# Modelling the radial and longitudinal variation in wood density and its sensitivity to climate in black spruce (*Picea mariana* (Mill.) B.S.P.)

(Spine title: Modelling wood density and its climate sensitivity)

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# *ABSTRACT*

Wood density variation affects structural timber performance and is correlated with different sources (genetic diversity, stand dynamics and climatic effects) which, to date, have not been comprehensively quantified in black spruce (*Picea mariana* (Mill.) B.S.P.). Controlling the confounding factors of ontogeny and stand dynamics allowed the effects of climate on annual wood density to be examined. The objectives of this study was to (1) to describe the variation in average ring density in black spruce as a function of cambial age, stem height and growth rate; (2) to identify climatic effect on density indicators (i.e. average ring density, minimum ring density, and maximum ring density) and determine the density-climate relationship according to tree size; and (4) to determine the effect of disc height on the density-climate relationship.

The dataset utilized densitometric data on a total of 35,127 annual rings from 450 radial strips collected in 107 black spruce trees sampled across 13 sites in northwest Ontario, Canada. Different aspects of the whole dataset were selected for various sub-studies.

We observed, when averaging the pith-to-bark profiles for all discs, that ring density (*RD*) was high near the pith and decreased rapidly in the first 12 growth rings, i.e. declined from 591.0 kg $m^{-3}$ to a minimum of 473.8 kg $m^{-3}$ between rings 10 and 15, followed by a slow increase until a consistent value was reached between rings 25 and 60. This average pattern till ring 60th corresponds to the type II pith-to-bark profile. However, thereafter, the dataset was separated into two groups. It was observed that 106 out of 450 radial samples showed a gradual decline in *RD* near the bark. These declining trends in annual ring density near the bark were found to be more common in old and slow-growing trees. We hypothesise that such trends reflect a gradual reduction in tree vigour over the life of the tree.

The climatic factors (monthly temperature and precipitation) were found to be significantly affecting density indicators across all dominance levels (dominant, co-dominant and intermediate trees). The density-climate relationships observed appears to be mediated according to dominance levels. This difference was assumed to be a result of dominance level related factors such as, thermal stress stratification and transpiration rate.

Additionally, it was evidenced that these density-climate relationships differed not only among dominance levels, but also along the length of the stem. The phenomenon of the various climatic sensitivities according to stem heights could be related to top-down auxin and carbon distribution, hydraulic effects and respiration rate among stem heights.

This work has provided a promising modelling method to disentangle the confounding sources of variation of wood density. It has also highlighted some of the future challenges which should be addresses on this research topic. Furthermore, this work has offered a starting point for studies on the effects of monthly climatic factors (temperature and precipitation) on density indicators and how these vary according to dominance level and stem height.

**Keywords:**

**average ring density; minimum ring density; maximum ring density; black spruce; modelling; density-climate relationship; dominance level; stem height; X-ray densitometry; boreal forest**

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# Chapter 1 INTRODUCTION

## 1.1 The change in global forestry and the impact on the Canadian industry: the necessity for wood property studies

Sustainable forest management is now widely accepted and the management of forests should follow the principles of sustainable development, called "Forest Principles" (United Nations, 1992). Forest managers traditional goals of forest planning for strictly commercial uses is changing to an integrated system of social, economic and environmental goals, which has led to some conflicts.

Many countries have established lists of criteria and indicators, and many forestry institutions have tested these in practice to assess if the objectives of sustainable forest management are being achieved at the management and operational level. The Forest Principles have also been embraced by Canadian society, which has experienced a range of fundamental changes relating to the environment and in particular in the forestry sector (e.g. Canadian Council of Forest Ministers, 2005).

As one of the most important renewable natural resources in Canada, forests benefit Canada's environment, social and economic wellbeing considerably. In order to improve the Canadian forest industry competitiveness in the global market place, it is necessary to move at least a portion of forest research and the forest industry towards value-added manufacturing. However, the forest research sector is still lacking an integrated model to simulate and optimize the value chain from forests to value-added products (ForValueNet, 2006). A first step to rectify this situation is to fully recognize the inherent wood quality properties of our species to allow better utilization of the forest resource.

