then generated with BioSIM using a varying uneven number of nearest stations (1, 3,...,15). A higher variance was associated with data obtained from the nearest weather station, with variation leveling off when data was simulated from 5-closest stations or more. Subsequently, climate data was generated from the five nearest weather stations for the period 1900–2000 for all plots.

2.6. Calibration of the periodic growth index model

The data set altogether spanned periodic growth index values between 1900 and 2000 but only very few plots had series that covered the entire period. Juveniles respond differently to climate when compared to older trees (Chhin et al., 2010) and also existing site index models are not reliable enough for young stands so growth data below 25 years of plot mean age was discarded (Nigh and Love, 1999). The data was subsequently divided into two datasets, from 1921 to 1960 and from 1961 to 2000. The first dataset was used to parameterize Eq. (4) (calibration data set) while the second was used to estimate its predictive ability (validation dataset).

We proceeded in four steps (Fig. 2). In a first step, we followed the methodology applied by Ung et al. (2001) when they developed biophysical site index models for boreal species, including trembling aspen:

$$S_{iH} = \bar{S}_{iH} \prod_{i=1}^{n} f_i(x_i) \tag{4}$$

where $\bar{S}_{iH}$ is the mean periodic growth index observed for the calibration data set and $\prod_{i=1}^{n} f_i(X_i)$ designates the product of n modifiers having a value close to unity when the variables X_i are equal to their mean $\bar{X}_i$ observed in the calibration data set and increase or decrease when moving further away from the mean. We considered two different estimations of the mean: (a) a mean estimated across time for all sample sites (regional mean model) and (b) a mean estimated through time for each sample plot (population model). In the regional mean model, it is assumed that the study area corresponds to one population reacting uniformly to an environmental variable. In the population model, the study area is assumed to have different populations reacting negatively or positively relative to their environmental mean conditions, but with a sensitivity common to all the sampled sites. For the population model, the temporal depth used to estimate the population means was varied between 5 and 50 years by steps of 5 years to choose the depth providing the lowest root mean square error for Eq. (4). We defined $f_i(x_i)$ as:

$$f_i(X_i) = 1 + \beta_{l.Xi}\left(\frac{X_i - \bar{X}_i}{\bar{X}_i}\right) + \beta_{q.Xi}\left(\frac{X_i - \bar{X}_i}{\bar{X}_i}\right)^2 \tag{5}$$

where $\beta_{l.Xi}$ and $\beta_{q.Xi}$ represent the linear and quadratic effects of the variable X_i on the periodic growth index. Potential X_i variables included total annual precipitation, degree-days above 5 °C, aridity index (*sensu* Ung et al., 2001), growing season precipitation, and growing season aridity index (AI). Growing season was considered as the months of June, July and August. Additionally, we added in the variable list previous year total precipitation, previous year growing season precipitation and previous year aridity index (Lapointe-Garant et al., 2010). Climate variables were estimated with the BioSIM model (Régnière and Saint-Amant, 2008).

Aspen experiences senescence at 60-years but this can start as early as 36 years for stands on more productive sites (Pothier et al., 2004). In order to account for senescence, we added stand mean age through time to the predictor variable list.

Finally, as a different way of expressing climate data as external factors affecting the physiological processes of the stand canopy (e.g. Coops et al., 2011), we further considered the yearly absorbed and utilized photosynthetically active radiation (YAPAR$_u$, mol m^{-2} ground year^{-1}). The YAPAR$_u$ was estimated with StandLEAP (Linking Ecophysiology and Productivity at the stand level – Hall et al., 2006; Girardin et al., 2008), a top-down light-use efficiency model derived from 3-PG (Landsberg and Waring, 1997). StandLEAP operates at the monthly time scale. Monthly APAR equals the photosynthetically active radiation above the canopy, derived from minimum and maximum monthly temperatures (Nikolov and Zeller, 1992), and intercepted by the canopy leaf area with a Beer–Lambert law (Gower et al., 1997; Chen, 1996). Monthly APAR$_u$ equals monthly APAR multiplied by the effects of environmental factors constraining canopy light-use efficiency. These modifiers account for the impact of frost (Aber et al., 1995), soil drought, vapor pressure deficit (Landsberg and Waring, 1997), monthly mean temperature, monthly radiation and leaf area index (Raulier et al., 2000; Hall et al., 2006). As in Pn-ET (Aber et al., 1995), monthly APAR is adjusted during the growing season for changes in leaf area due to phenological development and leaf fall is set at Julian day 270.

