Provided for non-commercial research and education use. Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/authorsrights

Forest Ecology and Management 302 (2013) 390-403



Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



The predominance of stand composition and structure over direct climatic and site effects in explaining aspen (*Populus tremuloides* Michaux) site index within boreal and temperate forests of western Quebec, Canada



Kenneth A. Anyomi^{a,*}, Frédéric Raulier^a, Yves Bergeron^b, Daniel Mailly^c

^a Centre d'Étude de la Forêt, Faculté de foresterie, de géographie et de géomatique, Université Laval, 2405 rue de la Terrasse, Québec, QC, Canada G1V 0A6 ^b NSERC/UQAT/UQAM Industrial Chair in Sustainable Forest Management, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, QC, Canada J9X 5E4

^c Direction de la recherche forestière, Ministère des Ressources naturelles, 2700 rue Einstein, Québec, QC, Canada G1P 3W8

ARTICLE INFO

Article history: Received 22 January 2013 Received in revised form 21 March 2013 Accepted 22 March 2013

Keywords: Trembling aspen Productivity Site index Landscape Stand composition Structure

ABSTRACT

Existing models that use the site-index concept (dominant canopy height of a tree species at a reference stand age) are fundamentally stand-level models that do not account for stand dynamics, limiting their use to only a part of successional trajectories. Given that stand dynamics is influenced by both large and fine scale processes, we took a multi-level look at aspen (Populus tremuloides Michaux) productivity by determining landscape- and plot-level factors related to productivity as rated with site index. The study area extends from latitude 45° to 50°N in western Québec, from which were sampled 62 landscapes made up of 4948 plots, 25% of which had aspen as dominant and/co-dominants in the canopy. There, aspen is most often found in mixed stands. A stepwise procedure with forward selection was used in building landscape- and plot-level models and models were then arranged hierarchically such that (a) predicted estimates of the landscape model were inputs to the plot-level model (top-down) and (b) significant landscape variables were added to selected plot level variables (bottom-up). For the plot-level model, none of the climate variables considered were selected but at the landscape level, annual sum of degree-days was only the third to enter. In both cases, aspen site index was more related to the proportion of spruce (Picea mariana (Mill.) B.S.P. and Picea glauca (Moench.) Voss). At the level of landscapes, this observation might be due to the existence of particular vegetation mosaics, of which spruce proportion could be a surrogate. At the level of plots, influence of spruce on aspen site index is probably indicative of niche sharing with aspen. A high random variability was associated with the plot-level model but not with the landscape-level model. The similarity in drivers of aspen site index at both levels and the fact that both top-down and bottom-up approaches provided the same information, suggest that the use of landscape variables when modelling site index in mixed stands may help distinguish peculiarities shared by plots located in a landscape and improve the signal between site index and explanatory variables by reducing the random noise observed at the level of plots.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

In North America, site index is a widely used tool for assessing forest site productivity and as the basis for constructing yield tables (e.g. Skovsgaard and Vanclay, 2007; Weiskittel et al., 2011b). Site productivity corresponds to the capacity of a site to produce plant biomass given the stand history and management (Skovsgaard and Vanclay, 2007) and, in turn, productivity models have aided in understanding the spatial and temporal dynamics of productivity

* Corresponding author. Tel.: +1 418 656 2131x11116.

E-mail address: kenneth-agbesi.anyomi.1@ulaval.ca (K.A. Anyomi).

(e.g. Landsberg and Waring, 1997; Coops et al., 2011; Weiskittel et al., 2011a). Moreover, yield tables are important tools in biomass carbon estimation for tracking ecosystem carbon balances (e.g. Kurz et al., 2008). Site index models are adequate for pure evenaged stands and even though generally not applicable for mixed-species stands (Weiskittel et al., 2011b, p. 39), there have been some attempts at extending their use to mixed temperate forests (e.g. Seynave et al., 2005; Pinto et al., 2008). Mixed stands are common, as is the case in most natural systems, and understanding productivity dynamics necessitates taking into account spatial and temporal changes in forest composition and structure. This is especially so in temperate and boreal forests where post-fire or

^{0378-1127/\$ -} see front matter @ 2013 Elsevier B.V. All rights reserved. http://dx.doi.org/10.1016/j.foreco.2013.03.035

post-logging succession is characterized by an intermediate mixedwood stage (Bergeron et al., 2004; Hart and Chen, 2008).

Due to the spatial variability in factors that influence productivity (Chen et al., 2002), the fact that different populations coexisting in a landscape may have a differential response to growth regulating factors (Rehfeldt, 1985; Rehfeldt et al., 2002), and the extent control of a factor can change with varying scale (Peterson, 2000), random variability in productivity modelling can exceed 50% at the tree or plot levels (e.g. McKenney and Pedlar, 2003; Miller et al., 2004; Monserud et al., 2006; O'Neil et al., 2008; Lapointe-Garant et al., 2010, Fig. 6a). One way to deal with such variability is to determine at which scale details actually matter when attempting to predict productivity (Hogg et al., 2005; Urban, 2005). Some studies (e.g. Hogg et al., 2008; Rehfeldt et al., 2009; Aertsen et al., 2012) have suggested that models that are calibrated for broader spatial extents tend to perform better when applied to finer scales, compared to scaling up model outputs that were obtained at finer scales to larger regions.

Existing site index models are single-level models and difficulties in obtaining sample sizes large enough to capture variability within a defined region of study is a major factor limiting their use (Zeilstra, 2008). Also, observations within a group may not be independent in some cases and, thus, may need to be modelled independently at that spatial unit (e.g. Wagner et al., 2011). Given that both broad-scale (e.g. fire regimes; Taylor and Chen, 2011) and fine-scale (e.g. soil surface deposits, Mansuy et al., 2010) processes could influence stand dynamics, multilevel models could be adequate tools to model site index. Further, hierarchical models can take either a top-down or a bottom-up approach (Jarvis, 1993, p. 121). These are multilevel models where the outputs at one scale (e.g. regional for a top-down approach versus local for a bottomup approach) serve as inputs to models at different scales, thereby making it possible to account for variability associated with each scale while allowing for interactions across scales (e.g. Wagner et al., 2011). In a top-down approach (e.g. Hamel et al., 2004), larger scale processes are accounted for first and models are arranged such that regional estimates serve as input at finer scales. A bottom-up approach (Jarvis, 1993, p.115) is known for being openended, while the top-down approach constrains finer scale observations to lie within the range of observations that are obtained at a larger scale. In this study, we considered both approaches.

Trembling aspen (Populus tremuloides Michaux) is the most abundant and widely distributed deciduous tree species in North America (Perala, 1990; Peterson and Peterson, 1992). It is an important broadleaf species for the forest products industry (Ondro, 1989; Christersson, 2010), and among aboriginal communities of boreal Canada, every part of the tree is considered useful, particularly from a medicinal perspective. For instance, ground fresh aspen leaves are remedies for bee stings, mosquito bites and cuts, while the sap is useful as a vermifuge (Uprety et al., 2012). Together with paper birch (Betula papyrifera Marshall), trembling aspen is a pioneer species, that is, one of the first tree species to colonize an area following a major disturbance event, such as catastrophic wildfire (Perala, 1990), given its clonal habit. Usually pure stands of aspen are converted over time into mixed-species stands, largely in combination with black and white spruce (Picea mariana (Mill.) BSP, and Picea glauca (Moench.) Voss, respectively), yellow or white birch (Betula alleghaniensis Britt. and B. papyrifera Marsh. respectively) or maple (Robitaille and Saucier, 1998). This study took a multilevel approach to aspen productivity by (a) determining landscape- and plot-level factors that influence aspen site index within the boreal and temperate forests of western Ouebec. Based on selected growth drivers, (b) we parameterized site index models at landscape and plot levels and (c) determined if variables at both plot and landscape scales concurrently influenced productivity. A top-down model was first constructed, assuming that plot-level site index is primarily influenced by landscape-level variables. A bottom-up model was then constructed to verify to what extent, once site index is explained at the plot level, landscape variables could further help in explaining the observed variability in site index. We hypothesized that major drivers may differ with scale given that major disturbances such as fire occur on scales larger than forest stands and since stands within a particular region may have a shared pedological history due to geology and climate, we also expected to encounter some homogeneity in productivity for stands within a particular landscape. Given that stand structure and composition change through time, we further hypothesized that aspen site index is influenced by these changes. Finally, we hypothesized that both fine-scale and dominant regional site features (soil characteristics and climate) could influence productivity and that, for mixed wood stands, structural and compositional changes could interfere with direct site effects.

2. Materials and methods

2.1. Location, forest classification and forest dynamics

The study area is a 6-degree wide latitudinal transect (45–50°N) within western Québec, Canada (longitude 76–79°W). Soil surface deposits, drainage, and relief vary considerably within the study region, due in part to its history of deglaciation and pedogenesis. Factors acting concurrently such as climate and disturbance regimes, together with soil conditions, have defined particular vegetation types, which is the basis for the system of ecosystem classification implemented by the Ministère des Ressources naturelles (MRN) of Quebec (Robitaille and Saucier, 1998).