Wood properties and composition display high variability between species, within a species, within a site and within a tree, based largely on genetic origin, site conditions, climate and forest management (Zhang *et al.,* 1993; Guilley *et al.,* 1999; Guilley *et al.,* 2004; Alteyrac *et al.,* 2005; Jyske *et al.,* 2008; Savva *et al.,* 2010). This high variability also means wood has potential for genetic and silvicultural improvement of wood properties for specific end products (Zobel and van Buijtenen, 1989). Therefore, to allow processing wood into a wide range of end products, researchers have to focus on formulating the high variability in wood properties. In other words, in order to produce the high quality and value-added forest products from Canadian forest resources, it is essential to accumulate extensive information on the various wood characteristics, especially to understand the significance variability has on species, growing conditions and silvicultural practices (Cown and Parker, 1979; Jozsa and Middleton, 1994; Evans *et al.,* 1994; Zhang and Morgenstern, 1995; Zhang *et al.,* 1997; Koubaa *et al.,* 2000).

## 1.2 The significance of wood density

### 1.2.1 Important wood quality indicator

A series of wood quality attributes, including fiber properties, knottiness, juvenile wood content, sapwood and heartwood content, dimensional stability and mechanical properties, are important for the quality and value of manufactured wood products (van Buijtenen, 1982; Zhang *et al.,* 1997). Of these attributes, wood density is well known to be one of the most significant wood quality attributes among most tree species (Panshin and de Zeeuw, 1980; Zobel and van Buijtenen, 1989). Wood density has been shown to be closely related to most mechanical properties of wood (Zhang *et al.,* 1993; Koga and Zhang, 2004) and certain strength properties of paper (van Buijtenen, 1982).

Specifically, higher wood density can result in higher timber strength as well as stiffness, and higher pulp yield. Commonly used industrial properties of conifers include lumber bending strength (modulus of rupture), stiffness (modulus of elasticity) and microfibril angle (MFA, the orientation of cellulose microfibrils of the S2 layer in the secondary cell wall), which are correlated with wood density (Evans *et al.,* 2000; Lenz *et al.,* 2010; Lachenbruch *et al.,* 2011; Moore, 2011). Therefore, it is not unreasonable to state that wood density is the most valuable single variable to represent wood quality.

### 1.2.2 Impact on the accuracy of aboveground biomass estimations

Additionally, wood density should not be limited to mechanical properties of timber, with growing interest in carbon sequestration of forest biomass; it can also be used in allometric equations as an essential component of aboveground biomass estimations (Ketterings *et al.,* 2001; Komiyama *et al.,* 2005). However, in many previous studies, growth rate was treated as a parameter to calculate biomass increments while wood density was introduced as a constant value into allometric equations (Ketterings *et al.,* 2001; De Vries *et al.,* 2006). In fact, wood density could be variable with growth rate, i.e. the higher ring width does not consequentially imply higher biomass accumulation as ring density could decline. It is logical to expect a substantial difference between observed and estimated biomass accumulation (Taki *et al*., 2007).

Therefore, a relative simple but accurate wood density model, which can be easily integrated into the equation for biomass estimations, is required.

### 1.2.3 Growing attention in growth-climate relationship studies

Furthermore, wood density is also of great importance in tracing growth and predicting tree productivity responses to climate. In the growth-climate relationship, tightly linked areas such as ring width sequences have been used as a tool to reflect climatic fluctuation and thus used for climatic history reconstruction over the last few decades (Fritts, 1976). Ring width chronologies can only be used after filtering out the non-climatic trends such as released growth due to competition and tree or site effects, referred to as a standardization procedure. Many complex functions, e.g. polynomials, cubic spline, or autoregressive models have been used to de-trend such non-climatic sources. However, uncertainty in the amount of climatic fluctuation was likely to be removed during such a procedure (Conkey, 1986).