For the variable inclusion in Eq. (4), a stepwise procedure was used with a forward selection. Each variable was first included into the model one after the other, and the variable that provided the lowest root mean square error (RMSE) and the highest correlation (R^2) was retained. PROC NLIN of SAS was used for this purpose. The same procedure was repeated until no more variable could be included. Since the inclusion of a variable into Eq. (4) requires the introduction of a modifier with two parameters (Eq. (5)), entry or exit of a modifier was tested with a likelihood ratio (Bates and Watts, 1988). To prevent over-fitting and maintain model robustness, variables were retained only if their inclusion reduced the RMSE of Eq. (4) by at least 5% (Raulier et al., 2000).

In a second step, a mixed modeling approach was used with the NLMIXED procedure of SAS. As we expected a spatio-temporal difference in height growth sensitivity to climate, a mixed modeling approach offered the opportunity to account for the structure of the dataset (Larreta-Vargas et al., 2009; Subedi and Sharma, 2011). The purpose was to detect at which level of categorization the addition of a random-effect could better explain the residual variability of Eq. (4). Hence we added a random-effect term (σ) into Eq. (4):

$$S_{iH} = (\bar{S}_{iH} + \sigma) \prod_{i=1}^{n} f_i(X_i) \tag{6}$$

As such, we assumed that the product represents the sensitivity of site index to climate within our study region (at the regional or population level) and that $(\bar{S}_{iH} + \sigma)$ could account for more specific sub-regional or local distinctive traits. Four levels of categorizations were considered: ecological sub-regions, ecological districts, ecological types (Saucier et al., 1998) and plots. Ecological sub-regions are characterized by the forest dynamics on mesic sites, either typical to the ecological region to which they belong or having a particular southern or northern character. Ecological districts are landscape units characterized by their topography, soil deposits and hydrology (Robitaille and Saucier, 1998). The expected climax vegetation characterizes ecological types. For each of the categories, the random-effect parameter takes a different value from one grouping to another.

In the third step, we sought to improve the predictive ability of Eq. (6) with prior information of the random variability (e.g. Larreta-Vargas et al., 2009; Subedi and Sharma, 2011). This step could then serve to provide information of climate sensitivity for specific populations. Hamel et al. (2004) have shown that soil properties interact with climate variables and improve the estimation of