The study region is composed of two vegetation zones: (a) the northern temperate forest, which is dominated by hardwood and mixed stands; and (b) the boreal zone, which is predominantly coniferous. Within the limits of our study region, six bioclimatic domains (areas described by characteristic vegetation found on sites with average soil conditions, drainage and exposure; Robitaille and Saucier, 1998) can be identified, including sugar maple-bitternut hickory, sugar maple-basswood, sugar maple-yellow birch, balsam fir-yellow birch, balsam fir-white birch, and black sprucefeather moss domains (Robitaille and Saucier, 1998). The first four bioclimatic domains are within the northern temperate zone, while the latter two are within the boreal vegetation zone. The study region can be further subdivided into ecological regions, ecological sub-regions, regional landscape units, and ecological districts. Ecological regions are characterized by a particular distribution of vegetation types. Ecological sub-regions show a transition towards more northern or southern bioclimatic domains. Regional landscape units are defined on the basis of similarity of biophysical factors and vegetation type. Finally, ecological districts are land units characterized by particular relief, soil deposits and drainage regimes (Robitaille et al., 1989), and are thus potentially useful units in studying productivity-climate-stand dynamics.

Mean annual temperature in the region ranges from $-0.2 \,^{\circ}$ C to 5.7 °C from north to south. Annual precipitation exhibits low variability (±48 mm year⁻¹) around a mean 970 mm year⁻¹, with no particular spatial trend. Fig. 1 illustrates the two major vegetation zones, the bioclimatic domains, as well as the ecological districts from which plots were sampled for this study.

2.2. Inventory data

The data set compiled for the study covers 62 ecological districts within which there were 4948 inventory plots, including 1247 plots with aspen as the dominant or co-dominant species K.A. Anyomi et al./Forest Ecology and Management 302 (2013) 390-403



Fig. 1. Study area map. Hatching refers to ecological districts with more than 50% of spruce proportion.

in the canopy and where aspen occurs in pure or mixed stands of varying species composition. In 1970, the MRN started its province-wide measurement program, where temporary circular plots of 0.04 ha were positioned in its forested lands following a stratified random sampling scheme. In every plot, all trees >9 cm DBH (diameter at breast height, 1.3 m) were measured by species and diameter. Height and age at 1 m (from ring counting) were recorded for one to five study trees (usually three individuals) and these are individuals of the upper canopy. During its third inventory phase (1992–2002), measurements were extended to include site characteristics (including soil texture, depth of B and C horizons, drainage class, surface deposit type, humus type), which hitherto were only part of permanent sample plot inventories (Rouleau, 1994). Data for this study were thus restricted to only the third inventory program.

Given the uneven distribution of aspen plots per ecological district, we suspected that, for some districts, their numbers of plots would be insufficient for providing reliable estimates at the scale of landscapes. To verify this, we selected seven ecological districts having the highest number of plots. We then computed the variances that were associated with mean site index estimates, which were obtained from varying the sampling intensity (number of plots per ecological district from 1, 2, 3,...,32). Using bootstrapping techniques, we obtained 143 samples for each of the ecological districts, yielding 1001 'ecological district' units $(=7 \times 143)$ for each sampling intensity. Mean site index and its variance were estimated for each district and sampling intensity, and variances were then averaged per sampling intensity. Reduction in sample variance increased as the number of plots increased until it stabilized when eight or more plots were used per landscape. Consequently, ecological districts having less than eight plots were excluded from the analysis.

2.3. Climate data

Annual mean temperature, total precipitation, sum of degreedays above 5 °C, vapour pressure deficit, and potential evapotranspiration were obtained from the BioSIM model (ver. 9, Régnière and Saint-Amant, 2008) for all of the sample plots considered in this study. Plot averages were also computed for each of these variables by ecological district. BioSIM interpolates climate from a specified number of weather stations nearest to the point of interest and accounts for differences in elevation and aspect of the weather stations that are used. It also accounts for the distance of the weather stations to the point of interest by assigning greater interpolation weights to nearer stations. The five nearest weather stations were used for interpolations of the climatic variables (Anyomi et al., 2012). Site index estimates represent mean height at a referenced age and in this study the reference age was 50years. In order to ensure that the time frame over which site index is calculated is the same for climatic variables, we also considered 50-year averages of climate variables. For plots younger than 50years-old, the time frame that was used corresponded to the stand age. Finally, climate data for the months of June, July and August, which represent the growing season period across most of the sites, was computed to isolate seasonal climate relationships from annual or long-term mean responses.

2.4. Landscape factors potentially linked to aspen productivity

Wiens et al. (1985) have defined landscapes according to the existence of recurring patterns of ecosystems that are primarily explained by edaphic patterns, and the patchiness of which depends on the spatial extent and type of disturbance. Hence, apart from the use of climate (point 2.3), as a surrogate for "edaphic patterns", we considered the dominant (by area) surficial deposit type and drainage class by ecological district. These variables were derived from the photo-interpreted forest maps that were produced by the MRN during its third inventory program (Létourneau et al., 2003). We also included in the analysis the dominant disturbances that could affect aspen productivity. Fire data covering the period 1924-2009 were obtained from the MRN for the entire territory of the study. The mean annual burn rate (% year ⁻¹) was estimated for each ecological district and landscape units by averaging the proportion of terrestrial area burnt between 1924 and 2009. A mean harvesting rate (% year ⁻¹) was also computed from data for annual areas that had been subjected to clear-cutting for the period 1970-2005 from the forest maps produced by the MRN. Insect defoliation and windthrow are other disturbances that occur within the study area, but these are partial disturbances (Gendreau-Berthiaume et al., 2012) the effects of which, although important for withinstand gap dynamics (e.g. recruitment), do not influence stand structure and growth barely two decades following disturbance events (Kneeshaw et al., 2011). We further considered mean plot age at the landscape-level because landscape mean stand age can be used as surrogate of the disturbance regime, such that areas with a higher disturbance rate are characterized by younger stands compared to areas with a lower disturbance rate (Bergeron et al., 2004). Two variables were used to characterize mean plot age by ecological district: (a) mean age of all plots within a landscape; and (b) mean age of plots having aspen as the dominant or co-dominant species.

Finally, vegetation composition results from the combined effects of edaphic patterns and disturbances and, thus, could be an overall indicator of productivity, including the dominant potential vegetation and the dominant ecological type by ecological district, which were derived from the MRN photo-interpreted forest maps. The potential vegetation corresponds to the vegetation that is expected at the end of succession. Ecological types correspond to the association of potential vegetation with a drainage class (Robitaille and Saucier, 1998). We also verified if varying proportions of companion species to aspen in the landscape could be linked to aspen productivity. Landscape species proportion represents the ratio of the number of plots having a particular species within a landscape unit to the total number of plots within that landscape unit. The proportions of black and white spruce (favourite companion species of aspen), jack pine (Pinus banksiana Lamb.) and aspen were estimated by ecological district.

2.5. Local traits of productivity

Local microclimatic traits can distinguish the productivity of one site from that of its neighbouring environment, such as aspect, slope and altitude, and were considered when modelling aspen productivity at the plot scale. Beers' aspect, which was estimated as $1 + \cos((45^\circ-aspect))^\circ$ slope) was found to have significant effects on forest productivity in boreal forests of Alaska (Beers et al., 1966) and, therefore, was also considered.

We verified if areas of particular surficial deposit-drainage combinations could be associated with higher or lower potential productivity. We regrouped 43 deposit types into six classes identified by Mansuy et al. (2010) to characterize the hydric regime of a site. These classes were coded VAVC, MM, MAM, MAC, ROC, and ORG (Mansuy et al., 2010). VAVC denotes moraine and juxtaglacial deposits that are characterized by a very high abundance of stones and boulders and very coarse texture with extremely high potential for drying. MM refers to undifferentiated thick (>1 m) tills with moderate stoniness, while MAM are undifferentiated thin (0.25–1 m) tills with moderately abundant stoniness. MAC refers to outwash with moderately abundant stoniness (sandy to sandy-silty texture) and xeric drainage. ROC are rock outcrops with excessive drainage but with a thin organic or till layer. Finally, *ORG* are organic deposits that characterize peatlands. Soil texture and drainage variables were further included in the list of potential explanatory variables. Specific area of the mineral soil layer (A_w), a variable that is linked to mineral weathering, was also considered since it has been found to be an important indicator of productivity (Hamel et al., 2004). We also considered the proportion of soil clay, percentage of rock, soil organic carbon content using the model of Périé and Ouimet (2008, their Table 3), and depth of organic layer, all within the B horizon (Rouleau, 1994).

The plot diameter distribution is an indicator of stand structural diversity, which varies with the site productive potential (Paquette and Messier, 2011). On more productive sites, one should expect more complex and diverse structures compared to less productive sites (Boucher et al., 2006; Larson et al., 2008; Ouzennou et al., 2008). We considered Shannon index (Eq. (1)), Shannon evenness index, Simpson index (Lexerød and Eid, 2006), the coefficient of variation for plot mean diameter, and skewness of diameter distributions (Boucher et al., 2006) as potential explanatory variables (Table 1).

$$S_h = -\sum_{i=1}^{s} p_i \ln(p_i) \tag{1}$$

where p_i is basal area proportion of a diameter class *i* relative to total stand basal area, *s* is number of diameter classes.

