

**COMPARING BALSAM FIR POTENTIAL SPECIES  
DISTRIBUTION IN TWO DISTINCT AREAS OF NEW  
BRUNSWICK, CANADA**

By

Yaquan Chang

HONOURS RESEARCH PROJECT

Supervisor: Charles P.-A. Bourque, Ph.D., Eco-hydrometeorology

THE UNIVERSITY OF NEW BRUNSWICK

NANJING FORESTRY UNIVERSITY

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## ABSTRACT

Forestland classification is a crucial element in the sustainable management of forests. Modelling tree site quality is a common approach to estimate tree species distribution at moderate spatial resolutions. In this study, I developed a framework to assess the potential tree species distribution of balsam fir [*Abies balsamea* (L.) Mill.] in two distinctive areas of New Brunswick (NB), Canada, specifically in the **NW-** and **SE-area** in northwest and southeast NB. Potential species distribution (PSD) is evaluated with the assistance of species-specific response functions to four site variables involving: (1) photosynthetically active radiation (PAR); (2) growing degree-days (GDD, a cumulative temperature index); (3) relative soil water content (SWC); and (4) near-surface wind speed (WS). To gauge the extent that calculations of PSD characterize site quality for balsam fir, PSD and site index (*SI*) calculations for balsam fir trees were compared. This comparison revealed: (1) overall better growing conditions for balsam fir in the NW-area; (2) modelled PSD was largely consistent with tree-based calculations of site index; (3) balsam fir generally grew taller in the NW-area, displaying no real difference in diameter at breast height (DBH) with trees in the SE-area; and (4) immature and mature balsam fir trees in the NW-area had lower radial growth as a result of increased tree competition. Although calculations of PSD are based entirely on abiotic-based inputs, the calculations provide a reasonable assessment of site quality and potential tree species distribution. Accounting for inner-stand processes of competition in the calculation of PSD may assist in refining associated calculations further.

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**Keywords:** balsam fir, biomass, PSD model, site index, tree structural dimensions

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# 1. INTRODUCTION

## 1.1 Background

Forests, as important dynamic systems, provide crucial ecological services to humans (Nadrowski et al., 2010). Forest management impacts ecosystem processes by affecting species diversity and structural forest compositions (Tilman et al., 1997). Forestland classification is one of the most important approaches associated with predicting forest management outcomes (Sims et al., 2012). However, classifying forestland is not easy, especially from a field-survey point of view (Kimmins, 1997), as a result of the complex (non-linear) interactions between site factors and tree growth. Some of these factors affecting tree growth, include solar radiation (Austin, 2002), growing degree-days (Zimmermann and Kienast, 1999), soil water content (Austin, 2007), surface wind speed (Bourque and Bayat, 2015), and several others. With the development of new statistical techniques and Geographic Information Systems (GIS) and associated tools, species distribution models have become popular in ecology (Guisan and Zimmermann, 2000). These spatially-explicit models provide a convenient way of classifying forestlands (Elith and Leathwick, 2009; Baah-Acheamfour et al., 2013).

## 1.2 Literature Review

Understanding the relationship between species and their environment is one of the most common approaches to describe species distribution (Guisan and Zimmermann, 2000). This approach uses data from biophysical surfaces (Zimmermann et al., 2007), which enhances our modelling capabilities by taking into account the myriad of environmental conditions prevalent at a site (Elith and Leathwick, 2009). There are various methods in parameterizing species distribution models. Minimum convex polygons are often used to model sparse data (Burgman and Fox, 2003) and expert opinions are often more reliable than actual species records (Elith and

Leathwick, 2009). Environmental envelope models, as the earliest form of species distribution models, define the limit of environmental factors in multi-dimensional space (Box, 1981). Regression-based models are commonly used in ecology because of species non-linear interactions to site conditions (Elith and Leathwick, 2009). For example, a Bayesian approach was recently used to analyze species distribution (Latimer et al., 2006). Gap models often define total species response by multiplying individual species response to specific site conditions (Acevedo et al., 1995).

### 1.3 Problem Statement

The scale of species distribution modelling varies from continent to grid-based for different analytical purposes (Elith and Leathwick, 2009). Conservation planning and forest management tend to use higher spatial resolutions to illustrate greater detail (Bourque and Bayat, 2015). Although model evaluations are always needed for prediction, it is also important to test the models' application in appropriate ways. Model testing through statistical methods and explanation from existing knowledge are two main approaches (Elith and Leathwick, 2009). Many species distribution models only refer to abiotic characteristics of forestland, since biotic factors, such as tree competition, are challenging to characterize independently from site environmental effects (Guisan and Thuiller, 2005).

### 1.4 Study Objective

In this study, I developed a framework for modelling potential species distribution (PSD) for balsam fir [*Abies balsamea* (L.) Mill] in two distinctive areas of New Brunswick, Canada, i.e., in the **NW-** and **SE-area** in northwest and southeast NB. Environmental variables pertinent to modelling PSD for balsam fir in this study, include: (1) incident photosynthetically active radiation (PAR, ~ 45% of incident solar radiation; Bourque and Gullison, 1998); (2) MODIS-image based

calculations of growing degree-days (GDD; Bourque et al., 2000; Hassan, 2008); (3) relative soil water content (SWC; Bourque et al., 2000); and (4) near-surface wind speed (WS; Bourque and Bayat, 2015). PSD-values for balsam fir range from 0.0 to 1.0, where 0.0 represents poor site quality and potential absence of the species and 1.0, optimal site quality and potential presence of the species. I subsequently compared median PSD for the NW- and SE-area against site index for balsam fir in assessing growing conditions in the highlands and lowlands of NB (i.e., NW- and SE-area; Fig. 1).