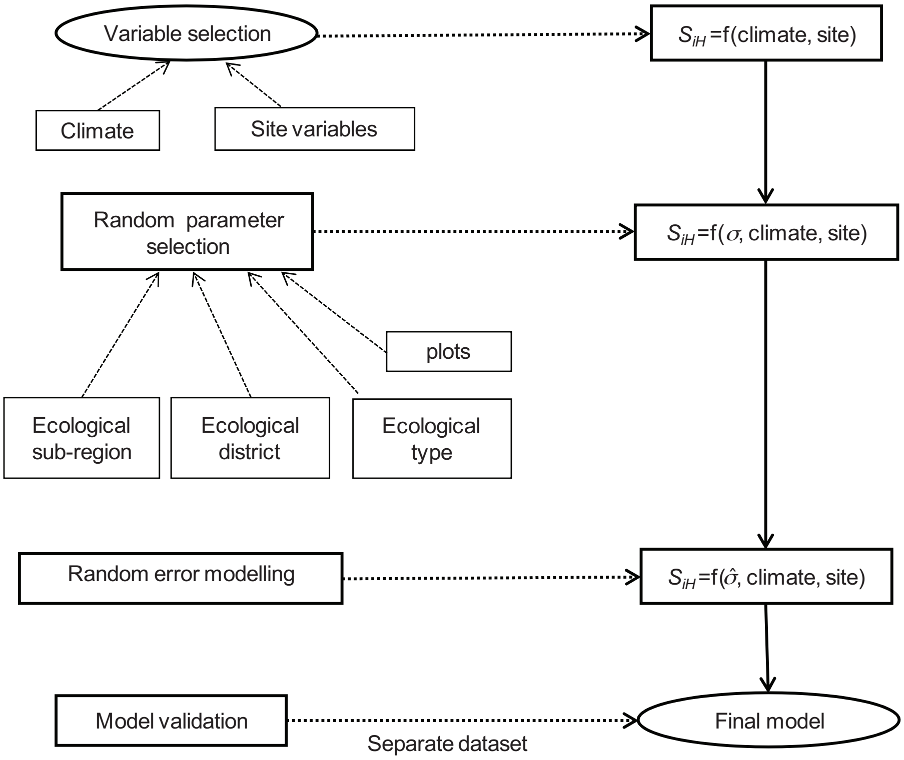

Fig. 2. Conceptual framework of the modeling approach.

site productivity. Soil variables such as type of soil deposit, texture and drainage observed on the sampling plots (MRN, 1994) were thus considered in the modeling of the random-effect parameter. We conducted an analysis of variance (ANOVA procedure in SAS) on all soil variables to first identify categorical variables that could most well predict the random error.

Specific area (A_W) of the mineral soil layer corresponds to the area exposed to mineral weathering and since it is related to the rate of release of base cations, it serves as an indicator of forest productivity (Jönsson et al., 1995; Hamel et al., 2004). Aspen defoliation effect on growth by forest tent caterpillar (*Malacosoma disstria* Hubner) was found to explain significant variation in aspen tree growth (e.g. Hogg et al., 2005), it was therefore considered in this study as well using data from Huang et al. (2008). Huang et al. (2008) identified aspen defoliation years by latitude and went further to differentiate between severe defoliation years and periods of less severe defoliation. Finally, site index estimated from dominant height and age was also considered since it is a widely available prior information of site productivity. We subsequently combined significant soil variables, defoliation effect, site index (estimated from mean height of the trees sampled for the stem analyses and age) and climate variables considered in the first step in covariance analyses.

In the fourth step, we re-estimated the model parameter estimates and verified the model predictive ability with the validation dataset. We regressed periodic growth index observed and predicted for the period 1961–2000. We also calculated 50-year moving averages of the entire observed and predicted data spanning 1921–2000 using PROC REG procedure in SAS to have a growth index equivalent to site index estimate from dominant height and age. We constructed 95% confidence intervals around observed and predicted estimates using the SUMMARY procedure in SAS in order to visually verify the concordance between predicted and observed estimates. Using PROC CORR procedure in SAS, we verified if model residuals were significantly correlated with predictor variables. Finally, model estimates were illustrated by site index classes (Table 1) established in Plonski's yield table (Plonski, 1956) and also separately for young (<60 years) and old (≥60 years) to be able to distinguish aspen stands in senescence (Pothier et al., 2004).

3. Results

3.1. Early growth suppression

In all, 124 aspen trees from 32 plots were corrected for early growth suppression. One plot had a mean age lower than the 25-year threshold and was excluded from further analysis. A good number of the trees (68%) were previously suppressed, i.e. they had clear suppression and acclimation phases (best fit with model 1). Twelve percent experienced previous suppression but only briefly (model 2) with only a few trees (20%) that were never suppressed (model 3). No particular trend in suppression by site and age classes was detected.

3.2. Temporal variability in productivity

Length of time series of periodic growth index varied among the different site classes as illustrated in Table 1. On the most productive site class (I^+), the periodic growth index reduced ($p < 0.05$) by 0.7% annually and increased ($p < 0.05$) by 0.2% per year for the other site classes. Grouping the data by age classes produced similar trends with a decrease (but $p > 0.05$) over time on the younger plots and an increase ($p < 0.05$) on older plots. Variability around mean periodic growth index was higher over time for the youngest age class compared to the oldest one. Except for the I^+ site class, variability around mean periodic growth index over time reduced from the low productivity site class through medium to high productivity class.

Table 1
PGI trend observed by age and site quality categorizations.

