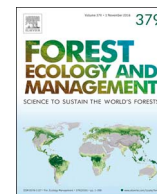




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## Climate-induced changes in the stem form of 5 North American tree species

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## ABSTRACT

Generally, the effects of climate change on tree growth focus on changes in one dimension of a tree. However, diameter increment along the main stem reacts differently to climatic variables, which in turn influences tree form. These differences can thus have important implications on stem volume, which could induce biases in future forest biomass estimation. A stem taper model including climatic variables was fitted to stem analysis data of five different species (*Abies balsamea*, *Betula papyrifera*, *Picea glauca*, *Picea mariana*, *Populus tremuloides*) distributed along a gradient from the temperate to the boreal forest of Eastern Canada. The effects of shifts in stem form on tree volume between different climatic scenarios were then estimated and related to different functional traits. Changes in stem form with climatic variables were observed for four of the five species, with up to 5% differences in stem volume between different climatic situations. Changes in stem volume were found to decrease with increasing waterlogging and shade tolerance. The most important differences in stem volume can induce changes of 3–4% in the biomass of a single tree. Not taking into account shifts in stem form could have implications in forest biomass estimations.

## 1. Introduction

According to the optimal partitioning theory (Thornley, 1972; McCarthy and Enquist, 2007), plants, and especially woody species, preferentially allocate their growth to the compartment (i.e. stem, branches, foliage, roots) which acquires the resource that is the most limiting to their growth. For example, a plant that is in a shaded environment will preferentially allocate its resources to increase its capacity in intercepting light, whereas plants in poor soils will expand their underground exploration (through root development or mycorrhizae). Moreover, plants change their allocation patterns with both environmental and local factors such as trees that reduce their foliage area in order to decrease their vulnerability to cavitation in arid conditions (Maherali and DeLucia, 2001) or increase their allocation to the roots in order to improve nutrient uptake in cold climates (Reich et al., 2014).

Moreover, the growth distribution within a given compartment also varies, which in turn can have important implications for estimating plant biomass. For example, foliage area is intimately related to the sapwood cross sectional area of the main stem (Shinozaki et al.,

1964b,a). Thus changes in foliage distributions help to understand shifts in tree stem form (Schneider et al., 2011a). The changes in the biomass allocation along the stem can also be explored through the study of the vertical growth profiles of a tree stem (Goudiaby et al., 2012). A few studies have worked on establishing such growth distributions within a tree stem at an annual level (Deleuze and Houllier, 2002; Cortini et al., 2013). When not considering butt flare, the growth rate is generally the largest at the crown base, in accordance with Pressler's law (Larson, 1963).

The within-compartment foliage distribution is known to be under the control of a large panel of factors, among them tree species, tree size, site conditions and competition (Schneider et al., 2011b). As for the main tree stem, both height and diameter growth have been shown to be closely related to temperature (Andalo et al., 2005; Goldblum and Rigg, 2005; Huang et al., 2010; Messaoud and Chen, 2011; O'Neill and Nigh, 2011; Girard et al., 2014) while the influence of precipitation was not as clear, at least in northern climates (Franceschini et al., 2016).

Instead of considering the longitudinal stem growth distributions, foresters generally use stem taper, defined as the diameter along the stem which corresponds to the cumulative sum of the annual growth at

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a given height. It has long been known that trees have more taper in open or in more fertile forests (Larson, 1963). Recent studies have shown that stem form is also influenced by climatic conditions (Nigh and Smith, 2012).

Shifts in stem form is often associated to changes in tree crown structure, as it has been demonstrated through modelling approaches (Valentine et al., 2012). The importance of crown characteristics have been explained by both hormonal (e.g. Larson, 1963) and biomechanical theories (e.g. Fournier et al., 2013). The first theory relies on the importance of auxins in general, and indole-3-acetic acid (IAA) in particular, on the initiation of radial growth of the stem (Nilsson et al., 2008). As IAA is formed in the apical meristems (Zhao, 2010), the xylem close to the apical meristems will receive the signal to initiate secondary growth earlier and thus have longer growth periods, thus leading to larger increments of the stem at crown base. The biomechanical theory on the other hand assumes that the stem must support both the branches and foliage to avoid buckling (Niklas, 2013). As a consequence, trees with bigger crowns must have larger diameter stems, and hence a larger stem increment at the base of the crown is required.

Changes in tree form have implications in estimating above ground biomass, as the main stem of the tree can account for up to 70% of a tree's biomass (Poorter et al., 2012). In order to estimate the above-ground biomass of a given tree, the volume of each compartment is generally multiplied by its basic density. Most studies have until recently focused on solely the changes in wood density with climatic variables (Franceschini et al., 2013), with very little attention on changes in tree forms. There are indications that the response of tree species to changes in climatic variables are determined by certain functional traits (Franceschini et al., 2016). Thus if tree form shifts with global changes, it should also be important to consider the effect of climate as forecasted by the International Panel on Climate Change (IPCC) on stem taper and volume. It is thus important to evaluate the magnitude of the climatic dependency of volume in order to avoid biases in the estimation of future biomass.