2.6. Estimating aspen productivity

To estimate productivity, we used the site index model of Pothier and Savard (1998), which was calibrated from temporary sample plots (Eq. (2)). This model is currently in use within the province of Québec for estimating growth and yield of commercial species:

$$S = b_1 H_d^{b_2} (1 - e^{-b_3 A})^{b_4 S^{-b_5}} + \varepsilon$$
⁽²⁾

where *S* is site index at a reference age of 50 years as predicted from plot dominant height H_d (m) at age *A* from a height of 1 m. The b_1 , b_2 , b_3 , b_4 and b_5 coefficients are species-specific parameters of the model (Pothier and Savard, 1998, their Table 4), *e* is the base of natural logarithm and *e* is model error. For the third inventory data that was used in this study, tree age was estimated at a height of 1 m (Ouzennou et al., 2008). Stand dominant height which is the mean height of four trees of largest diameters per 400 m² area was first estimated using the following equation:

$$H_{d} = 1.3 + \left[\frac{\overline{D}_{4}}{\left(\frac{\overline{D}}{\overline{H}-1.3}\right) + \lambda_{2}(\overline{D}_{4} - \overline{D})} \right]$$
(2a)

where H_d is predicted dominant height, \overline{D}_4 is mean diameter of four largest trees on a plot, \overline{D} and \overline{H} are respectively mean diameter and height of study trees, λ_2 is a parameter (Pothier and Savard, 1998). Plot estimates of site index were averaged for each ecological district as an estimate of the landscape mean site index of aspen.

2.7. Modelling approach

Two types of models were constructed, viz., a plot-level and a landscape-level model. A variance analysis was first used for each model to preselect the variables that were significantly correlated (P < 0.05) with the site index at that scale using a combination of PROC MIXED and REG approaches in SAS (SAS Institute, Cary, NC). We then applied the approach used by Ung et al. (2001), in which the mean value of site index is modulated by modifiers:

$$S = \overline{S} \prod_{i=1}^{n} f_i(x_i) \tag{3}$$

Author's personal copy

394

K.A. Anyomi et al./Forest Ecology and Management 302 (2013) 390-403

Table 1

Variables considered in productivity modelling.

Climatic variables	Soil variables	Stand structural and disturbance related variables
Plot level variables		
Annual mean temperatures (2.19, [], 1.02 °C year $^{-1}$)	Aspect (120, [], 119.7°)	Shannon index (2.45, [], 0.40)
Total precipitation (969.6, [], 47.8 mm)	Slope (7.7, [], 7.2%)	Shannon evenness index (1.02, [], 0.17)
Growing season days (134.5, [], 9.7 days)	Altitude (300, [], 38.58 m)	Simpson index (0.89, [], 0.06)
Potential evapotranspiration (512.7, [], 21.16 mm)	Beers' aspect (0.94, [], 0.7)	Spruce basal area proportion (11.48, [], 16.1%)
Annual sum of degree-days above 5 °C over a year (1464, [], 135 °C year ⁻¹)	Soil texture ([13])	Aspen basal area proportion (48, [], 24.2%)
Vapour pressure deficit (173.8, [], 7.9 kPa)	Drainage ([10])	Mean plot age (50, [], 15 years)
	Specific area of the mineral soil layer (52,721, [], 29,914 $m^2m^{-3})$	Mean aspen age (47, [], 16 years)
	Depth of organic layer (6.7, [], 6.1 cm)	Potential vegetation ([T3])
	Soil surface deposit ([7])	Ecological type ([T3])
	Soil clay proportion (31, [], 22%)	Ecological district ([T3])
	Soil organic carbon content (187.7, [], 0.6 g kg ⁻¹)	Landscape unit ([T3])
	Percentage of rock/stoniness (17, [], 21%)	Ecological sub-region ([T3])
Landscape level variables		
Mean degree days (1500, [], 136 °C year ⁻¹)	Dominant surface deposit ([8])	Spruce plot proportion (68, [], 18%)
Annual precipitation (977.5, [], 48.8 mm)	Dominant drainage ([3])	Plots proportion with spruce in dominant/co-dominant
		position (33, [], 17%)
	Dominant texture ([3])	Jack pine proportion (18, [], 16%)
	Mean stoniness (0.21, [], 0.12%)	Aspen proportion (48, [], 18%)
	Mean depth of organic matter (6.48, [], 1.21 cm)	Plots proportion with aspen in dominant/co-dominant position (30, [], 16%)
	Mean clay content (0.25, [], 0.14%)	Dominant potential vegetation ([10])
		Dominant ecological type ([18])
		Regional landscape unit ([9])
		Mean age ^a (47, [], 9 years)
		Mean age ^b (54, [], 9 years)
		Annual burn rate per ecological district (0.044, [], 0.1)
		Annual harvest rate (76.3, [], 1.7 ha year $^{-1}$)

[] Contains degrees of freedom from which mean and standard error values were estimated; where degrees of freedom is not provided, it implies 1247 for plot level variables and 62 for landscape level variables. [T3] means that it is provided in Table 3.

^a Mean age estimated using plots within an ecological district having aspen as dominant and/co-dominants.

^b Mean age estimated from all plots within an ecological district.

Table 2 Plot model parameter values.					
Order of entry	Variable	Mean	Parameter	Estimate (Std. Err.)	Contribution to R^2 (%)
1	Basal area proportion in spruce	0.115	$\beta_{LGspr.p}$	-0.051 (0.0045)	12
			$\beta_{q.Gspr.p}$	0.006 (0.0014)	
2	Stoniness	0.175	$\beta_{L.Ston.p}$	-0.0404 (0.0047)	6.9
			$\beta_{q.Ston.p}$	0.0062 (0.0021)	
3	Shannon index	2.45	$\beta_{l.Shan.p}$	0.2473 (0.0217)	3.5
4	Mean aspen age (years)	47.0	$\beta_{l.AspenAge.p}$	-0.09 (0.011)	4.6
			S _d	0.329 (0.1179)	8.2
			\overline{S}_p	19.5	

where \overline{S} is mean site index estimated from the calibration data set which represents a regional level mean for the landscape model. Eq. (3) is the product of *n* modifiers having a value close to unity when the variables x_i are equal to their average x_i observed values, and increase or decrease when moving further away from the average:

$$f_i(x_i) = 1 + \beta_{lxi} \left(\frac{x_i - \bar{x}_i}{\bar{x}_i} \right) + \beta_{qxi} \left(\frac{x_i - \bar{x}_i}{\bar{x}_i} \right)^2 \tag{4}$$

where $\beta_{l,Xi}$ and $\beta_{q,Xi}$ represent the linear and quadratic effects respectively of the variables x_i on site index. Categorical variables

Table 3

Plot-level model fits under varying assumptions of random parameter units. *P*-value are given for the nested random component of the model.

(0.103)

8			
Level of categorization	Ν	R^2	P-value
Ecological region	9	0.29	0.34
Ecological sub-region	13	0.28	0.42
Landscape unit	23	0.31	0.07
Ecological district	62	0.35	0.01
Potential vegetation	10	0.28	0.37
Ecological type	18	0.28	0.30

K.A. Anyomi et al. / Forest Ecology and Management 302 (2013) 390-403

Parameter values of the landscape-level model.					
Order of entry	Variable	Mean	Parameter	Estimate (Std. Err.)	Contribution to R^2 (%)
1	Plot proportion with spruce	0.684	$\beta_{LSpr.L}$	-0.0649 (0.0214)	34
2	Mean plot stoniness	0.205	$\beta_{LSton.L}$	-0.0336 (0.010)	9
3	Degree-days (°C year ⁻¹)	1500	βl.dd.l	0.281 (0.059)	8
4	Mean plot age (years)	48.5	$\beta_{LAge.L}$	-0.128 (0.030)	11
			\overline{S}_L	19.7 (0.118)	

(soil surface deposit types, texture, etc.) were converted to dummy

Table 4

variables so that they could be used in NLMIXED procedure in SAS. From the pre-selected pool of variables, we retained the climate variables that provided the highest correlation with the response variable, together with the lowest root mean square error (RMSE) and, subsequently, added other variables one by one. Inclusion of covariates in the model was in two stages: (a) we first studied model residuals to verify which variables were most significantly (P < 0.05) related with site index; and (b) through a stepwise procedure with forward selection, we selected the variable combination that most explained the variability in aspen site index. As a preventive measure against model over-fitting, a covariate was only retained in the model if it was significant (P < 0.05) in the model and additionally contributed significantly (at least 1%) to the variance explained (or in reducing RMSE). Entry or exit of a modifier was determined with a likelihood-ratio test (Bates and Watts, 1988).

In order to capture random variation, we introduced a random (*s*) component into Eq. (3) to account for locally distinctive traits (Anyomi et al., 2012), thereby obtaining the following equation:

$$S = (\overline{S} + s) \prod_{i=1}^{n} f_i(x_i)$$
(5)

The parameters of Eq. (5) were estimated with the NLMIXED procedure. For the landscape model, the random component could imply characteristics that are associated with specific dominant species, potential vegetation or other characteristics peculiar to landscape units, while for the plot-level model, it will depend on the selected level of categorization. For instance, a random plot-level parameter could imply particular local traits (e.g. same population) while a random parameter at the level of ecological districts might imply the influence of a regional factor (e.g. effects of climate on plot-level productivity).