	Class	Number of plots	Data span	Mean age (SDev)	PGI trend
Site index	I$^+$ (>25.4 m)	12	1979–2000	36 (7)	–
	I (21.7–25.4 m)	9	1953–2000	57 (10)	+
	II (17.9–21.6 m)	7	1942–2000	71 (11)	+
	III (14.1–17.8 m)	4	1907–2000	82 (25)	+
Age	I (<60)	16	1970–2000	45 (10)	=
	II (≥60)	16	1907–2000	75 (14)	+

+, = and – denote increase, no trend and decrease, respectively.

Table 2
Climate variable selection for model building.

Climate variable – 1st candidates	Lin	Quad	R^2 (regional mean model)	R^2 (population model)
Vapor pressure deficit	sig	sig	0.02	0.08
Aridity index	ns	ns	0.00	0.00
Total annual precipitation	sig	sig	0.04	0.11
Degree days	sig	sig	0.12	0.22
APAR	sig	sig	0.06	0.19
APARu	sig	ns	0.11	0.22

Table 3
Selection of local level of categorization.

Level	*p*-Value	YAPAR$_U$ (R^2)	DD (R^2)
Plot	0.001	0.679	0.692
Ecological types	0.001	0.634	0.645
Ecological districts	0.001	0.652	0.644
Ecological sub-regions	0.001	0.291	0.317
Entire region	0.001	0.217	0.221

3.3. *Selection and spatio-temporal variability of climate variables*

Root mean square error (RMSE) values and strength of correlation (R^2) served for the climate variable selection. Degree-days (DD) and yearly absorbed and utilized photosynthetically active radiation (YAPAR$_u$) as a single climate variable gave best and very close fits (Table 2). For the population models, the best fits were obtained with means estimated over a time span of 20 years. Comparing aspen height growth sensitivity to climate in the study area as a regional or a population response function, we observed a better fit with the latter (Table 2). Maintaining both regional and population effects of DD or YAPAR$_u$ in the model did not result in significant differences ($p > 0.05$) in model fit when compared to a model with only the population effect of DD or YAPAR$_u$ (results not shown). Co-variables that would enter the model together with DD or YAPAR$_u$ were then selected. Even though the RMSE decreased with the addition of other variables, only mean plot age as a regional variable met the selection criteria (more than a 5% decrease in RMSE). Inclusion of mean plot age as a population variable was non-significant ($p > 0.05$). Results of the second calibration step further showed that residual variation in site index when explained by DD and mean plot age could most be explained at the plot level when compared to the other three considered categories or when YAPAR$_u$ was used instead of DD (Table 3). Consequently, DD and mean plot age were selected as the environmental variables for the remaining steps of model building.

Regionally, DD did not exhibit any particular significant ($p > 0.05$) temporal trend over the study period. On the most productive site classes (I$^+$ and I), DD increased over time and reduced ($p < 0.05$) at the medium and poor sites (classes II and III). Variability around mean DD decreased ($p < 0.05$) over time both regionally as well as for each of the site productivity classes. This might be due to the increase in plot number over time.

3.4. *Model calibration*

3.4.1. *Periodic growth index*

In the model, both DD and stand age behave similarly by having insignificant ($p > 0.05$) quadratic effects but significant linear effects on productivity. The interaction between DD and stand age explains 77% of variation in the periodic growth index of aspen. There were some variations among site classes. For instance, explained variance was 82% on the most productive site and 65% on the poorest site. Seventy-nine percent and 74% were explained respectively for the youngest and oldest age classes.

3.4.2. *Random error model*

A combination of site index (S_H) estimated from mean height and age and lacustrine clay deposit (z_{Dep}, a binary variable) provided the best explanation of variation in the random parameter (Eq. (7), Table 4).

$$\hat{\sigma} = \beta_1 + (\beta_2 + \beta_3 z_{\mathrm{Dep}})S_H \tag{7}$$

An alternate error model was also developed to exclude site index as a variable so this model could help in estimating sensitivity of specific forest stands without existing prior knowledge on site index. With the latter, significant input variables included 50-year moving average of DD ($\bar{D}_{50}$ – as a surrogate of site index on a comparable time frame), soil surface deposit (z_{Dep}) and surface area (A_w) and with these, one is able to predict 63% of variation in the random error parameter (Eq. (8), Table 4):

$$(\bar{S}_{iH} + \hat{\sigma}) = (\bar{S}_{iH} + \varphi \times z_{\mathrm{Dep}}) \times f_{\bar{D}_{50}} \times f_{A_{\mathrm{w}}} \tag{8}$$

where φ is a parameter related to the soil surface deposit variable, and $f_{\bar{D}_{50}}$ and $f_{A_{\mathrm{w}}}$ are modifiers of $\bar{D}_{50}$ and A_w as defined in Eq. (5).