In the 1960s, Polge (1963, 1966) applied the X-ray film technique in dendroclimatology studies in France and since then it has attracted increased attention in the forestry field. Density data has proven to be a successful complementary data source for climate construction in the conifers because of its main anatomical cell type - tracheids, representing 90% of the wood volume (Conkey, 1986; Tsoumis, 1991), which has density that is reliant on lumen size and cell-wall thickness (Wang *et al.,* 2002). It has also been found that a strong correlated link exists between maximum density and late summer temperature in conifers of northern Canada (Parker, 1976; Briffa *et al.,* 1998; Wang *et al.,* 2002). Density characteristics (e.g., minimum or earlywood density, maximum or latewood density and average ring density values) have therefore been used more and more in later studies (Conkey, 1986; Briffa *et al.,* 1998; Franceschini *et al.,* 2012). Compared to the ring width series, which require standardization, density chronologies display less variation in long-term trends. The density chronologies were therefore, always standardized by using straight lines in subsequent studies (Conkey, 1986; Wang *et al.,* 2002).

### 1.3 The importance of black spruce (*Picea mariana* (Mill.) B.S.P.) in Canada

With a broad distribution across Canada (Figure 1-1), the natural range of black spruce (*Picea mariana* (Mill.) B.S.P.), extends from Newfoundland to Alaska, south to British Columbia, Minnesota, and east to Rhode Island and Massachusetts (Little, 1971). Thus, it is one of the most important and valuable species for both lumber and pulpwood in eastern and central Canada, and the most important commercial and reforestation species from the Atlantic Coast to Manitoba (Hall, 1984; Risi & Zeller, 1960; Boyle *et al.,* 1987; Zhang & Jiang, 1998). With the importance of its wood and fiber to the forest industry, this species has pivotal significance in Canada.

Generally, this species can often be found on wet organic soils such as wet peat bogs or swamps, most of the time as a pure stand, but it can also tolerate a variety of nutrient-poor soil conditions in mixed stands associated with other species such as jack pine (*Pinus banksiana* Lamb.), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.) and white birch (*Betula papyrifera* Marshall) (Hosier, 1979). Normally, the size of black spruce reaches between 20 and 30 metres tall, between 23 and 26 centimetres in diameter at maturity in Ontario (Arnup, 1988). Compared to black spruce grown on upland high and dry sites, the size of black spruce in wetlands will be much smaller (Farjon, 1990). Black spruce is designated along with balsam fir and jack pine in the lumber category Spruce-Pine-Fir (SPF) in eastern Canada for marketing purposes (Mullins and McKnight, 1981). It is also a very important and widely used reforestation species in Eastern Canada. In order to maintain the resource for a steady supply of logs to mills into the future, large-scale reforestation with improved or selected genotypes have been planted in many parts of Canada (McKenney *et al.,* 1992; Weng *et al.,* 2011). Currently, wood density variation of many commercial species has been well documented (Zobel & van Buijtenen, 1989). However, for black spruce, in spite of this species importance, the relationship between wood density and tree growth is limited compared to some other commercial species. Most of the knowledge that is related to this species is descriptive (Zobel & van Buijtenen, 1989; Zhang *et al.,* 1993; Zhang *et al.,* 1996; Alteyrac *et al.,* 2005; Alteyrac *et al.,* 2006). Therefore, with its importance to the Canadian industry, the study of wood density needs to be expanded upon to help further our understanding of this species and focus on integrating wood density into models relating to forest growth, management and utilization.

Figure 1-1 Geographic distribution of black spruce in North America (Little 1971).

## 1.4 Objectives

**Overall objective**

The main objective of the study is to examine the impacts of different sources (i.e. cambial age, growth rate, stem heights, tree effect, dominance effect, site effect and climatic effect) on ring density through modelling to explain the density profile from pith to bark and base to a merchantable top of the stem in black spruce from naturally-regenerated, unmanaged stands.