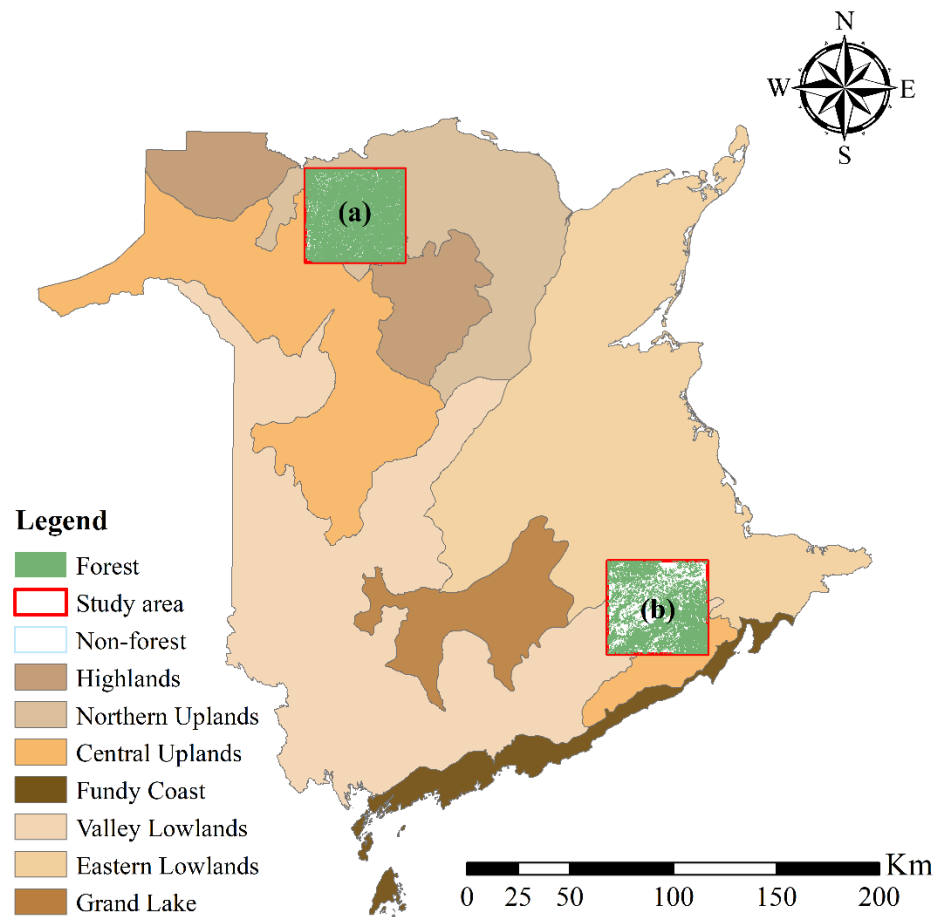
## **2. METHODS**

### 2.1 Study Area

#### *2.1.1 Climate conditions*

New Brunswick (NB) is located in eastern Canada, next to the Atlantic Ocean. The province is divided into seven ecoregions, which are defined by climate differences (generally in terms of precipitation and temperature), elevation, landforms, and marine influences (Zelazny et al., 2007). NB has a humid continental climate influenced by the cool Bay of Fundy to the south of the province (Fig.1). The elevation of NB ranges from 0–834 m and mean temperature decreases with increasing elevation. Tree species distribution largely follows the ecoregions of NB. The province is home to both broad- and needle-leaf forests, including 55% spruce-fir, 14% other softwood species, and 32% hardwood species (Chen et al., 2017). Based on long-term weather records from the Saint Leonard airport, the NW-area is characterized by a mean annual temperature of 3.5°C and total precipitation of 1104 mm. The SE-area is mostly warmer than the NW-area, with a mean annual temperature of 6.1°C and total precipitation of 1124 mm, based on weather records from the Moncton Airport, [http://climate.weatheroffice.ec.gc.ca/climate\\_normals/index\\_e.html](http://climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html), last accessed on April 2018.



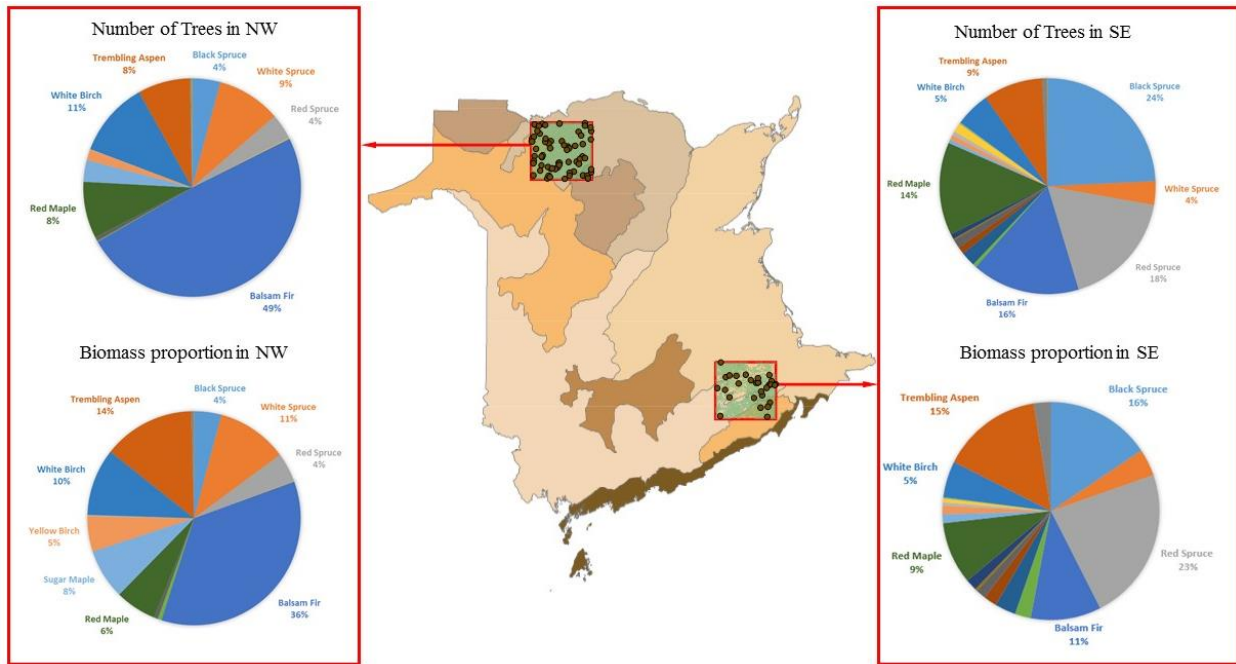


**Fig. 1.** Location of the two study areas in the province of New Brunswick (NB), i.e., (a) the NW- and (b) SE-area.

### 2.1.2 Proportion of tree amount and biomass

Balsam fir is one of two dominant species in NB, making up 20% of the public forest ([Management Alternatives for New Brunswick’s Public Forest](#)). In the study areas, balsam fir trees make up the largest proportion of forests in the NW-area at 49%, followed by white birch (*Betula papyrifera*, 11%), white spruce (*Picea glauca*, 9%), red maple (*Acer rubrum*, 8%), and trembling aspen (*Populus tremuloides*, 8%; Fig. 2). Although the biomass of balsam fir accounts for 36% of the total tree biomass, it contributes to the single largest forest component in the NW-area, followed by trembling aspen (14%), white spruce (11%), and white birch (10%; Fig. 2). In the SE-

area, the dominant species is black spruce (*Picea mariana*, 24%), followed by red spruce (*Picea rubens*, 18%), balsam fir (16%), and red maple (14%; Fig. 2). Red spruce makes up the largest proportion of biomass (23%) in the SE-area, more than twice of that of balsam fir (11%; Fig. 2). Black spruce and trembling aspen account for 16 and 15% of the total tree biomass in the area.

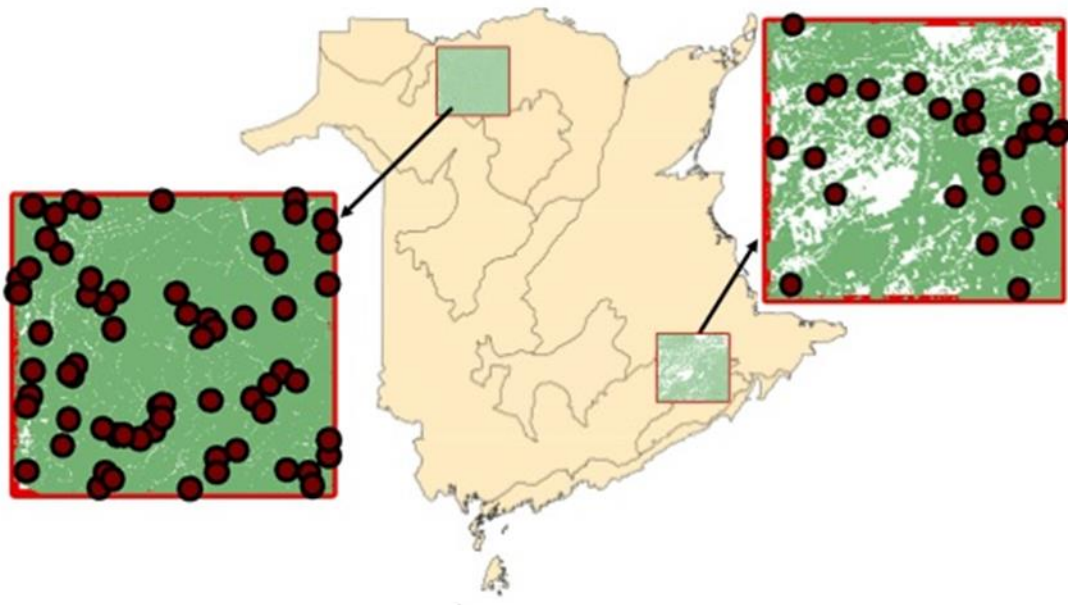


**Fig. 2.** Within-plot proportion of biomass and trees according to tree species; note that stem density in the NW- and SE-area is roughly 1357 and 1181 stems ha<sup>-1</sup>, respectively.