The present study has the objective to estimate the effects of climatic variables on tree volume for the main commercial species growing in northeastern America. This was performed by (i) integrating climatic variables in a previously published stem taper equation (Schneider et al., 2013); (ii) converting stem taper into volume (Fortin et al., 2013); (iii) compare the effects of different global change scenarios on tree volume and biomass estimates. The tested hypothesis is that stem taper decreases with temperature and increases with precipitations. We also hypothesized that global change will result in increases in tree volume and tree biomass for a given dbh and tree height which will be higher for conifers than for broadleaves. The analysis however relies on the assumption that the influence of future climatic conditions on tree development will remain constant.

## 2. Materials and methods

### 2.1. Study area

The database used in this study was originally collected to establish links between site fertility and forest ecotypes (Lafleche et al., 2013). A total of 8558 trees in 1328 plots distributed over a land base of 761,000 km<sup>2</sup> in the province of Quebec, Canada, were used to fit stem taper models (Table 1). The studied species were white birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* Moench. Voss), black spruce (*Picea mariana* Mill. Britton), trembling aspen (*Populus tremuloides* Michx) and balsam fir (*Abies balsamea* L. Mill). The study area ranges (Fig. 1) from the sugar maple-basswood bioclimatic domain in the temperate forests to the south to the black spruce-moss domain in boreal forest to the north (e.g. between 45° and 51°N) and between the eastern and western borders of the province of Quebec, Canada (i.e. 60° and 80°W).

**Table 1**

Dataset statistics (standard deviations in parentheses) and species functional traits (Waterlogging and drought tolerance: Niinemets and Valladares (2006); Shade tolerance: Humbert et al. (2007)).

	Trembling aspen	White birch	White spruce	Black spruce	Balsam fir
Number of plots	258	134	312	562	645
Number of trees	799	657	1321	2802	2979
Mean diameter at breast height (mm)	288 (60)	197 (48)	289 (68)	193 (43)	221 (47)
Mean total tree height (m)	22.41 (2.84)	17.44 (2.44)	18.86 (3.57)	15.71 (2.84)	16.74 (2.90)
Mean altitude (m)	336 (99)	373 (104)	428 (188)	420 (127)	421 (181)
Mean annual precipitation sum (mm)	1010 (93)	1023 (98)	1072 (123)	982 (77)	1059 (112)
Mean annual temperature (°C)	1.91 (1.22)	1.75 (1.19)	1.64 (1.32)	0.22 (1.12)	1.31 (1.55)
Waterlogging tolerance	2	1.25	1.02	2	1.77
Drought tolerance	1	2.02	2.88	2	1.77
Shade tolerance	9	7	4	4	3

### 2.2. Data collection

A stratified random sampling design was used to select the sample trees. The five most important ecotypes were identified in each ecological region of the province based on the forest ecological classification system established by the Quebec Ministry of Natural Resources (Robitaille et al., 2015). Within these ecotypes, a minimum of 5 temporary sample plots of 400 m<sup>2</sup> were established. A forest inventory within these plots was carried out where the species and diameter at breast height (DBH) of all the living trees were recorded in order to obtain stand basal area (BA, m<sup>2</sup>.ha<sup>-1</sup>) and density (SD, stems.ha<sup>-1</sup>).

Sample trees were then randomly selected within a 25-m radius from the plot centre, whereby the trees had to belong to the dominant species of the ecotype, be a dominant or codominant tree, not have any forks nor decay and a relatively straight main stem. On average, between five and ten trees per plot were chosen. The DBH (mm) of the sample trees was measured. Once the tree felled, total height (HT, m) was taken and disks cut out at 0.15, 0.60, 1.00, 1.30, 3.00 m and every 2 m until the stem apex. The disk diameter was measured with a circumference tape, as well as bark width at four points in order to obtain the under bark diameter of the cross section (d, mm).

### 2.3. Stem taper model

The stem taper model used is based on the work of Schneider et al. (2013). It is an adaptation of the model originally proposed in Sharma and Oderwald (2001) and later modified by Sharma and Zhang (2004). The model relates the under bark diameter d (in mm) at any point along the stem to DBH (in mm), HT (in m) and the height at which diameter d is taken (h, m) as follows

$$d_{ijk}^2 = \frac{1}{1 + e^{(\alpha + b_{i,1} + b_{ij,1})}} \times DBH_{ij}^2 \times \left( \frac{HT_{ij} - h_{ijk}}{HT_{ij} - 1.3} \right) \times \left( \frac{h_{ijk}}{1.3} \right)^{2 - (x_{ijk}\beta + b_{i,2} + b_{ij,2})} + \varepsilon_{ijk} \quad (1)$$

for  $i = 1, 2, \dots, q$ ;  $j = 1, 2, \dots, n_i$  and  $k = 1, 2, \dots, o_{ij}$ .

Where:

- $\alpha$  and  $\beta$  are a fixed effect or a vector of fixed effects parameters estimated by the regression, respectively,
- $q$ ,  $n$  and  $o_{ij}$  the total number of plots, the total number of trees and the number of disks in the tree  $i$  of plot  $j$ , respectively.
- $i$ ,  $j$ , and  $k$  the plot, tree within plot and disk within tree within plot indices, respectively, such that

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