We considered two approaches: (i) a top-down approach, where a landscape model was first constructed and variability in model residuals at the level of plots was explained using plot-level variables (Fig. 2); and (ii) a bottom-up approach, where a plot-level model was first constructed and variability in model residuals at the plot-level explained with landscape variables (Fig. 2). The variable selection and model building procedure were done following the same criteria as described earlier. Mixed models are used in hierarchical modelling due to their potential for capturing both fixed and random effects that may occur at different spatial scales (Zeilstra, 2008), in which case the fixed effect explains variability at one scale while the random component could be made to vary at a different scale. Together they could best explain the variability in the response variable. Alternatively, two models could be arranged hierarchically, where outputs of a second-level model provide inputs into a first-level model (Wagner et al., 2011). For the top-down approach, we applied this procedure in linking the landscape-level model to the plot-level model (Fig. 2) by replacing the



Fig. 2. Conceptual framework of the modelling approach. \hat{S}_p , \hat{S}_L are predicted estimates of site index and \bar{S}_p , \bar{S}_L are mean site indices estimated from plot and landscape level site index values respectively. S_L , S_p are random error variables respectively at landscape and plot levels.

mean site index value of Eq. (3) (which, for the plot-level model, **3. Results**

3.1. Observed variability in site index

would have referred to the mean site index estimate) with site index estimates that were predicted with the landscape-level model. Conversely, the plot-level model accounts for landscape-level variability in site index that corresponds to a homogeneity in productivity associated with stands that are located within a defined landscape (e.g. stands of similar origin, topography, disturbance regime, etc.). For the bottom-up approach, we maintained the structure of Eq. (3), to which we introduced significant landscape-level variables as modifiers. To verify if plot and landscape variables concurrently influenced plot-level site index, we compared a model that was calibrated at the plot-level and hereafter referred to as 'partial model' with a 'full' model that includes plot-level variables and selected landscape variables in predicting plot-level site index. The two models were compared using the Akaike information criterion (AIC) and a maximum likelihood-ratio test for nested models.

Finally, we verified if the level of ecological districts was the appropriate scale when modelling aspen site index. For this purpose, seven alternative models at the plot level were tested by including different levels of categorization in the random-effect parameter. Two types of categorization were used. One type corresponded to spatial units of different size: ecological regions, ecological sub-regions, regional landscape units and ecological districts. The second type referred to land stratification: potential vegetation and ecological types. These models were rated against the model that included only fixed effects with a likelihood-ratio test (Bates and Watts, 1988).



Fig. 3. Variability in productivity as a function of (a) latitude, (b) aspen proportion and (c) aspen age. Both histograms in (a) and (c) denote the number of plots at each latitude and age class respectively. The dark lines in (a) each represent two standard deviations while the red line in (b) and (c) represents a linear fit to the distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

We observed only a slight latitudinal decrease (Fig. 3a) in site index from south (45°N) to north (49°N), despite the change in the length of the growing season over the transect (from 95 days in northern plots to 190 days in southern plots, with a mean value of 143 days). Most plots (83%) were found in mixed stands (with aspen contribution to total plot basal area less than 75%). In general, site index of aspen was higher in pure stands and decreased in mixed stands (Fig. 3b). Younger stands also exhibited higher site index values, both when mean plot age was considered and when only aspen age was singled out (Fig. 3c). The slope of decline in site index was steeper for stands that were younger than 60 years of aspen age, while stands about 60 years and older exhibited low and stable site index (Fig. 3c). There was also a relatively high variability in site index for younger stands and a decrease of variability with stand age (Fig 3c).

At the level of ecological districts, aspen proportions ranged from 7 to 67% (mean of 30%) while spruce proportions ranged from 11% to 97% (mean of 68%). The mean proportion of aspen in plots increased moderately (r = 0.47, P < 0.05) in ecological districts where aspen was more abundant (Fig. 4a), with aspen abundance itself being related to mean clay content of the B horizon (r = 0.43, P < 0.05) but not to the mean disturbance rate (fire, harvest, or both cumulated; r = 0, P = 0.43). For spruce, which was the main companion species of aspen in mixed stands, its proportion per plot increased with the abundance of spruce in the landscape (Fig. 4b). Yet, the mean proportion of aspen per plot was not related (r = -0.29, P = 0.10) to the abundance of spruce in the landscape (Fig. 4c). Mean proportion of spruce per plot tended to increase moderately (r = 0.63, P = 0.00) with dominant soil deposit type and also moderately (r = 0.35, P = 0.05; Fig. 4d) with mean stand age. While this response was also true (r = -0.58, P < 0.05) for aspen regarding the mean age of all (aspen and non-aspen) plots, it was not the case when mean age was estimated from aspen plots only (r = -0.29, P = 0.10). Nevertheless, the two estimates of age were highly correlated (*r* = 0.79, *P* < 0.05). Contrary to expectation, the mean age of plots that included aspen was not related to the disturbance rate (fire, harvest, or both) at the level of ecological districts. We also observed no significant correlation between burn rate and aspen site index at the scales of both ecological district (P = 0.60) and regional landscape unit (P = 0.49). Mean age that had been estimated from all plots, however, was weakly and negatively related with burn rate at the level of landscape units only (r = -0.28, P = 0.03).

3.2. Plot-level drivers of aspen productivity as rated with site index

Even though we observed a significant correlation between site index and growing season days (P = 0.001) and site index vs. vapour pressure deficit (P = 0.03), none of the plot-level climatic variables were retained by the stepwise procedure with forward selection, due to the selection criterion. We observed significant effects of soil surface deposit (explaining 7% of variability in aspen site index) and soil texture (7%). Negative effects on site index were observed with the inclusion of spruce basal area proportion (12%), stoniness (8%), stand age (7%), aspen age (6%), soil organic carbon content (6%), slope (2%), and depth of the organic layer (1%). In contrast, the specific area of mineral soil layer exhibited a positive effect (6%) on aspen plot-level site index, as did clay content (5%), and Shannon and Simpson indices (each explaining 1% of the variation). Insignificant correlations were observed with Beers aspect, altitude, and all other variables listed in Table 1.

K.A. Anyomi et al./Forest Ecology and Management 302 (2013) 390-403



Fig. 4. Relationships between (a) aspen plot proportion computed from basal area and the plot proportion within the landscape having aspen (b) spruce plot proportion computed from basal area and the plot proportion within the landscape having spruce (c) aspen proportion computed from basal area and plot proportion having spruce and (d) spruce proportions computed from basal area and stand age.



Fig. 5. Main drivers of aspen productivity at the plot level.

Of the significant variables, the first that was selected was spruce basal area proportion, and by using forward selection, we further added stoniness, Shannon index, and aspen mean age (Table 2, and Fig. 5a–d):

$$S_p = (S_p + s_d) f_{Gspr.p} f_{Ston.p} f_{Shan.p} f_{AspenAge.p}$$
(6)

where \hat{S}_p and \bar{S}_p denote respectively the predicted and mean values of site index at the plot-level, $f_{Gspr,p}$ is a modifier (Eq. (4)) accounting for spruce basal area proportion, $f_{Ston,p}$ for substrate stoniness, $f_{Shan,p}$ for stand structural diversity as measured by Shannon index, $f_{AspenAge,p}$ for aspen age at the plot level, and s_d is a random parameter. This combination of fixed effects (when s_d is fixed to 0) explained 29% of variation in plot-level site index (Table 2). There were some gains in explained variance when levels of categorization were included in the random-effect parameter; gains made (6%) by using ecological districts were slightly but significantly higher (Table 3), both compared to the rest of the other levels of categorization and to the model including only fixed effects. Despite the fact that there was instability in variability of site index with stand aging, the final model does not exhibit any heteroscedasticity.

3.2.1. Main drivers of aspen productivity at the landscape level

The annual sum of degree-days was the only climatic variable that met the selection criterion. Mean aspen site index linearly increased with degree-days with a coefficient of determination of 8% (Fig. 6a). The mean stand age that was estimated from all plots in an ecological district, and which was estimated from plots having aspen as dominant or co-dominants, explained respectively 14% and 23% of variation in site index, with both exhibiting a significant linear negative effect on aspen site index at the scale of landscapes (Fig. 6b for the latter). We subsequently selected the latter in the following steps of analysis. The proportion of spruce in the landscape had a stronger and negative influence on aspen site index, explaining 34% of variation in the latter. As spruce proportion increased in the landscape, site index of aspen reduced accordingly, especially when the proportion of spruce was higher than 50% (Fig. 6c). The mean stoniness of the B-horizon by landscape was also found to have a significant positive effect on aspen site index, explaining 17% of variability (Fig. 6d). The harvest rate was significantly correlated with aspen site index even though it did not meet our variable selection criteria (results not shown). Aspen proportion in the landscape was not a significant (P = 0.80) indicator of aspen site index, as was also the proportion of jack pine (P = 0.62) and the proportion of other species (non-spruce and non-aspen) combined. The model (Eq. (7)) explains 63% of variation in landscape site index (Table 4).

$$S_L = (S_L + s_L) f_{Spr.L} f_{Ston.L} f_{Age.L} f_{DD.L}$$
(7)

where \hat{S}_L is site index predicted at landscape level, $f_{Spr.L}$, $f_{Ston.L}$, $f_{Age.L}$, and f_{DDL} are respectively the modifiers (Eq. (4)) for the plot proportion of spruce in an ecological district, the mean stoniness of the B horizon, the mean age of aspen in an ecological district, and the

mean degree–days. s_L is a random parameter and \overline{S}_L is the mean site index at landscape level. Table 3 summarizes the parameter values for the landscape model (Eq. (7)). The random parameter s_L was found not to be significant (P > 0.05).