### 2.1.3 Permanent sample plots

Permanent sample plots (PSPs) were established by the Canadian Forest Service and NB Department of Energy and Resource Development (NB ERD) in 1987, including more than 3000 PSPs (Porter et al., 2001). The NW- and SE-area contain 66 and 31 PSPs, respectively (Fig. 3). All PSPs identified in Fig. 3 have a component of balsam fir. Diameter at breast height (DBH), tree height (H), and age classes (Table 1) are used in this study to test the PSD model and explore the growing trends in balsam fir for the two study areas. Diameter at breast height was measured for all commercial species, whereas H was collected from all commercial trees with a DBH > 9

cm (Dunlap, 1987). Age class is divided into four groupings, including young (Y), immature (I), mature (M), and overmature (O). Table 1 shows the age range for each age class and species. The age information was collected from trees outside the plot, with increment coring of at least two trees for each species/age class characteristic of the plot (Porter et al., 2001).



**Fig. 3.** Permanent sample plots (PSPs) with some balsam fir content.

**Table 1.** Age class according to development stages in major tree species, after Porter et al. (2001).

<b>Species</b>	<b>Young (Y)</b>	<b>Immature (I)</b>	<b>Mature (M)</b>	<b>Overmature (O)</b>
Balsam fir	25-35	36-50	51-70	71+
Red spruce	30-45	46-70	71-110	111+
Black spruce	30-45	46-70	71-110	111+
White spruce	20-40	41-60	61-110	111+
White pine	30-50	51-90	91-160	161+
Jack pine	20-40	41-70	71-110	111+
Red pine	20-40	41-70	71-110	111+
Eastern cedar	30-45	46-70	71-110	111+
Eastern hemlock	30-50	51-90	91-140	141+
Larch	20-45	46-70	71-110	111+
Tolerant hardwoods	30-50	51-80	81-160	161+
Intolerant hardwoods	20-35	36-50	51-70	71+
Grey birch	15-25	26-40	41-50	51+

## 2.2 PSD Model

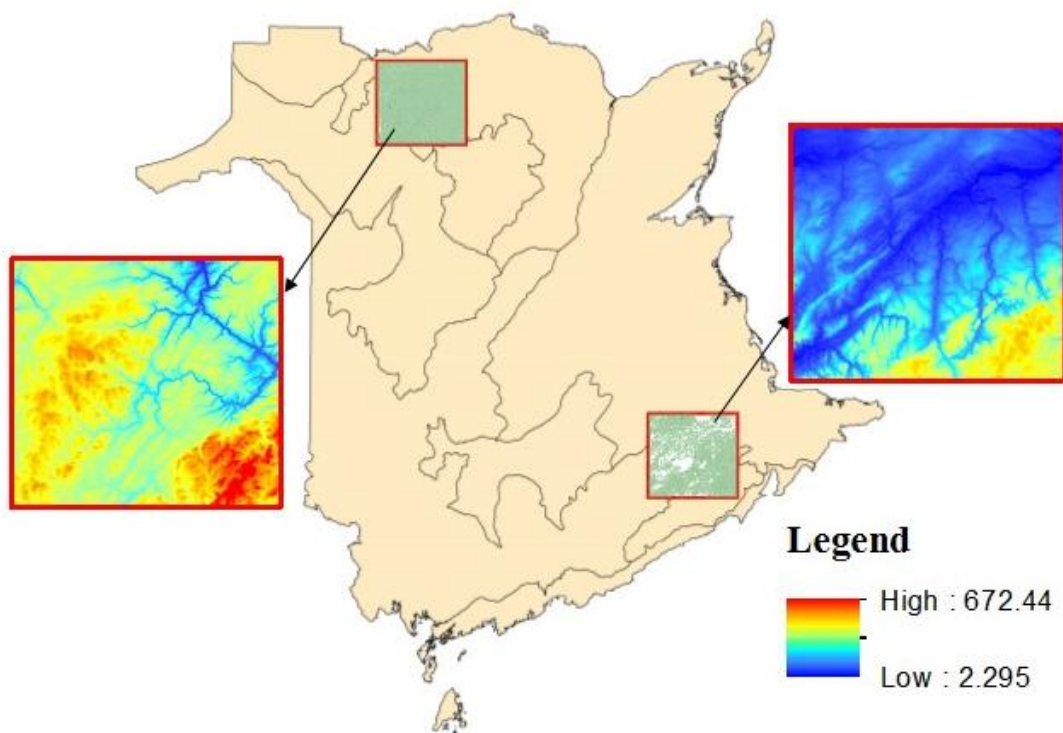
### 2.2.1 Data requirement and processing

The potential species distribution (PSD) model accounts for the effects of four biophysical variables in its calculation of species distribution. The input data for the calculation of PSD includes: (1) a digital elevation model (DEM) of NB based on the NASA Shuttle Radar Topography Mission (SRTM v. 3.0), 1-arc second (30-m resolution) product (<https://earthexplorer.usgs.gov/>; Fig. 4); (2) PAR (Fig. 5a); (3) GDD (Fig. 5b); (4) SWC (Fig. 5c); and WS (Fig. 5d). Surfaces of PAR and SWC are estimated with the **Landscape Distribution of Soil moisture, Energy, and Temperature model (LandSET**; Bourque and Gullison, 1998; Bourque et al., 2000), whereas GDD is based on the processing of remote sensing images (Hassan et al., 2007c). The 3D wind field is determined through a numerical solution of the Reynolds-averaged

Navier-Stokes equations (Lopes, 2003). Input to its calculation includes the DEM and upwind weather station wind speed and direction.

### 2.2.2 Digital elevation model

One of the most important inputs to the calculation of PSD is the DEM (Fig. 4), since landforms have a deep influence on the redistribution of water (Schoorl et al., 2002) and the distribution of incident solar energy and associated energy balance. Although there are some valleys in the NW-area, the average elevation of NW-area is greater than that of the SE study area.



**Fig. 4.** Elevation differences between the NW- and SE-area.

### 2.2.3 Biophysical surfaces

Every species distribution and growth patterns have different responses to PAR. To calculate PAR (Fig. 5a), DEM-derived terrain factors of slope, aspect, horizon angle, view factor, and terrain

configuration factor were considered (Bourque and Gullison, 1998). The mean mid-afternoon value of 0.7 was used to calculate atmospheric transmissivity to correct for the diffused PAR that does not reach the earth's surface (Bourque and Gullison, 1998). Assuming climate factors, such as cloud, have no effect on solar radiation, PAR was estimated by LandSET as an integration of hourly values over the entire growing season (Hassan et al., 2006).