3.5. *Model performance*

Residuals of the final model were not correlated ($p > 0.05$) with mean stand age, DD or YAPAR$_u$. Parameter estimates of the modifiers of DD and mean stand age are illustrated in Table 5. Moving averages with a 50-year window of periodic growth index estimates predicted from this model and observed correlate very highly ($R^2 = 79\%$). Fig. 3 illustrates mean site indices observed and predicted from the model with their 95% confidence interval. There seem to be stronger differences in the observed and predicted mean values from 1960 to 1970 but confidence bands continuously overlap. Correlation was highest ($R^2 = 92\%$) on the most productive site

Table 4
Parameter values for the random error ($\hat{\sigma}$) model and the alternate random error model.

	Random error model			Alternate random error model				
	β_1	β_2	β_3	φ	$\beta_{l.\bar{D}_{50}}$	$\beta_{q.\bar{D}_{50}}$	$\beta_{l.Aw}$	$\beta_{q.Aw}$
Estimate	18.329	0.938	−0.156	−6.258	0.914	−1.449	0.325	−0.249
SE	0.252	0.012	0.004	0.467	0.061	0.377	0.019	0.023

SE, standard error.

Table 5
Model parameter estimates and their standard errors.

Parameter	Estimate (SE)
$\beta_{l.\mathrm{DD}}$	0.500 (0.031)
$\beta_{q.\mathrm{DD}}$	−3.107 (0.309)
$\beta_{l.\mathrm{age}}$	0.075 (0.013)
$\beta_{q.\mathrm{age}}$	−0.115 (0.018)
$\bar{S}_{IH}$	19.990 (0.142)

$\overline{X}_{\mathrm{age}} = 47.37$ years; $\mathrm{Min}_{\mathrm{age}} = 25$; $\mathrm{Max}_{\mathrm{age}} = 121$ years; $\overline{X}_{\mathrm{DD}} = 1400.6$ degree-days; $\mathrm{Min}_{\mathrm{DD}} = 880.3$; $\mathrm{Max}_{\mathrm{DD}} = 2137.6$ degree-days.

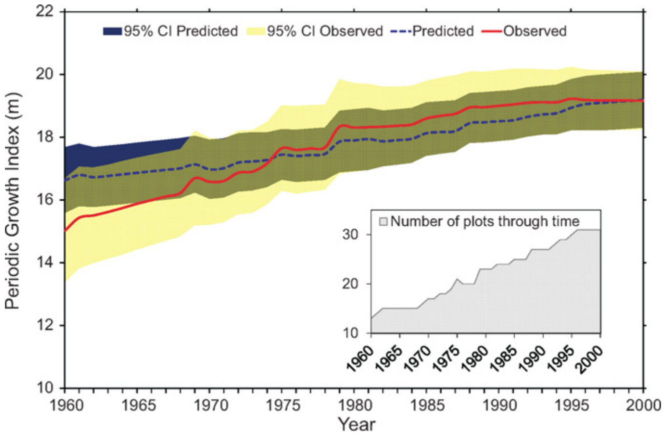

Fig. 3. Temporal variation in site index with 95% confidence interval for both observed and predicted values. The red smooth line represents observed value while dark-blue dotted line represents model prediction. The dark green is the overlapping area of predicted and observed confidence bands. The small gray graph shows plot variation through time. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

class, while it was 70%, 67% and 85% respectively for classes I, II and III. There was not much difference in the model performance on young stands compared to older stands.

4. Discussion

In this study, we attempted to explain climate–productivity relationships using height growth measurements of trembling aspen, an important boreal tree species. We first built models to predict productivity of trembling aspen from climate variables. We then employed a mixed modeling approach offering the opportunity to capture both fixed and random effects (Littell et al., 2006) of site variables that also represent between and within site variability.