3.2.2. Landscape vs plot-level productivity drivers – are they complementary?

With a bottom-up approach, analysis of variance of plot-level residuals of Eq. (6) and the stepwise procedure with forward selection led to a model with entries in the order; (a) spruce plot proportion within landscape and (b) landscape mean degree-days together explained 34% of variability in plot-level site index:

$$\widehat{S}_{p.bottom-up} = (\overline{S}_p + S_d)(f_{Cspr.p}f_{Ston.p}f_{Shan.p}f_{AspenAge.p})(f_{Spr.L}f_{DD.L})$$
(8)

where $\widehat{S}_{p.bottom-up}$ corresponds to the predicted value of site index at the plot-level with a bottom-up approach. Parameter values are provided in Table 5. The top-down approach led to the following model that explained 35% of variability in plot-level site index:

$$\widehat{S}_{p.top-down} = (\widehat{S}_L + S_d) f_{Gspr.p} f_{Ston.p} f_{AspenAge.p}$$
(9)

where $\hat{S}_{p,top-down}$ corresponds to the predicted value of site index at the plot-level with a top-down approach.

Given the high degree of similarity in major drivers of site index at both scales and using both approaches, we verified that the selected landscape variables operated concurrently with plot-level factors in driving plot-level site index. We compared Eq. (6) with only fixed effects, i.e., plot-level or 'partial' model, to two 'full' models (either Eqs. (8), or (9), depending on the approach), with the latter having landscape variables nested within Eq. (5). Likelihood-ratio tests show that the full model could not be rejected in favour of the partial model (F_{obs} = 28.18) either for the top-down approach or for the bottom-up approach (F_{obs} = 51.35). Likewise, AIC values justify selecting the full model that was obtained from the bottom-up approach (5593) over the partial model (5632), even though we did not observe same (AIC = 5633) with respect to the full model from top-down approach. In the present case, a hierarchical (bottom-up) approach to modelling site index thus better accounts for cross-scale concurrent effects of site index drivers.

Table 5

Parameter values of the plot-level model with nested landscape variables

Order of entry	Variable	Mean	Parameter	Estimate (Std. Err.)	Contribution to R^2 (%)
1	Basal area proportion in spruce	0.115	$\beta_{l.Gspr.p}$	-0.0486 (0.0045)	12
			$\beta_{q.Gspr.p}$	0.006 (0.0014)	
2	Stoniness	0.175	$\beta_{L.Ston.p}$	-0.0436 (0.0051)	6.9
			$\beta_{q.Ston.p}$	0.0079 (0.0022)	
3	Shannon index	2.45	$\beta_{l.Shan.p}$	0.2342 (0.0219)	3.5
4	Mean aspen age (years)	47.0	$\beta_{l.AspenAge.p}$	-0.0929 (0.011)	4.6
5	Plot proportion with spruce	0.684	$\beta_{l.Spr.L}$	-0.0466 (0.019)	1
6	Degree-days (°C year ⁻¹)	1500	$\beta_{l.DD.L}$	0.1806 (0.0526)	1
			S _d	0.176 (0.082)	5.7
			\overline{S}_p	19.52 (0.1160)	

4. Discussion

4.1. Structure and compositional changes drive aspen productivity

Inter-stand variability was observed to be important in explaining site index variation (Table 2) and included spruce basal area proportion, stoniness, stand structure as measured by Shannon index, and aspen age. Negative effects of spruce proportions on aspen site index were an indication of the sensitivity of site index to stand species composition (Pinto et al., 2008) and perhaps also signalled a temporal instability in site index (Bontemps et al., 2009; Cavard et al., 2011) driven by stand dynamics. Over time, understory shade-tolerant species (mostly fir and spruce) occupy canopy gaps and gradually replace shade-intolerant aspen, with the apparent consequence of declines in aspen productivity. These dynamics are thus competition induced as a result of species composition and stocking (Pinto et al., 2008; Vallet and Perot, 2011) with consequences for site productivity. Compositional changes such as an increase in spruce proportion can also have more direct effects on site fertility through negative impacts of spruce litter on nutrient mineralization and availability, since it decomposes slowly compared to hardwood litter (Légaré et al., 2005; Prescott et al., 2000), leading to an increased depth of organic layer, making soils cold and constraining aspen growth (Figs. 5a and 6c). In this study, we suspect more the latter even though teasing apart these two phenomena was beyond the scope of this study. Given the sensitivity of aspen to soil moisture (e.g. Hogg et al., 2008), stoniness was expected to be an important inter-site variable. Given that aspen has a preference for fine textured, well-drained and moist clay soils (Peterson and Peterson, 1992, p. 65; Paré et al., 2001), with high stone fraction, soils tend to have more rapid drainage and less available moisture (Alexander and McLaughlin, 1990) and, hence, lower productivity. Pinto et al. (2008) and Seynave et al. (2005) made similar observations for Norway spruce and silver fir, an observation they attributed to a soil depth effect. Shannon index has been widely used as a measure of stand structural complexity (Boucher et al., 2006), given that gap dynamics lead to release of suppressed trees (Groot and Hökkä, 2000) and, hence, diversity (Boucher et al., 2006) in the diameter distribution (except under conditions where all species are present and have different diameters, then the Shannon index might mirror stand composition). We observed a direct relationship between Shannon index and site index, consistent with findings of Paquette and Messier (2011) and Long et al. (2007). Indeed, the biophysical site index model of Ung et al. (2001), which has been calibrated within pure stands, did not exhibit a significant influence of Shannon index on aspen site index, further re-enforcing the fact that it is an index related to stand dynamics.

At the scale of landscapes (ecological districts), the annual sum of degree-days was the most important climatic driver of aspen growth, as is the case for many other boreal species (Huang et al., 2010). In contrast to earlier studies (e.g. Seynave et al., 2005; Pinto et al., 2008; Lapointe-Garant et al., 2010; Vallet and Perot, 2011), this variable was only the third variable to enter the landscape-level site index model (Table 4). This is also apparent in Fig. 3a, where there is only a slight decrease in site index with change in latitude mostly because aspen tends to occupy rich clay sites in the north (Paré et al., 2001). We observed a major negative effect of landscape spruce proportion on aspen site index suggesting (1) niche sharing between aspen and spruce, which creates identifiable vegetation patterns at the scale of landscapes (Fig. 4), and (2) an influence of spruce on aspen site index. Other studies in the region (e.g. Harvey et al., 2002; Lecomte et al., 2005; Belleau et al., 2011) have reported more frequent colonization by pioneer hardwoods on specific soil deposits, largely aspen, in relation to the mean clay content of the B horizon (Belleau et al., 2011, their Figs. 2 and 3). Irrespective of site-specific variability (for instance, site nutrient status) or spruce canopy position within a stand, which were previously reported to confound aspen–spruce relations (e.g. Légaré et al., 2005; Calder and St. Clair, 2012), some identifiable patterns exist at the landscape scale regarding the influence of spruce cover on aspen site index. Results also show that aspen mean site index at landscape scale is reduced by a high stone fraction (>20%) (consistent with plot-level observations and also with earlier observations of Paré et al. (2001) who reported higher site index estimates on clay sites compared to till, the latter substrate having relatively higher stone proportions), and that this reduction is more important than a direct climate effect (Fig. 6d).

Results from the analysis of nested models (Eqs. (8) and (9)) showed a concurrence of both landscape and plot-level drivers in terms of stand site index. So we ask in what respect do more spruce in the landscape affect stand productivity when spruce abundance is already accounted for in the plot-level model (Eq. (6)). Given the moderate correlation with dominant soil surface deposit (r = 0.63, P = 0.000), spruce plot proportion could be a surrogate of the deposit type at that scale and that vegetation homogeneity within a defined landscape could be associated with geology, landscape topography (Fekedulegn et al., 2003), or history of deglaciation (Veillet, 1994) that produced particular dominant surface deposits at that scale. Thus, at landscape level, spruce plot proportion does not have a direct causal effect on aspen stand-level site index; rather, it is indicative of a more regional factor that influences aspen productivity. Fire is a major driver of stand dynamics across all latitudes in western Québec with varying intensities and return intervals, and is capable of creating particular mosaics of forests across landscapes (e.g. Bergeron et al., 2004). Forest harvesting in the past has also contributed to particular mosaics and could also contribute to landscape forest composition (Barrette and Bélanger, 2007; Alvarez et al., 2011). The influence of landscape spruce proportion on site index could also be linked to the past disturbance regime such that it is a surrogate of past disturbances at that scale. Indeed, we observed spruce to vary in composition across the study landscapes from south to north (Fig. 1), even outside its expected zone, as detailed by the Quebec forest classification system (Robitaille and Saucier, 1998, black sprucemoss bioclimatic domain). Our observations are consistent with some earlier studies (Barrette and Bélanger, 2007; Alvarez et al., 2011). With the available fire (1924-2009) and harvest (1970-2005) data for our landscapes, we could however not confirm this hypothesis, since we suspect that our disturbance data did not span a sufficient period of time to be significantly correlated with spruce proportion but the observed moderate correlation with mean age could be indicative of this. Studies (e.g. Drever et al., 2006) have indeed confirmed that distinct assemblages of canopy species are associated with particular fire regimes, re-emphasizing our hypothesis that spruce landscape proportions are likely a surrogate of the disturbance regime at that scale. Since disturbances are driven by climate (Ali et al., 2012), spruce landscape proportion could also be a consequence of an indirect effect of past climate or climate averaged over a longer time span.