Temperature is one of the primary determinants of plant metabolic processes (Gillooly et al., 2001). Growing degree-days (GDD) represent the level of warmth plants require for growth over the growing season. The GDD map (Fig. 5b) at 28.5-m resolution was developed from a compilation of Landsat-7 ETM+ and MODIS satellite images (Hassan et al., 2007b), whereby

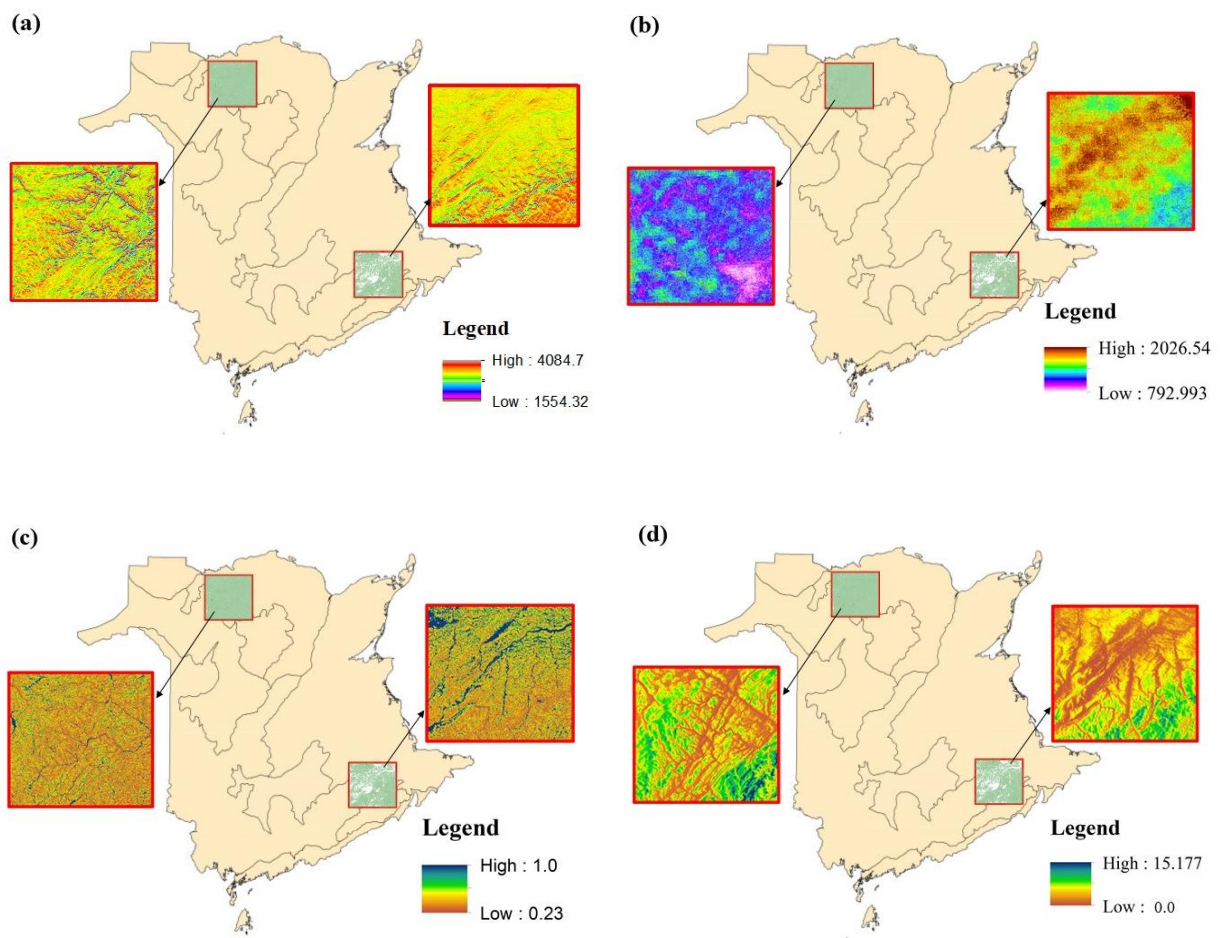
$$GDD = \sum_{i=1}^{i=n} (T_{mean} - T_{base}), \text{ when } T_{mean} - T_{base} > 0, \quad [1]$$

where  $T_{mean}$  is the average temperature,  $T_{base}$  is the base temperature of 5°C, and  $i$  goes from 1 to  $n$ , where 1 and  $n$  represent the beginning and last day of the growing season, respectively (Hassan et al., 2007b). The final GDD map was standardized to a normal (30-year) period using long-term temperature data from selected weather stations (Hassan et al., 2007c).

Tree species have different soil water requirements (Oliver and Larson, 1996). Annual mean SWC was calculated with the LandSET model (Gallant, 1996; Moore et al., 1993). A DEM cell-by-cell water-budget calculation of SWC was performed by taking into account annual total precipitation, lateral flow from upslope to downslope positions, infiltration, percolation, evapotranspiration, surface runoff, and changes in soil water storage (Bourque et al., 2000). Other inputs include cell-size specification (30-m) and all-wave radiative fluxes (in MJ m<sup>-2</sup>; Bourque et al., 2000) for an energy-balance calculation of evapotranspiration. Relative soil water content

(SWC) is represented by a value that ranges between 0.0 and 1.0, with SWC approaching 1.0 for very wet sites.

Wind affects plant growth due to both mechanical (e.g., flagging) and physiological effects (Retuerto and Woodward, 1992). Wind-tunnel studies of tree growth have shown relative growth-rate rises with increasing wind speed, but these growth rates soon drop as wind speed continues to increase beyond an optimal level, especially when the trees are young (Wadsworth, 1959).



**Fig. 5.** Distribution of biophysical surfaces; (a) photosynthetically active radiation (PAR), (b) growing degree-days (GDD), (c) relative soil water content (SWC), and (d) wind speed (WS).

#### 2.2.4 Species response functions and potential species distribution

To model PSD for different species, generic species response functions were previously developed for PAR (Fig. 6a), GDD (Fig. 6b), SWC (Fig. 6c), and WS (Fig. 6d; Smith, 1998; Bourque et al., 2000; Bourque and Bayat, 2015). These response functions consider physiological and morphological traits of species and their relative abundance along environmental gradients. A final assessment of PSD was obtained by multiplying the various response values at the pixel level (Fig. 6; Bourque et al., 2000).

$$PSD = R_{PAR} \cdot R_{GDD} \cdot R_{SWC} \cdot R_{WS}, \quad [2]$$

where  $R_{PAR}$ ,  $R_{GDD}$ ,  $R_{SWC}$ , and  $R_{WS}$  are the individual species response functions for PAR, GDD, SWC, and WS, respectively.

Species response function for PAR is defined by:

$$R_{PAR} = c_1 \cdot \left\{ 1 - \exp \left[ -c_2 \left( \frac{PAR}{PAR_{max}} - c_p \right) \right] \right\}, \quad [3]$$

where  $c_1$  is a scaling factor,  $c_2$  is the slope of the response function,  $c_p$  is the light compensation point, and  $PAR_{max}$  is the maximum PAR on south-facing slopes in the northern hemisphere (Bourque et al., 2000; Fig. 6a).

Species response function for GDD is given by:

$$R_{GDD} = \frac{4(GDD - GDD_{min}) \cdot (GDD_{max} - GDD)}{(GDD_{max} - GDD_{min})^2}, \quad [4]$$

where  $GDD_{min}$  and  $GDD_{max}$  are the minimum and maximum values of GDD, respectively (Hassan and Bourque, 2009; Fig. 6b). Plants have an optimal growth at the mid-point between



$GDD_{min}$  and  $GDD_{max}$ . In this study,  $GDD_{min}$  and  $GDD_{max}$  are the north-south limits of GDD for the geographic range of balsam fir (Bourque et al., 2000).