Canopy height estimates from stem analysis data may underestimate past dominant heights and overestimate future dominant heights (Weiskittel et al., 2009; Raulier et al., 2003). Our site index estimates (mean of 19.9 m (SE: 0.7)) are however within the range of those obtained in other studies for trembling aspen. For instance, in British Columbia, a range of 5.5–30.7 m was obtained by Chen et al. (2002) in a study done from stem analysis data. Ung et al. (2001) obtained a mean of 20.7 m (SE: 0.1) for aspen in Québec using temporary sample plot data.

Degree-days were the single climate variable explaining most of the periodic height growth variability and its explanatory capacity was as good as more sophisticated variables based on our understanding of processes affecting growth, such as $\mathrm{YAPAR_u}$. Part of this result is due to the fact that temperature is the main climatic variable controlling aspen growth in Western Quebec and that drought events remain infrequent in our study area (Girardin et al., 2009), when compared to other regions within the distribution range of this species (e.g. Hogg et al., 2002, 2005). Yet, this robust result matches that of other studies that typically relate site index to degree-days (Monserud, 1984b; Ung et al., 2001).

Most studies relating site index to climatic variables assume that the sensitivity of a species to climate remains stable across the geographic range of their study area (e.g. Ung et al., 2001; Monserud et al., 2008). Agreeing with findings that speak to the contrary (e.g. Chen et al., 2002), our results show that the periodic height growth index of trembling aspen is better explained with a simple population model. The low number of populations ($n = 32$ plots) in the present study did not allow us testing for more complex models. Despite this, these results concur with provenance trials of tree species that specific populations have a different response function to climate and are adapted to their local climatic conditions (Rehfeldt et al., 1999, 2002). Monserud and Rehfeldt (1990) further showed a strong empirical link between site index estimated from stem analysis and genotype. This has implications when predicting the response to climatic change for forest growth models that assume that irrespective of location, conspecifics respond to climate similarly (e.g. Peng et al., 2002; Girardin et al., 2008; Coops et al., 2010).

There were marked differences in climate influence by scale i.e. regional, sub-regional and local levels (Table 3). Variation in periodic growth index explained by the model increases as one moved from a more regional to local scale. Soil properties interact with climate variables in a way that improves site productivity (Paré et al., 2001; Hamel et al., 2004; Pinno and Bélanger, 2011). There was, however, not much difference between locally defined ‘ecological districts’, ‘ecological types’ and ‘plots’ with respect to climate–growth relations (Table 3). For this study, plot level was identified as the unit at which most variation in growth was explained and was selected for the modeling. Yet ‘ecological districts’ or ‘ecological types’ could also be chosen for planning purposes (Beaulieu et al., 2011).

Local climate and mean stand age explained 77% of periodic growth index and 79% of the variation of aspen growth over a period of 50 years. Even though there were some minor differences in variance explained by site quality classes, the observation is largely the case across site quality and age classes of stands considered in this study. On the most productive sites, where trees have a mean age of 37 years (Table 1), and for which tree growth represents recent decades (1979–2000), an annual reduction of 0.7% year^{-1} was observed with an increase in degree-days. One hypothesis would be that senescence has commenced on these sites. Pothier et al. (2004) observed aspen senescence as early as 36 years of stand age, especially for more productive stands. Cavard et al. (2011) also observed that on richer clay soils of the Québec clay belt region, aspen growth decreased after 37–54 years. Testing if DD-periodic growth relations differ between lacustrine clay and non-clay soil deposit types, we observed a positive linear effect ($p < 0.05$) of DD on periodic growth at lacustrine clay sites while on non-clay sites this relationship was non-existent. Aspen periodic growth index is lower on non-clay soil deposits with lower pH and lower calcium and nitrogen contents (Paré et al., 2001; Pinno and Bélanger, 2011).