Finally, site index is assumed to be constant through time (Skovsgaard and Vanclay, 2007) but consistent with studies that observed the contrary (e.g. Bontemps et al., 2009; Cavard et al., 2011), the present study showed negative effects of both aspen and stand aging (Figs. 3c and 4d) on aspen site index. Stand age and dominant height are derived from measurements on dominant and co-dominant trees (Cumming et al., 2000), the canopy position of which may be unstable through time (Raulier et al., 2003), especially for shade-tolerant species (Mailly et al., 2009). Individuals currently dominant or co-dominant in the canopy may not have always been in those positions, thus leading to the influence of stand dynamics on tree height growth and then subsequently on site index. Existence of productivity changes is another hypothesis that may explain the effect of stand age on site index (e.g. Bontemps et al., 2009). Also, the risk of underestimating actual post-disturbance age with stand age increases through time (Garet et al., 2012), even with shade-intolerant species such as trembling aspen (Cumming et al., 2000). Yet, stand age remains a widely used measure of successional stage and cohort assignment to early, mid- or late successional phases (Harvey et al., 2002). We considered two age variables that were estimated by district, one using all 4948 stands located within our 62-districts and the other with only 1247 plots, which have aspen in a dominant or co-dominant canopy position and both age variables showed an inverse relationship with aspen site index, even though only the latter was included as fourth entry variable into the landscape-level model (Table 4).

4.2. Scale and productivity

With the plot-level model (Eq. (6)), which assumes random variability among ecological districts, there was still a high percentage (66%) of unexplained variation, which was consistent with several studies that have been conducted within the study region and elsewhere. O'Neil et al. (2008) reported random inter-site variability of 59% and Lapointe-Garant et al. (2010) reported 54% unexplained variability, attributable to between-tree variability within plots. In explaining such high plot-level random variability in site index, we hypothesize that it was because we extended the use of site index to mixed-species stands, when in fact site index models are normally calibrated for single-species and even-aged stands (Skovsgaard and Vanclay, 2007; Weiskittel et al., 2011b). That notwithstanding, changing the scale of study reveals a different pattern. Of the 72% of variability that the landscape model explained (Eq. (7)), a nonsignificant (P = 0.49) 10% was due to random variability. This was a marked difference from plot-level observations, suggesting that the plot scale or actual plot size (400 m^2) might be too small a scale for site index modelling in mixed stands. Given the striking similarity in the factors that influence aspen landscape- and plotlevel site index, the overall variance that was explained by these factors at both scales, and the cross-scale combined effects of these factors (Eqs. (8) and (9)), we argue that a hierarchical bottom-up approach to modelling site index is appropriate. It also suggests that, for both operational and predictive purposes, a mixed landscape- and plot-level model (especially Eq. (8)) is more appropriate than a single plot-level model (Eq. (6)).

4.3. Model evaluation and applications

The plot-level model provides an opportunity for studying productivity within mixed-species stands, which has not been addressed in earlier studies carried out within the boreal region (e.g. Ung et al., 2001; Chen et al., 2002; Bravo-Oviedo et al., 2010; Lapointe-Garant et al., 2010; Périé et al., 2012) even though some evidence exists from the temperate forests (e.g. Vallet and Perot, 2011). The landscape model obtained from 62 districts with four fixed-effect variables is also parsimonious, explains most of the variation ($R^2 = 62\%$) in the data, and is unbiased.

The landscape model presents a practical and useful tool for forest management and decision-making, given the effects between climate and landscape processes (Soja et al., 2007; Kurz et al., 2008; Girardin et al., 2011; Girardin et al., 2012), and their effects on productivity can be better understood. The landscape model could be useful in understanding regional variation in productivity due to increases in growing season lengths (e.g. Kim et al., 2012), resulting in species expansions (e.g. Huang et al., 2008), niche movements (Pearman et al., 2007), and biome shifts (e.g. Beck et al., 2011). For instance, climate could affect aspen productivity through direct positive effects (Fig. 6a), or indirectly through disturbance-driven stand dynamics (Fig. 6b and c). Even though species-specific growth responses are to be expected (e.g. Drobyshev



Fig. 6. Main drivers of aspen productivity at the landscape level.

K.A. Anyomi et al. / Forest Ecology and Management 302 (2013) 390-403

et al., 2013), given evidence of species interactions (Figs. 5a and b and 6c), losses in aspen productivity could be realized through spruce gains. Moreover, the proportion of spruce plots in the landscape has consequences for wildlife habitats (Stam et al., 2008). Given the high spruce proportion in mixed landscapes, even in the southern boreal forest (Fig. 1), a re-characterization of vegetation categories might be considered (Barrette and Bélanger, 2007; Alvarez et al., 2011). Finally, given that accurate biomass carbon estimation hinges upon the precision of yield tables (Kurz et al., 2008), and that yield tables are normally constructed for singlespecies stands (Weiskittel et al., 2011b), calibrated models could aid in more accurately tracking the dynamics of aboveground carbon pools within these ecosystems.

5. Conclusion

Site index, a widely used measure of site productivity in North America, is generally assumed to be constant through time and over varying stocking intensities. While this assumption could be tenable within single-species and even-aged stands (Skovsgaard and Vanclay, 2007), our results demonstrate the contrary for aspen in mixed-species stands. This study reveals the predominance of stand dynamics over direct climatic and site effects on aspen site index within mixed stands. Given that site index is an important input variable to growth and yield models and, hence, carbon management, caution should be exercised when applying site index models that have been calibrated in pure stands to mixed stands. Our results also show that plot-level site index estimation is associated with high random and unexplained variability, suggesting that scaling-up could be an appropriate strategy when modelling site index. Given that dominant deposit and indirect climatic effects create some homogeneity within the landscape, a hierarchical approach that accounts for this homogeneity could be useful in adequately explaining the ecological links. Since this study solely investigated aspen site index, we suggest similar studies be conducted for spruce and other major species. A potential limitation of the present study has to do with selection of study trees; in Quebec, three or four largest (diameter) trees are not systematically selected as top height trees within a 400 m² plot. Therefore, top height is estimated using a specific equation (Pothier and Savard, 1998). Insufficient top height trees could thus lead to under- or over-estimation of site index for individual species. Moreover, given that dominant species may be unstable through time (Raulier et al., 2003; Mailly et al., 2009), the use of an index of site productivity that is independent of species but that accounts for stand dynamics may help deal with this problem.

Acknowledgments

Inventory, fire and harvest data were obtained from the Ministère des Ressources naturelles of Quebec. Data on dominant potential vegetation that was computed by ecological districts were obtained from Guillaume Cyr and Martin Després (Direction des Inventaires Forestiers, MRN). We thank Nicolas Mansuy for suggesting testing Beer's aspect variable, Hakim Ouzennou for statistical help, and Dr. W.F.J. Parsons for correcting the English text. Funding for the study came from an NSERC (Natural Sciences and Engineering Research Council of Canada) project grant to Dr. Yves Bergeron.

References

- Aertsen, W., Kint, V., Muys, B., Van Orshoven, J., 2012. Effects of scale and scaling in predictive modelling of forest site productivity. Environmental Modelling & Software 31, 19–27.
- Alexander, E.B., McLaughlin, J.C., 1990. Soil porosity as an indicator of forest and rangeland soil condition (compaction) and relative productivity. In: In

Proceedings of the Soil Quality Standards Symposium, October 23, San Antonio, TX, USDA Forest Service, Washington, DC, WO-WSA-2, pp. 52–61.