Species response function for SWC is defined as shown below:

$$R_{SWC} = \max\left(0, kS^\alpha(1 - S)^{\frac{1}{\alpha}}\right),$$

where

$$S = \frac{SWC - SWC_{min}}{SWC_{max} - SWC_{min}}$$

$$x = \frac{t - SWC_{min}}{SWC_{max} - SWC_{min}}, \quad SWC_{min} < t < SWC_{max}, \quad [5]$$

$$k = \frac{1}{x^\alpha(1 - x)^{\frac{1}{\alpha}}}, \text{ and}$$

$$\alpha = \sqrt{\frac{x}{1 - x}}.$$

Here,  $SWC_{max}$  and  $SWC_{min}$  are the SWC-tolerance limits; plants will not grow when actual SWC is lower or greater than the lower and upper limits of the response function (Fig. 6c). Variable,  $t$ , is the SWC for optimal growth (Bourque et al., 2000).

Species response function for WS shows that:

$$R_{WS} = \max\left(0, \sigma WS_{new}^\gamma \cdot (1 - WS_{new})^{\frac{1}{\gamma}}\right),$$

where

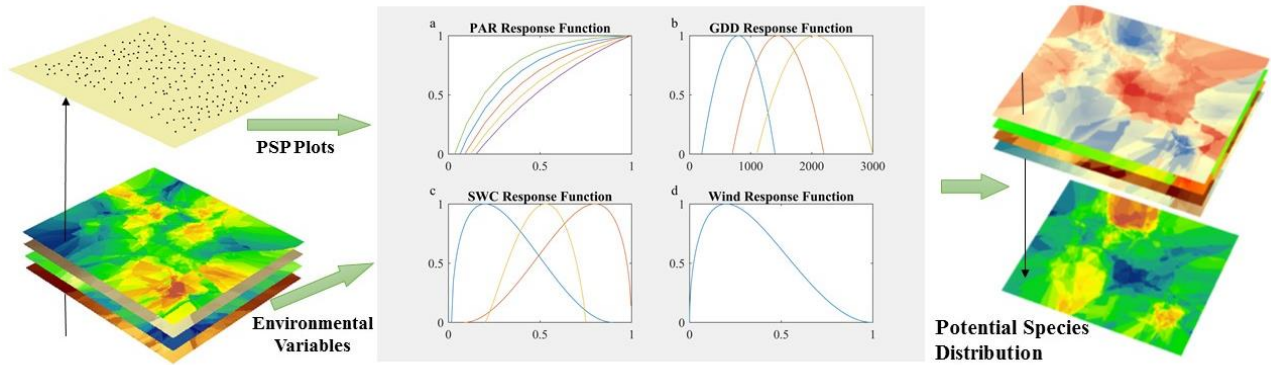
$$\sigma = \frac{1}{WS_{maxnew}^\gamma} \cdot (1 - WS_{maxnew})^{\frac{1}{\gamma}}$$

$$\gamma = \sqrt{\frac{WS_{maxnew}}{1-WS_{maxnew}}} \quad [6]$$

$$WS_{new} = \frac{WS}{12}, \text{ and}$$

$$WS_{maxnew} = 0.2.$$

Here,  $WS_{maxnew}$  is the wind speed coinciding with optimal tree growth (Fig. 6d);  $WS_{new}$  represents the normalized wind speed between 0.0 and 1.0.



**Fig. 6.** Conceptual diagram in the production of species distribution maps; the different colored lines represent response curves for different tree species; note that for balsam fir model parameters  $c_1 = 1.05$ ,  $c_2 = 3.29$ ,  $c_p = 0.06$ ,  $GDD_{min} = 563$ ,  $GDD_{max} = 2011$ ,  $SWC_{max} = 0.999$ ,  $SWC_{min} = 0.087$ ,  $t = 0.5$ , and shade-tolerance class = 4.

### 2.3 Site Index

Different site quality results in different patterns of polymorphic height growth (Carmean, 1972). Site index ( $SI$ ) equations are widely used throughout the world, especially in North America (Aertsen et al., 2010; Doolittle, 1958; Ker and Bowling, 1991; Watt et al., 2015). This is a simple approach to assess site quality based on tree height growth and breast-height age (Carmean and Lenthall, 1989). The equation applied to balsam fir in NB calculates height at the index age of 50

years (Ker and Bowling, 1991) and is derived from a generalized Chapman-Richards' equation (Richards, 1959) mathematically constraining  $SI$  (Clutter et al., 1983), i.e.,

$$H = 1.3 + (SI - 1.3)[1 - \exp(-b_2 50)]^{-b_3 SI^{b_4}} \cdot [1 - \exp(-b_2 A)]^{b_3 SI^{b_4}}, \quad [7]$$

where  $H$  and  $SI$  are the tree height and site index (m),  $A$  is the tree age (in years), and  $b_i$  are species-specific regression coefficients (Ker and Bowling, 1991). Site index in eqn. [7] is normally solved numerically, using, e.g., the Newton-Raphson or bisection-secant rule, given actual tree  $H$  and age.

## 2.4 Site Characteristics

Change in annual diameter at breast height ( $\delta DBH$ ) was calculated in young, immature, mature, and overmature trees as an indicator of tree vigor (Fortin et al., 2008). Although consecutive measurement intervals vary (3 to 5 years), I calculated mean DBH-increment (i.e.,  $\delta DBH$ ) to eliminate this effect.

## 2.5 Biomass

Biomass is one of the important factors in gauging tree competition (Bonser and Reader, 1995; Reader et al., 1994). Allometric models are commonly used to estimate biomass to avoid using destructive harvesting methods (Brown, 1997). However, models can vary from area to area, mainly in their coefficients (Chave et al., 2014). Aboveground biomass can be calculated by tree biomass equations based on DBH (Lambert et al., 2005). This report bases total biomass by summing individual aboveground biomass for foliage, branches, stem, and bark. The DBH-based equations are:

$$Y_{\text{wood}} = \beta_{\text{wood}1} D^{\beta_{\text{wood}2}}$$

$$y_{\text{bark}} = \beta_{\text{bark}1} D^{\beta_{\text{bark}2}}$$

$$y_{\text{foliage}} = \beta_{\text{foliage}1} D^{\beta_{\text{foliage}2}} \quad [8]$$

$$y_{\text{branches}} = \beta_{\text{branches}1} D^{\beta_{\text{branches}2}}$$

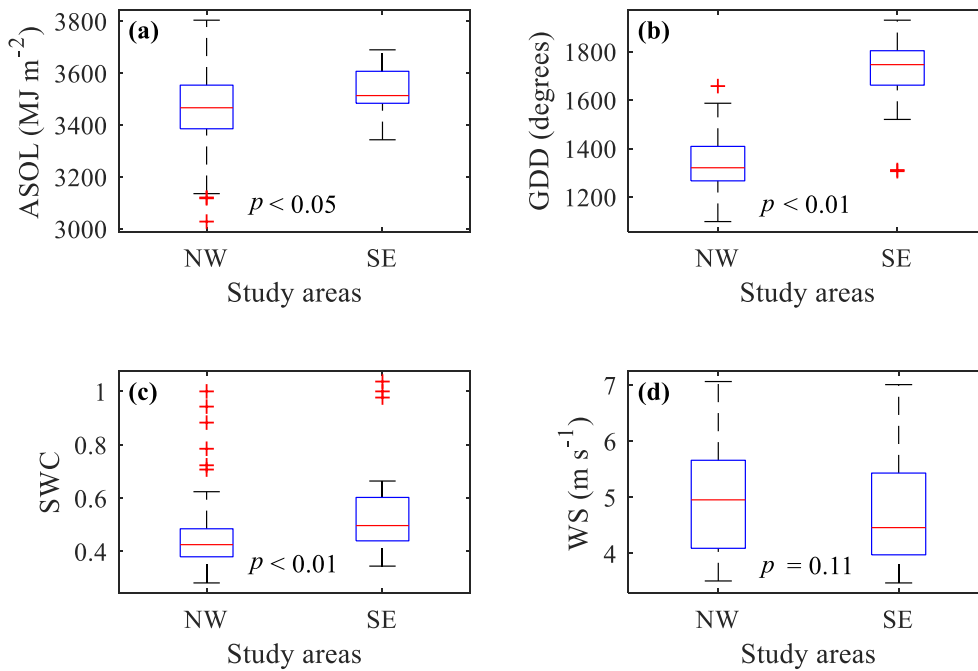
$$y_{\text{AGB}} = y_{\text{wood}} + y_{\text{bark}} + y_{\text{foliage}} + y_{\text{branches}}$$