With the other site classes (i.e. I, II and III) where mean age ranged from 57 to 82 years (Table 1), an annual increase of 0.2% year^{-1} was observed. A number of recent studies observed increased productivity over the 20th century (e.g. Boisvenue and Running, 2006; Zhang et al., 2008; Girardin et al., 2011) attributed largely to global warming. But in this study, no significant temporal increase in DD for these classes was observed for the period, so either growth was due to an increase in the sensitivity of trees to warming (Wilmking et al., 2005) or some other local factors might have positively interacted with local climate to enhance aspen growth (Hamel et al., 2004). A plausible explanation includes an increase of the available soil moisture over our study area as reported by Girardin et al. (2009) and Girardin et al. (2011). When we studied precipitation trends for our data by site index classes, we did not observe significant increases, except for class II where significant increases ($p = 0.016$) were observed from 1942 to 2000. We suspect that for these sites, there might have been some relaxation of summer moisture stress owing to the marginal increases in precipitation accounting for the 0.2% annual increase in growth. These stands are mostly located on clay deposits with therefore the potential for an increased growth (Paré et al., 2001). Also, we observed that older stands on clay deposits had positive linear ($p < 0.05$) relations with climate compared to younger stands on similar sites. Older stands might have been less affected by moisture stress owing to a denser, more stratified vegetation cover that reduces water losses through evapotranspiration (Bunn and Goetz, 2006). As height growth is averaged over approximately 3–5 years, infrequent droughts probably remain undetected.

4.1. Model performance

The final model explains 77% of variation in periodic growth index in the calibration dataset and predicted estimates correlate quite well ($R^2 = 60\%$, RMSE = 1.8, CV = 9.8) with observed periodic growth index estimates in the validation dataset. When 50-year means of observed and predicted estimates were compared, the model fit further improved ($R^2 = 79\%$, RMSE = 0.97, CV = 5.2). It was also observed that 95% confidence interval of model predictions lie within the 95% confidence band of the observed values. Moreover, obtaining future growth from two predictor variables (degree-days and stand age) makes the model attractive from the viewpoint of the rule of parsimony (Sauerbrei et al., 2007). Previous work e.g. with the zone-specific aspen model of Chen et al. (2002) from British Columbia obtained a better fit ($R^2 = 82\%$) than observed in this study but this can be expected owing to the number of predictor variables in their model ($n = 24$). Compared with other previous attempts at modeling climate-growth relationships (e.g. Ung et al., 2001; Lapointe-Garant et al., 2010; Beaulieu et al., 2011), the model presented is simpler and therefore expected to be quite robust. Since climate influences on growth have been identified as a population event (Eq. (7)) as well as a mix of population and regional processes (Eq. (8)), the ability to capture random plot level variations and model it deterministically presents an opportunity to be able to understand periodic growth dynamics of future populations (Schmidtling, 1994). From the alternative random error model, one is also able to predict random error estimates for populations without existing prior knowledge on the site index.

5. Conclusion

The model presented here provides periodic estimates of productivity which could serve as an interesting alternative to existing models in understanding climate–site–growth relations of specific populations. It also presents an opportunity to capture climate variability thereby potentially reducing biases induced by time-invariant site index curves. As shown before by Lapointe-Garant et al. (2010), a mixed-modeling approach helped to distinguish between regional and local facets of forest productivity as measured with site index. But contrary to Lapointe-Garant et al. (2010), our results showed that a multiple site index - climate relationship is more appropriate to account for a differential response to climate of specific populations. Even though this has been proven with provenance trials, to our knowledge, our study is the second to corroborate this fact with site indices of naturally regenerated stands (after Monserud and Rehfeldt, 1990).

Site index values as estimated from height increments measured with stem analyses spread across a wide latitudinal gradient provided a spatio-temporal dimension otherwise unavailable in studies relating site index to climatic variables. Since the dataset for this study covered a wide latitudinal gradient which also represents a gradient of varying species mixture, we suggest that a further study investigates the influence of changing proportions of other species to the productivity of aspen (Cavard et al., 2011; Paquete and Messier, 2011). The age variable in the predictor list could also be replaced with time since last fire to monitor productivity over time, hence offering the potential to improve our understanding of stand succession processes. Finally, the area covered by the study area is very large and there may be different sub-regional trends in precipitation and degree-days. Since our study had only 32 plots, the identified trends in productivity could also be driven by a particular sub-region having a larger weight on the entire dataset (Fig. 1). A further study with a larger dataset would be necessary to confirm or dismiss these results.

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