**Specific objectives**

Ideally, the established model should be able to comprehensively interpret the effects of the confounding sources at the same time. However, it is not possible to incorporate all sources in the model at once using current statistical methods. Therefore the above general objective was separated into four objectives:

I. Investigating the ring density profile and its variation in response to cambial age, growth rate, stem heights, tree effect, dominance effect and site effect from natural unmanaged forests;

II. Understanding the impact of integrating climatic variables (temperature-related and precipitation-related variables) with sources from objective I on wood density at breast height, and to determine the climate sensitivity of wood density according to tree size;

III. To determine the climate sensitivity of wood density along the stem height.

## 1.5 Organization of the thesis

This thesis is organized into 6 chapters. In Chapter 1, the general background, motivations and objectives are presented. Chapter 2 covers a literature review on the frequently used sources of wood density; available information on the current understanding of the relationship between the major sources of variation of wood density and density indicators.

Chapter 3 presents a two-step model to formulate variation of ring density and link this with external stimuli by using densitometry data. Chapter 4 focuses on studying the density-climate relationships among tree size. Chapter 5 describes climate sensitivity of wood density variation based on different stem heights. Chapters 3 is under review, chapter 4 and 5 will soon be submitted.

Finally, Chapter 6 also summarizes the main contributions and conclusions of the thesis. Based on the general discussion, recommendations for future research are provided.

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# Chapter 2 LITERATURE REVIEW

It is essential to clarify the definition of wood density before getting into the discussion on the sources of variation of wood density. The term wood density is frequently expressed as a wood substances mass for a given volume of wood (Zobel and van Buijtenen, 1989), or the mass of a material per unit volume (Bowyer *et al.,* 2003). In practice, this terminology sometimes could become complicated depending on the research area, for example the weight of a wood product needs to account for the moisture content in addition to the wood substance. Although in the United States wood density is normally calculated based on moisture-free wood also referred to as oven-dry wood, in many other countries wood moisture content can be calculated using green weight or weight at a specific moisture content. Therefore, the best strategy before discussing wood density is to determine which values were used? Density can therefore be calculated from oven dry weight and volume, green weight and volume, or weight and volume at specific moisture content (Bowyer *et al.,* 2003). Additionally, wood density can also be strongly affected by chemical deposits within and between the cells such as resinous deposits and sugars (Zobel and van Buijten, 1989). However, no extractions were performed in this study, as the extractive content of black spruce wood is known to be very low (Lohrasebi *et al.*, 1999). In the present study, the term 'wood density' refers to the wood density at 12% moisture content.

Where does the variation in wood density come from? Variation in wood density is due to many intrinsic and extrinsic sources and exists radially from pith to bark and longitudinally along the stem (Koga and Zhang, 2004; Alteyrac *et al.,* 2005), and within the tree, sites and regions for the same species (Zobel and van Buijten, 1989).

For convenience, there are many ways to classify the sources of variation of wood density, such as:

1) internal sources which govern age-related changes during tree development: i.e. those intrinsic controls from gene expression; external sources namely environmental controls which might impact gene expression (Cown and Ball, 2001; Day *et al.,* 2002; Day and Greenwood, 2011; Lachenbruch *et al.,* 2011);

2) using data structure to organize the dataset, the variation of wood density exists not only among individual trees of the same species (Zobel & van Buijten, 1989), but also within a tree (Guilley *et al.,* 1999) which is normally expressed as inter-tree variation and intra-tree variation, respectively (Koga and Zhang, 2004). It is a common practice in studies to use the individual tree as the boundary at the management unit level.

Those separation methods are often varied depending on the objective of the research and they thus seem miscellaneous and fickle, but the essence of these methods is the same for simplifying data structure to select informative sources of the density variation. The present study will use the second method since this is a plain but effective way to split the variation at the management unit level.

More specifically, the intra-tree variation of wood density also can be further partitioned into three categories:

(a) Intra-ring variation;
(b) Radial variation from the pith to the bark;
(c) Axial variation from the stem stump to the stem apex.