where  $y_i$  is the dry biomass component of living trees (i.e., wood, bark, foliage, or branches; in kg),  $D$  is the DBH (cm),  $\beta_{jk}$  are equation parameters for wood, bark, foliage, and branches, and  $k=1$  or  $2$  (Lambert et al., 2005). Due to missing information on the characteristics of pin cherry, serviceberry, and striped maple, I used the characteristics of black cherry and average hardwood for informing the calculations associated with these three species.

### 3. RESULTS AND DISCUSSION

#### 3.1 Biophysical Conditions

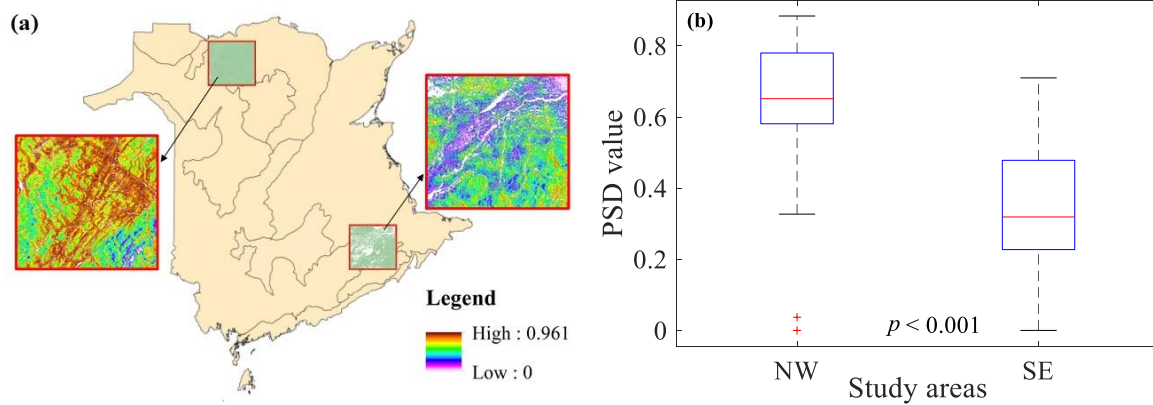
The biophysical conditions of PAR, SWC, GDD, and WS in both study areas were evaluated (Fig. 7). Student t-tests showed PAR (Fig. 7a) and GDD (Fig. 7b) having significant difference ( $p \leq 0.01$ ) between the two areas (Fig. 1). The average values of PAR and GDD in the NW- and SE-area were 3,456.1 and 3,532.3 MJ m<sup>-2</sup> and 1,343.8 and 1,707.5 degrees respectively. This means that plants in the SE-area generally received more solar radiation and heat to grow. Statistically, SWC was greatest in the SE-area, based on a Mann-Whitney Rank Sum test (the conditions of equal variance and normality failed for a t-test;  $p < 0.01$ ), albeit the presence of many extreme values in the NW-area (Fig. 7c). Wind speeds in the NW- and SE-area were not statistically different ( $p = 0.11$ ; Fig. 7d).



**Fig. 7.** Boxplots of environmental variables associated with balsam fir in the two study areas (Fig. 1). The red lines in the boxes represent the median of plotted values. The bottom and top edges of the box indicate the 25<sup>th</sup> and 75<sup>th</sup> percentiles, respectively. The end of the whiskers represent the 10<sup>th</sup> and 90<sup>th</sup> percentile, and the red crosses are data points with values beyond the 10<sup>th</sup> and 90<sup>th</sup> percentile.

### 3.2 Modelling Results

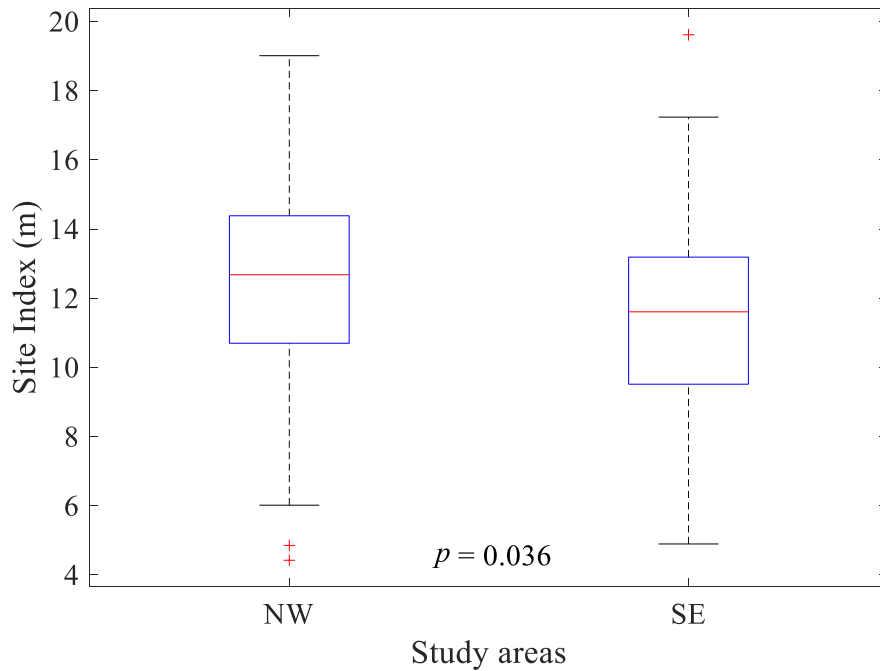
According to a Mann-Whitney Rank Sum test, spatial distribution (Fig. 8a) and boxplot of modeled PSD (Fig. 8b) showed that balsam fir possessed a significantly greater potential of occurrence in the NW-area (median PSD = 0.65) than in the SE-area (median PSD = 0.32;  $p < 0.001$ ). This suggests that balsam fir has preference for the growing conditions in high elevation areas of the province (Fig. 4), which is noted for its lower PAR, SWC, and GDD (Fig. 7). This is consistent with the ecological land classification system of the province (Godin and Roberts, 1994; Taylor and MacLean, 2005). In general, balsam fir trees tended to do better in the valleys (low elevation areas) of northwest NB.



**Fig. 8.** Comparing modeled PSD (habitat suitability) for balsam fir in the two study areas (Fig. 1). The red lines in the boxes represent the median of plotted values. The bottom and top edges of the box indicate the 25<sup>th</sup> and 75<sup>th</sup> percentiles, respectively. The end of the whiskers represent the 10<sup>th</sup> and 90<sup>th</sup> percentile, and the red crosses are data points with values beyond the 10<sup>th</sup> and 90<sup>th</sup> percentile.