- Ali, A.A., Girardin, O., Ginries, M.P., Hély, C., Tinquaut, F., Guellab, A.E., Valsecchi, V., Terrier, A., Bremond, L., Genries, A., Gauthier, S., Bergeron, Y., 2012. Control of the multimillennial wildfire size in boreal North America by spring climatic conditions. PNAS USA. 109 (51), 20966–20970. http://dx.doi.org/10.1073/ pnas.1203467109.
- Alvarez, E., Bélanger, L., Archambault, L., Raulier, F., 2011. Portrait préindustriel dans un contexte de grande variabilité naturelle : une étude de cas dans le centre du Ouébec (Canada). Forestry Chronicle 87, 5.
- Anyomi, K., Raulier, F., Mailly, D., Girardin, M., Bergeron, Y., 2012. Using height growth to model local and regional response of trembling aspen (*Populus tremuloides* Michx.) to climate within the boreal forest of western Québec. Ecological Modelling 243, 123–132.
 Barrette, M., Bélanger, L., 2007. Reconstitution historique du paysage préindustirel
- Barrette, M., Bélanger, L., 2007. Reconstitution historique du paysage préindustirel de la region écologique des hautes collines du Bas-Saint-Maurice. Canadian Journal of Forestry Research 37, 1147–1160.
- Bates, D.M., Watts, D.G., 1988. Non-Linear Regression Analysis and Its Applications. John Wiley & Sons, New York, p. 359.
- Beck, P.S.A., Juday, G.P., Alix, C., Barber, V.A., Winslow, S.E., Sousa, E.E., Heiser, P., Herriges, J.D., Goetz, S.J., 2011. Changes in forest productivity across Alaska consistent with biome shift. Ecology Letters 14, 373–379.
- Beers, T.W., Dress, P.E., Wensel, L.C., 1966. Aspect transformation in site productivity research. Journal of Forestry 64, 691–692.
- Belleau, A., Leduc, A., Lecomte, N., Bergeron, Y., 2011. Forest succession rate and pathways on different surface deposit types in the boreal forest of northwestern Quebec. Ecoscience 18 (4), 329–340.
- Bergeron, Y., Gauthier, S., Flannigan, M., Kafka, V., 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in Northwestern Québec. Ecology 85 (7), 1916–1932.
- Bergeron, Y., Cyr, D., Girardin, M.P., Carcaillet, C., 2010. Will climate change drive 21st century burn rates in Canadian boreal forest outside of its natural variability: collating global climate model experiments with sedimentary charcoal data. International Journal of Wildland Fire 19, 1127–1139.
- Bontemps, J.-D., Hervé, J.-C., Dhote, J.-F., 2009. Long-term changes in forest productivity: consistent assessment in even-aged stands. Forest Science 55 (6), 549–564.
- Boucher, D., Gauthier, S., De Grandpré, L., 2006. Structural changes in coniferous stands along a chronosequence and productivity gradient in the northeastern boreal forest of Québec. Ecoscience 13 (2), 172–180.
- Bravo-Oviedo, A., Gallardo-Andrés, C., del Rio, M., Montero, G., 2010. Regional changes in *Pinus pinaster* site index in Spain using a climate-based dominant height model. Canadian Journal of Forest Research 40, 2036–2048.
- Calder, W.J., St.Clair, S.B., 2012. Facilitation drives mortality patterns along succession gradients of aspen-conifer forests. Ecosphere 3 (6), 57. http:// dx.doi.org/10.1890/ES12-00119.1.
- Cavard, X., Bergeron, Y., Chen, H.Y.H., Paré, D., Laganière, J., Brassard, B., 2011. Competition and facilitation between tree species change with stand development. Oikos 120 (11), 1683–1695.
- Chen, H.Y.H., Krestov, P.V., Klinka, K., 2002. Trembling aspen site index in relation to environmental measures of site quality at two spatial scales. Canadian Journal of Forest Research 32, 112–119.
- Christersson, L., 2010. Wood production potential in poplar plantations in Sweden. Biomass and Bioenergy 34, 1289–1299.
- Coops, N.C., Gaulton, R., Waring, R.H., 2011. Mapping site indices for five Pacific Northwest conifers using a physiologically based model. Applied Vegetation Science 14, 268–276.
- Cumming, S.G., Schmiegelow, K.A., Burton, P.J., 2000. Gap dynamics in boreal aspen stands: is the forest older than we think? Ecological Applications 10, 744–759. Drever, C.R., Messier, C., Bergeron, Y., Doyon, F., 2006. Fire and canopy species
- Drever, C.R., Messier, C., Bergeron, Y., Doyon, F., 2006. Fire and canopy species composition in the Great lakes-St. Lawrence forest of Tèmiscamingue, Quèbec. Forest, Ecology and management 231, 27–37.
- Drobyshev, I., Gewehr, S., Berninger, F., Bergeron, Y., 2013. Species specific growth responses of black spruce and trembling aspen may enhance resilience of boreal forest to climate change. Journal of Ecology. 101 (1):231-242.
- Fekedulegn, D., Hicks Jr., R.R., Colbert, J.J., 2003. Influence of topographic aspect, precipitation and drought on radial growth of four major tree species in an Appalachian watershed. Forest Ecology and Management 177, 409–425.
- Garet, J., Raulier, F., Pothier, D., Cumming, S., 2012. Forest age structures as indicators of sustainability in boreal forests: are we measuring them correctly? Ecological Indicators 23, 202–210.
 Gendreau-Berthiaume, B., Kneeshaw, D.D., Harvey, B.D., 2012. Effects of partial
- Gendreau-Berthiaume, B., Kneeshaw, D.D., Harvey, B.D., 2012. Effects of partial cutting and partial disturbance by wind and insect on stand composition, structure and growth in boreal mixedwoods. Forestry 85, 551–565.
- Girardin, M.P., Bernier, P.Y., Gauthier, S., 2011. Increasing potential NEP of eastern boreal North American forests constrained by decreasing wildfire activity. Ecosphere 2 (3), 23. http://dx.doi.org/10.1890/ES10-00159.1.
- Girardin, M.P., Guo, X.J., Bernier, P.Y., Raulier, F., Gauthier, S., 2012. Changes in growth of pristine boreal North American forests from 1950 to 2005 driven by landscape demographics and species traits. Biogeosciences 9, 2523–2536.
- Groot, A., Hökkä, H., 2000. Persistence of suppression effects on peatland black spruce advance regeneration after overstory removal. Canadian Journal of Forest Research 30, 753–760.
- Hamel, B., Bélanger, N., Paré, D., 2004. Productivity of black spruce and Jack pine stands in Quebec as related to climate, site biological features and soil properties. Forest Ecology and Management 191, 239–251.

Author's personal copy

402

K.A. Anyomi et al. / Forest Ecology and Management 302 (2013) 390-403

- Hart, S.A., Chen, H.Y.H., 2008. Fire, logging and overstory affect understory abundance, diversity and composition in boreal forest. Ecological Monographs 78 (1), 123–140.
- Harvey, B.D., Leduc, A., Gauthier, S., Bergeron, Y., 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. Forest Ecology and Management 155, 369–385.
- Hogg, E.H., Wein, R.W., 2005. Impacts of drought on forest growth and regeneration following fire in southwestern Yukon, Canada. Canadian Journal of Forest Research 35, 2141–2150.
- Hogg, E.H., Brandt, J.P., Michaelian, M., 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Canadian Journal of Forest Research 38, 1373–1384.
- Huang, J.-G., Tardif, J., Denneler, B., Bergeron, Y., Berninger, F., 2008. Tree ring evidence extends the historic northern range limit of severe defoliation by insects in the aspen stands of western Quebec, Canada. Canadian Journal of Forest Research 38, 2535–2544.
- Huang, J.G., Tardif, J., Bergeron, Y., Denneler, B., Berninger, F., Girardin, M.P., 2010. Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. Global Change Biology 16, 711–731.
- Jarvis, P.G., 1993. Prospects for bottom-up model. pp. numbers. In: Ehleringer, J.R., Field, C.B. (Eds.), Scaling Physiological Processes. Leaf to Globe. Academic Press, UK, p. 388.
- Kim, Y., Kimball, J.S., Zhang, K., McDonald, K.C., 2012. Satellite detection of increasing Northern Hemisphere non-frozen seasons from 1979 to 2008: implications for regional vegetation growth. Remote Sensing of Environment 121, 472–487.
- Kneeshaw, D.D., Harvey, B.D., Reyes, G.P., Caron, M.-N., Barlow, S., 2011. Spruce budworm, windthrow and partial cutting: do different partial disturbances produce different forest structures? Forest Ecology and Management 262, 482– 490.
- Kurz, W.A., Stinson, G., Rampley, G., 2008. Could increased boreal forest ecosystem productivity offset carbon losses from increased disturbances. Philosophical Transactions of the Royal Society B 363, 2285–2299.
- Landsberg, J.J., Waring, R.H., 1997. A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. Forest Ecology and Management 95, 209–228.
- Lapointe-Garant, M.-P., Huang, J.-G., Gea-izquierdo, G., Raulier, F., Bernier, P.Y., Berninger, F., 2010. Use of tree rings to study the effect of climate change on trembling aspen in Québec. Global Change Biology 16, 2039–2051.
 Larson, A.J., Lutz, J.A., Gersonde, R.F., Franklin, J.F., Hietpas, F.F., 2008. Potential site
- Larson, A.J., Lutz, J.A., Gersonde, R.F., Franklin, J.F., Hietpas, F.F., 2008. Potential site productivity influences the rate of forest structural development. Ecological Applications 18 (4), 899–910.
- Lecomte, N., Simard, M., Bergeron, Y., Larouche, A., Asnong, H., Richard, P.J.H., 2005. Effects of fire severity and initial tree composition on understory vegetation dynamics in a boreal landscape inferred from chronosequence and paleoecological data. Journal of Vegetation Science 16, 665–674.
- Légaré, S., Paré, D., Bergeron, Y., 2005. Influence of aspen on forest floor properties in black spruce-dominated stands. Journal of Plant and Soil 275, 207–220.
- Létourneau, J.-P., Bard, A., Lambert, J., 2003. Normes de cartographie écoforestière. Troisième inventaire écoforestier. Ministère des Ressources naturelles, de la Faune et des Parcs, Direction des inventaires forestiers, Québec. http://www.mrn.gouv.qc.ca/publications/forets/connaissances/norme-cartographieecoforestiere.pdf> (cited 01.11.12).
- Lexerød, N.L., Eid, T., 2006. An evaluation of different diameter diversity indices based on criteria related to forest management planning. Forest Ecology and Management 222, 17–28.
- Long, Z.T., Bruno, J.F., Duffy, J.E., 2007. Biodiversity mediates productivity through different mechanisms at adjacent trophic levels. Ecology 88, 2821–2829. Mailly, D., Gaudreault, M., Picher, G., Auger, I., Pothier, D., 2009. A comparison of
- Mailly, D., Gaudreault, M., Picher, G., Auger, I., Pothier, D., 2009. A comparison of mortality rates between top height trees and average site trees. Annals of Forest Science 66, 202.
- Mansuy, N., Gauthier, S., Robitaille, A., Bergeron, Y., 2010. The effects of surficial deposit-drainage combinations on spatial variations of fire cycles in the boreal forest of eastern Canada. International Journal of Wildland Fire 19 (8), 1083–1098.
- McKenney, D.W., Pedlar, J.H., 2003. Spatial models of site index based on climate and soil properties for two boreal tree species in Ontario, Canada. Forest Ecology and Management 175, 497–507.
- Miller, J.R., Turner, M.G., Smithwick, E.A.H., Dent, C.L., Stanley, E.H., 2004. Spatial extrapolation: the science of predicting ecological patterns and processes. Bioscience 54 (4), 310–320.
 Monserud, R.A., Huang, S., Yang, Y., 2006. Predicting lodgepole pine site index from
- Monserud, R.A., Huang, S., Yang, Y., 2006. Predicting lodgepole pine site index from climatic parameters in Alberta. Forestry Chronicle 82, 562–571.
- Ondro, W.J., 1989. Utilization and market potential of poplar in Alberta. Forestry Canada, Northern Forestry Centre, Edmonton, AB. Information Report Nor-X-30 S, p. 72.
- O'Neil, G., Hamann, A., Wang, T., 2008. Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. Journal of Applied Ecology 45, 1040–1049.
 Ouzennou, H., Pothier, D., Raulier, F., 2008. Adjustment of the age-height
- Ouzennou, H., Pothier, D., Raulier, F., 2008. Adjustment of the age-height relationship for uneven-aged black spruce stands. Canadian Journal of Forest Research 38, 2003–2012.
- Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. Global Ecology and Biogeography 20, 170–180.