The inter-tree variation can be separated into three main categories:

(a) Variation across the individual tree within a site (tree effect);
(b) Variation among sites within a relatively small geographic location in the same ecologic zone (site effect);
(c) Difference caused by climate (climatic effect).

In the review, the effect of human interference will also be discussed generally.

To facilitate expression of some inter-tree variations, the major source of each type of variation will be used to represent this type of variation, for example using site effect to represent the influences of site-related sources. However, we should note that many sources impact both intra-tree variations and inter-tree variations, for example climate effect is able to impact both intra-tree and inter-tree variations. This method of classification is not attempting to relate each variation to the mechanism of variation of density, but only for sorting sources conveniently.

Among the properties of wood, wood density is a notable variable: it is closely related to many wood quality properties (strength, stiffness), pulp yield and quality, is a meaningful record of climate variation and is an essential intermediate variable for aboveground biomass estimations.

In addition, wood density is directly related to aspects of the microscopic anatomical structure of wood. Anatomical structure refers to the radial and tangential diameter of tracheids and the thickness of the cell wall. There are two major types of cells in all conifers: longitudinal tracheids and ray parenchyma cells with the tracheid making up over 90 percent of the volume of the stem in conifers (Panshin and de Zeeuw, 1980). Under the same moisture content, wood density is determined by two characteristics: 1) the porosity or proportion of void space; and 2) cell wall thickness and the microstructure within the cell wall which is species-specific. The formation of tracheids, are under the control of genetic and environmental sources influencing cambial activity. Two questions are then raised: what is the genetic influence on variations in anatomical structure when environmental sources are controlled; and how do anatomical structure responses to environmental stimulations occur. Therefore, the relationship between environment-related anatomical structures with wood density needs to be understood.

## 2.1 Intra-tree variation

### 2.1.1 Intra-ring variation

In boreal forest, following a period of dormancy, trees reactivate with certain temperature related stimulus in the early spring. Varied levels of hormones and availability of photosynthate result in the newly produced cells displaying non-uniform size and arrangement during the growth season. Cells formed in the early part of the growing season display larger radial diameter, thinner cell walls with a larger lumen and relatively lower density when compared to cells formed later in the growing season. Cells formed later in the growing season display smaller radial diameter, thicker cell walls with a small lumen and higher density when compared to cells formed earlier in the growing season (Panshin and de Zeeuw, 1980). Cells are classified as latewood when their double cell wall thickness is greater than the lumen size (Zobel and van Buijtenen, 1989). For the conifers, the less dense and normally lighter-colored wood is known as earlywood or springwood and the latter denser and darker wood is called latewood or summerwood (Panshin and de Zeeuw, 1980).

A number of studies have revealed significant wood density changes from earlywood to latewood. The reason for this change in density has been exhaustively discussed by Larson (1969) where he proposes cell diameter is driven by auxin (plant hormone) produced in apical meristems. Any factors leading to reduced apical activity will cause less auxin production and consequently smaller diameter cells, typically resulting in increased cell wall thickness and therefore higher wood density. The supply of photosynthate has also been suggested to be involved in the whole complicated physiologic process. The competition early in the growing season between the development of new shoots and their new needles, and the vascular cambium for resources leads to less photosynthate available for radial growth, thereafter when crown development ceases or slows, more resources will received in vascular cambium region (Panshin and de Zeeuw, 1980).

It has been proposed that earlywood is formed during the tree elongation phase of growth early in the season and latewood is produced later in the season once bud formation has completed for the season (Zobel and van Buijtenen, 1989; Larson *et al*., 2001). However, some sources controlling the formation of latewood still remain unclear, many studies have indicated there are more than the above two mentioned sources controlling the cambium to produce latewood cells instead of earlywood cells (Lachenbruch *et al*., 2011). It might be attributed to the confounding effects of both genetic and environmental sources (Zobel and van Buijtenen, 1989).