### 3.3 Test Results

According to a Student t-test, the *SI* in the NW-area was statistically greater than the *SI* in the SE-area ( $p < 0.05$ ; Fig. 9), again suggesting that the NW-area provided better site conditions for balsam fir establishment and growth. Mean *SI* in NW-area was 12.5 m, whereas in the SE-area it was 11.5 m. On average, balsam fir in the NW-area had the potential to grow about 1 m taller than balsam fir in the SE-area at the same index age of 50 years. This is consistent with my earlier conclusions based on modeled PSD.

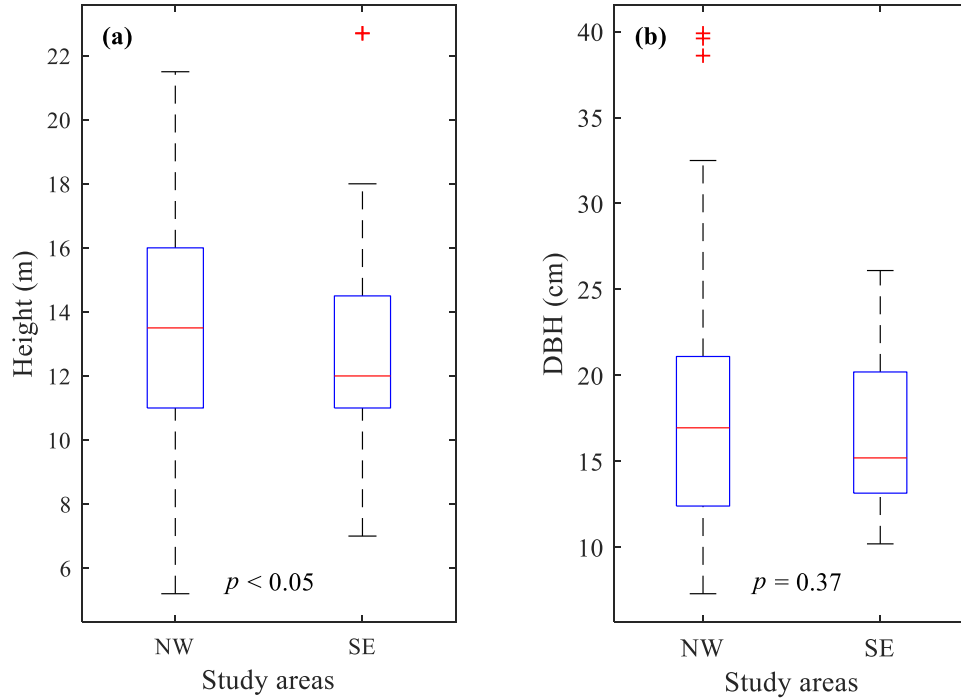


**Fig. 9.** Site index for balsam fir in the two study areas (Fig. 1). The red lines in the boxes represent the median of plotted values. The bottom and top edges of the box indicate the 25<sup>th</sup> and 75<sup>th</sup> percentiles, respectively. The end of the whiskers represent the 10<sup>th</sup> and 90<sup>th</sup> percentile, and the red crosses are data points with values beyond the 10<sup>th</sup> and 90<sup>th</sup> percentile.

### 3.4 Site Characteristics

#### 3.4.1 Height and DBH

Balsam fir in the NW-area tended to be taller than the trees in the SE-area, based on actual tree height measurements ( $p < 0.05$ ; Fig. 10a). According to a t-test, the mean tree height in the NW-area was 13.4 m, whereas in SE-area it was 12.6 m. For actual on-the-ground-conditions, balsam fir in the NW-area grew ~1 m taller than trees in the SE-area, consistent with the study-area differences in *SI*. In contrast, DBH did not show significant difference; a Mann-Whitney Rank Sum test produced a  $p = 0.37$ . The median DBH of balsam fir in the NW-area was 17.0 cm, whereas in the SE-area it was 15.2 cm. This suggests that balsam fir trees in better growing conditions tended to grow taller (Lines et al., 2012) at the expense of radial growth or increment in DBH.



**Fig. 10.** Balsam fir height and DBH in the two study areas (Fig. 1). The red lines in the boxes represent the median of plotted values. The bottom and top edges of the box indicate the 25<sup>th</sup> and 75<sup>th</sup> percentiles, respectively. The end of the whiskers represent the 10<sup>th</sup> and 90<sup>th</sup> percentile, and the red crosses are data points with values beyond the 10<sup>th</sup> and 90<sup>th</sup> percentile.

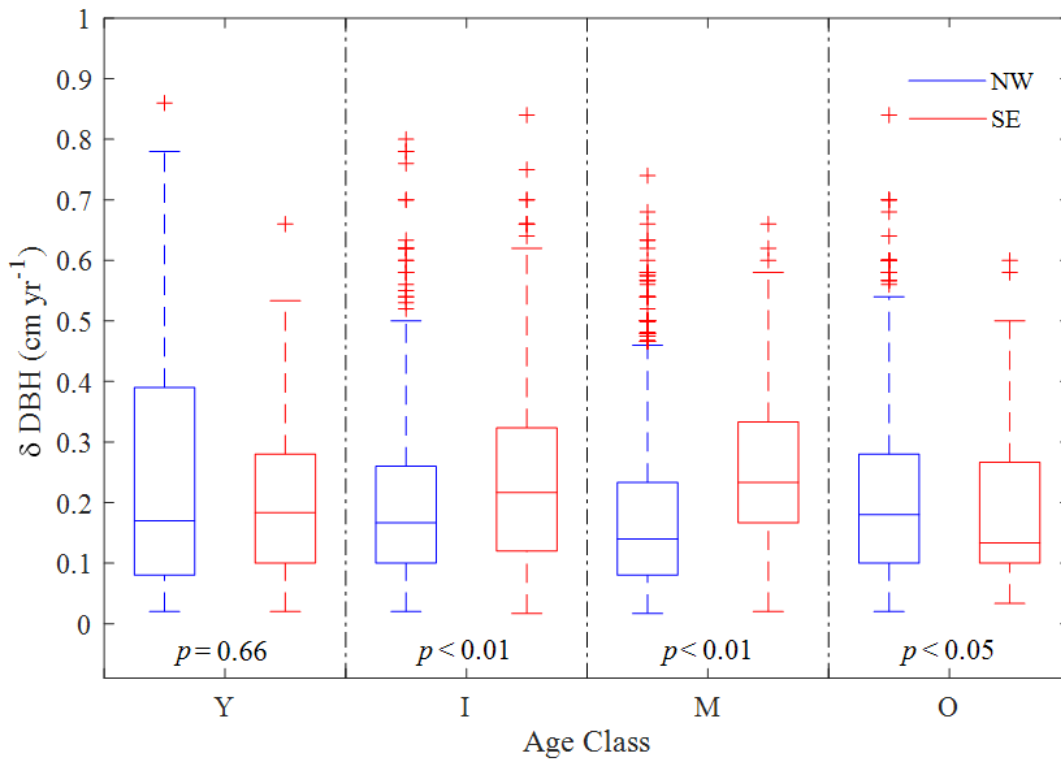
### 3.4.2 Dynamic change

Radial growth rates (i.e.,  $\delta\text{DBH}$ ) in the four age classes (i.e., young, immature, mature, and overmature) were distinctly different. In the young age class, balsam fir in the NW- and SE-area showed no significant difference ( $p = 0.66$ ), with their individual median radial growth rates being 0.17 and 0.18  $\text{cm yr}^{-1}$ , respectively. In contrast,  $\delta\text{DBH}$  varied for the other age classes (i.e.,  $p < 0.05$  with a Mann-Whitney Rank Sum tests; Fig. 11).