- Paré, D., Bergeron, Y., Longpré, M.-H., 2001. Potential productivity of aspen cohorts originating from fire, harvesting and tree-fall gaps on two deposit types in northwestern Quebec. Canadian Journal of Forest Research 31, 1067–1073.
- Pearman, P.B., Guisan, A., Broennimann, O., Randin, C.F., 2007. Niche dynamics in space and time. Trends in Ecology and Evolution 23 (3), 149–158.
- Perala, D.A., 1990. Populus tremuloides Michx. quaking aspen. Salicaceae Willow family. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America. Hardwoods. Agriculture Handbook 654, vol. 2. USDA Forest Service, Washington, DC, p. 877.Périé, C., Ouimet, R., 2008. Organic carbon, organic matter and bulk density
- Périé, C., Ouimet, R., 2008. Organic carbon, organic matter and bulk density relationships in boreal forest soils. Canadian Journal of Soil Science 88, 315– 325.
- Périé, C., Duschesne, L., Lambert, M.-C., 2012. Prédire la croissance potentielle des arbres au Québec à l'aide des caractéristiques cartographiables des peuplements et des stations. Mémoire de Recherche Forestière No. 164. http://www.mrn.gouv.qc.ca/publications/forets/connaissances/recherche/ Perie-Catherine/Memoire164.pdf> (accessed when).
- Peterson, G.D., 2000. Scaling ecological dynamics: self-organization, hierarchical structure and ecological resilience. Climate Change 44 (3), 291–309.
- Peterson, E.B., Peterson, N.M., 1992. Ecology, management and use of aspen and balsam poplar in the prairie provinces, Canada. Forestry Canada, Northwest Region Northern Forestry Centre, Edmonton, AB. Special Report 1, p. 252.
- Pinto, E.P., Gégout, J.-C., Hervé, J.-C., Dhote, J.-F., 2008. Respective importance of ecological conditions and stand composition on *Abies alba* Mill. dominant height growth. Forest Ecology and Management 255, 619–629.
- Pothier, D., Savard, F., 1998. Actualisation des tables de production pour les principales espèces forestières du Québec. Ministère des Ressources naturelles du Québec. Direction de la recherche forestière, Québec, p. 183.
- Prescott, C.E., Zabek, L.M., Staley, C.L., Kabzems, R., 2000. Decomposition of broadleaf and needle litter in forests of British Columbia: influences of litter type, forest type, and litter mixtures. Canadian Journal of Forest Research 30, 1742–1750.
- Raulier, F., Lambert, M.-C., Pothier, P., Ung, C.-H., 2003. Impact of dominant tree dynamics on site index curves. Forest Ecology and Management 184, 65–78.
 Régnière, J., Saint-Amant, R., 2008. BioSIM 9 Manuel de l'utilisateur. Ressources
- Régnière, J., Saint-Amant, R., 2008. BioSIM 9 Manuel de l'utilisateur. Ressources naturelles Canada, Service canadien des forêts. Centre de foresterie des Laurentides. Rapport d'information LAU-X-134F. ftp://www.ftp.cfl.scf.rncan.gc. ca/regniere/Data/Weather/ (accessed 04.02.11).
- Rehfeldt, G.E., 1985. Genetic variances and covariances in *Pinus contorta*: estimates of genetic gains from index selection. Silvae Genetica 34 (1), 26–33.
 Rehfeldt, G.E., Tchebakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A.,
- Rehfeldt, G.E., Tchebakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A., Milyutin, L.I., 2002. Intraspecific responses to climate in *Pinus sylvestris*. Global Change Biology 8, 912–929.
- Rehfeldt, G.E., Ferguson, D.E., Crookston, N.L., 2009. Aspen, climate, and sudden decline in western USA. Forest Ecology and Management 258, 2353–2364.
- Robitaille, A., Saucier, J.-P., 1998. Paysages régionaux du Quebec méridional, MRN (Ministère des Ressources naturelles), Gouvernement du Québec. Les publications du Québec, p. 213.
- Robitaille, A., Robert, D., Saucier, J.-P., Chénard, F., 1989. Cartographie des districts écologiques; normes et techniques. Ministère des ressources naturelles du Québec. Direction de la gestion des stocks forestiers, service des inventaires forestiers, p.118.
- Rouleau, R., 1994. Comparaison entre les programmes d'inventaire de 1970 à aujourd'hui. Unpublished legend explaining MRNFQ's inventory programme, p. 106.
- Seynave, I., Gégout, J.-C., Hervé, J.-C., Dhote, J.-F., Bruno, E., Dumé, G., 2005. Picea abies site index prediction by environmental factors and understorey vegetation: a two-scale approach based on survey databases. Canadian Journal of Forestry Research 35, 1669–1678.Skovsgaard, J.P., Vanclay, J.K., 2007. Forest site productivity: a review of the
- Skovsgaard, J.P., Vanclay, J.K., 2007. Forest site productivity: a review of the evolution of dendrometric concepts for even-aged stands. Forestry 81 (1), 14– 31.
- Soja, A.J., Tchebakova, N.M., French, N.H.F., Flannigan, M.D., Shugart, H.H., Stocks, B.J., Sukhinin, A.I., Parfenova, E.I., Chapin III, F.S., Stackhouse Jr., P.W., 2007. Climate-induced boreal forest change: predictions vs. current observations. Global and Planetary Change 56, 274–296.Stam, B.R., Malechek, J.C., Bartos, D.L., Bowns, J.E., Godfrey, E.B., 2008. Effect of
- Stam, B.R., Malechek, J.C., Bartos, D.L., Bowns, J.E., Godfrey, E.B., 2008. Effect of conifer encroachment into aspen stands on understory biomass. Rangeland Ecology and Management 61, 93–97.
- Taylor, A.R., Chen, H.Y.H., 2011. Multiple successional pathways of boreal forest stands in central Canada. Ecography 34, 208–219.
- Ung, C.-H., Bernier, P., Raulier, F., Fournier, R.A., Lambert, M.-C., Régnière, J., 2001. Biophysical site indices for shade tolerant and intolerant boreal species. Forest Science 47 (1), 83–95.
- Uprety, Y., Asselin, H., Dhakal, A., Julien, N., 2012. Traditional use of medicinal plants in the boreal forest of Canada: review and perspectives. Journal of Ethnobiology and Ethnomedicine 8, 7. http://dx.doi.org/10.1186/1746-4269-8-7.
- Urban, D.L., 2005. Modeling ecological processes across scales. Ecology 86 (8), 1996–2006.
- Vallet, P., Perot, T., 2011. Silver fir stand productivity is enhanced when mixed with Norway spruce: evidence based on large scale inventory data and a generic modelling approach. Journal of Vegetation Science 22, 932–942.
- Veillet, J.J., 1994. Evolution and paleohydrology of glacial lakes Barlow and Ojibway. Quaternary Science Reviews 13, 945–971.

K.A. Anyomi et al. / Forest Ecology and Management 302 (2013) 390-403

- Wagner, T., Diefenbach, D.R., Christensen, S.A., Norton, A.S., 2011. Using multilevel models to quantify heterogeneity in resource selection. Journal of Wildlife Management 75 (8), 1788–1796.
- Weiskittel, A.R., Crookston, N.L., Radtke, P.J., 2011a. Linking climate, gross primary productivity, and site index across forests of the western United States. Canadian Journal of Forest Research 41, 1710–1721.
- Weiskittel, A.R., Hann, D.W., Kershaw, J.A., Vanclay, J.K., 2011b. Forest Growth and Yield Modeling. John Wiley & Sons, Ltd., UK, p. 405.
 Wiens, J.A., Crawford, C.S., Gosz, J.R., 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos 45, 421–427.
 Zeilstra, A.S., 2008. Regional Labour Markets in a Cross-Country Perspective. PPI
- Publishers Enschede, The Netherlands, p. 214.