In the immature and mature age classes, balsam fir in the SE-area grew significantly faster radially than the trees in the NW-area ( $p < 0.01$ ). In the immature age class, balsam fir radial growth rate in the NW-area remained unchanged at 0.17  $\text{cm yr}^{-1}$ , whereas in the SE-area it increased from 0.04 to 0.22  $\text{cm yr}^{-1}$ . Balsam fir grew more slowly in the NW-area ( $\sim 0.14 \text{ cm yr}^{-1}$ ),



whereas in the SE-area the radial growth rate of balsam fir rose to  $0.23 \text{ cm yr}^{-1}$ . However, in the overmature age class, their radial growth rates reversed ( $p < 0.05$ ). The median radial growth rate in balsam fir in the NW-area increased sharply to  $0.18 \text{ cm yr}^{-1}$ . After climbing to a peak in the mature age class, the growth rate in the SE-area decrease to  $0.13 \text{ cm yr}^{-1}$ . In the young age class, balsam fir in both study areas generally had similar radial growth rates ( $p = 0.66$ ). In the immature and mature age classes, the radial growth rates of balsam fir were statistically greater in the SE-area than in the NE-area. In the overmature age class, balsam fir in the NW-area exhibited a greater radial growth rate.

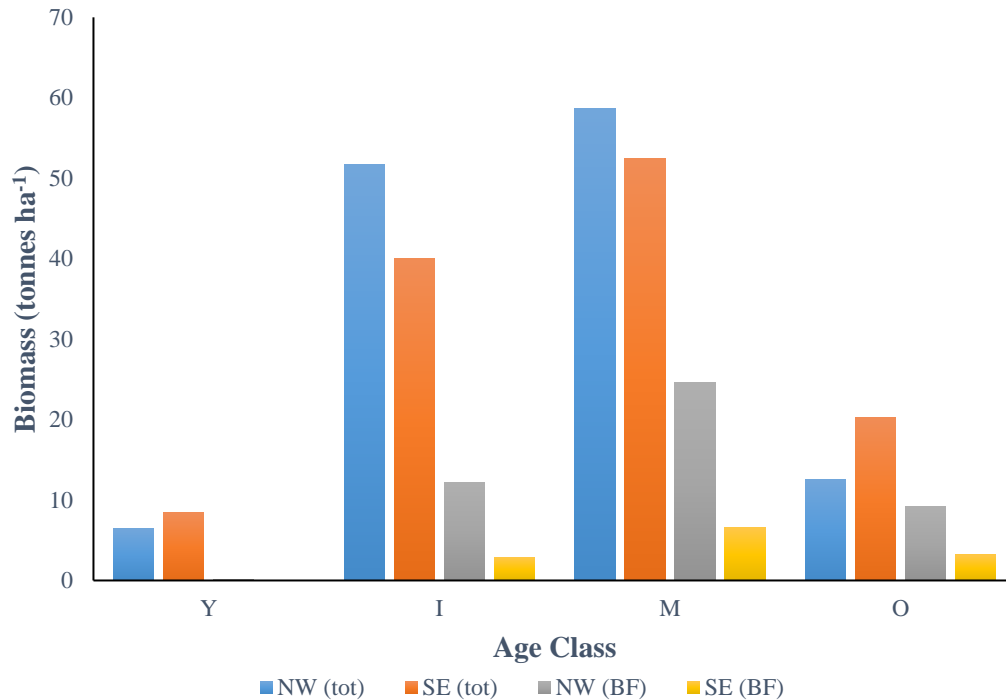


**Fig. 11.** Radial growth rate ( $\delta\text{DBH}$ ) among four age classes, i.e., young, immature, mature, and overmature. The blue or red horizontal lines in the boxes represent the median of plotted values. The bottom and top edges of the box indicate the 25<sup>th</sup> and 75<sup>th</sup> percentiles, respectively. The end of the whiskers represent the 10<sup>th</sup> and 90<sup>th</sup> percentile, and the red crosses are data points with values beyond the 10<sup>th</sup> and 90<sup>th</sup> percentile.

### 3.5 Biomass

Biomass of balsam fir in the NW-area was 45.9 tonnes ha<sup>-1</sup>, whereas in SE-area it was 12.7 tonnes ha<sup>-1</sup>, suggesting that the NW-area at the time of measurement contained almost three times more biomass of balsam fir than in the SE-area. Biomass in the NW-area was consistently greater than the biomass in the SE-area across all age classes (Fig. 12).

Total biomass in the NW- and SE-area was 129.2 tonnes ha<sup>-1</sup> and 121.2 tonnes ha<sup>-1</sup>, indicating that the NW-area was able to produce a greater amount of biomass than the SE-area by about 8.1 tonnes ha<sup>-1</sup>. In the young and overmature age classes, total biomass in NW-area was less than that in the SE-area, whereas in the immature and mature age classes, total biomass in the NW-area was greater than that in the SE-area. In the young age class, total biomass in the NW- and SE-area was 6.5 and 8.4 tonnes ha<sup>-1</sup>. In the overmature age class, total biomass in the NW-area accounted for 12.6 tonnes ha<sup>-1</sup>, or about three-fifths of the biomass appearing in the SE-area (i.e., 20.2 tonnes ha<sup>-1</sup>). In contrast, total biomass in immature-aged trees in the NW-area was 51.7 tonnes ha<sup>-1</sup>, which was significantly greater than the biomass in the SE-area (40.0 tonnes ha<sup>-1</sup>) by about 11.7 tonnes ha<sup>-1</sup>. In the mature age class, total biomass in the NW-area was 58.6 tonnes ha<sup>-1</sup>, and 52.5 tonnes ha<sup>-1</sup> in the SE-area, exhibiting smaller overall differences than exhibited in the immature-tree component.



**Fig. 12.** Total biomass and biomass of balsam fir as a function of age class; note that the biomass for balsam fir in the NW- and SE-area for the young age class is 0.08 and 0.05 tonnes ha<sup>-1</sup>, respectively.

In the immature and mature age classes, with a greater total biomass in the NW-area (Fig. 12), balsam fir exhibited a slower radial growth (Fig. 11), which may have been a result of the greater level of competition that would have been present. Competition is known to have a negative effect on radial tree growth (Taylor and MacLean, 2005). As sunlight is an important variable for tree growth and crown shaping, competition has the effect of increasing relative height growth over radial growth (Duchesneau et al., 2001). In conditions of elevated competition, plants tend to grow taller to access more sunlight to become more competitive (Lines et al., 2012). In the overmature age class, with a reduction in biomass and presumably lower competition in the NW-area, balsam fir did not need to compete for sunlight as much, leading to increased radial growth in the trees.

#### 4. CONCLUSION

Although the NW-area experienced lower PAR, GDD, and SWC, it provided better growing conditions for balsam fir than did the SE-area. PSD-model results and interpretation were largely consistent with tree-based calculations of *SI*. Based on actual tree measurements from the NW-area, balsam fir trees were found to grow taller, whereas no significant difference existed with tree DBH with trees from the SE-area.

According to tree radial growth rates and total biomass accumulation in the NW-area, balsam fir demonstrated slower radial growth rates in both the immature and mature age classes due to higher total biomass and competition. However, radial growth rates increased in the overmature age class, which may have been associated with a corresponding reduction in biomass and, therefore, competition. Although calculations of PSD were based entirely on abiotic-based inputs, the calculations provided a reasonable assessment of site quality and potential tree species distribution. Accounting for inner-stand processes of competition in the calculation of PSD may assist in refining associated calculations further.

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