Indeed, characteristics from anatomical structure could offer more detailed information at a finer scale. These characteristics such as, radial and tangential diameter of tracheids (or lumens), and the thickness of cell walls are preferable variables adopted by some researchers (Bannan, 1965; Lundgren *et al*., 2004). However, constrained by the cost of these types of measurements, some other more general variables such as earlywood density, latewood density and average ring density were used. They are not the most precise variables at the anatomical level, however in practice these ring density characteristics have been more frequently used (Guilley *et al*., 1999; Alteyrac *et al*., 2005). The anatomical structure within these characteristics is, however presumed to be evenly-distributed throughout. Normally, earlywood and latewood density can be calculated through the mean value of earlywood and latewood widths, respectively. Ring density can also be calculated by a simple geometrical equation (equation 1) as a function of earlywood density, latewood density and proportion of latewood as follows:

$$RD = EW * (1 - LW\%) + LW * LW\% \qquad (1)$$

where $RD$ is the ring density, $EW$ is the earlywood density, $LW$ is the latewood density and $LW\%$ is the ratio of latewood within an individual ring.

Intra-ring wood density variation displays useful information relating to wood formation and physiological processes that occurred during past environmental conditions. Average ring density could be a comprehensive variable to describe general information during a growing season and across several growing seasons.

Variation in wood density within rings is usually referred to as the intra-ring density profile. In black spruce, the difference between earlywood and latewood within a ring can be remarkable. The earlywood density can reach the minimum value of 260 kg/m$^{-3}$ while latewood density can attain maximum values of 800 kg/m$^{-3}$ (Koubaa *et al.,* 2002). The density is constant at the beginning of the ring and increases gradually to the maximum value, thereafter, followed by a rapid decrease. This intra-ring profile is well known and has been described in many other spruce species such as Norway spruce (*Picea abies* (L.) Karst.) (Franceschini *et al.,* 2013a) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (Moore, 2011).

Recently, with the expansion of X-ray film techniques, many models were established based on densitometric data for intra-ring density profiles (Koubaa *et al*., 2002). Microscopic structures of earlywood and latewood have also been investigated (Lindström, 1997) as well as their relationships with densitometric characteristics (Wang *et al.,* 2002). However, some other important sources in the radial direction such as cambial age (ring count from pith outwards) and ring width have not been comprehensively integrated into these models.

### 2.1.2 Radial variation from the pith to the bark

In addition to intra-ring variation, radial variation in wood structure and properties within the main stem is pronounced in relation to cambial age and growth rate (Zobel and van Buijtenen, 1989). In many conifers, cambial age has been used to describe density variation for the radial pattern (Kennedy, 1995; Lachenbruch *et al.,* 2011). Indeed, cambial age is physiologically related to the radial pattern to a great extent since cambial age partially represents the difference in anatomical structure between juvenile and mature wood. Tree vigour may also be related to growth-regulating hormone levels and the availability of photosynthate.

Radially, wood properties and the structure of stems, branches, and roots display variation from pith to bark (Lachenbruch *et al.,* 2011). In conifers, wood near the pith usually displays a larger proportion of earlywood (tracheids with larger diameter and thinner cell walls) compared to latewood (tracheids with smaller diameter and thicker cell walls) in a growth ring, and is generally referred to as 'juvenile wood' (JW) (Cown, 1992, Larson *et al.,* 2001, Lachenbruch *et al.,* 2011). Juvenile wood is also referred to as pith wood or inner wood, and has further been defined as secondary xylem produced by cambial regions influenced by activity in the apical meristem (Bowyer *et al.,* 2003). Following several years of JW production the tree begins producing wood with more consistent properties including a lower earlywood to latewood ratio within growth rings and is referred to as ‘mature wood’ (MW) (Cown, 1992, Larson *et al.,* 2001, Lachenbruch *et al.,* 2011). Separating the stem into the JW core and the surrounding MW recognizes the distinct difference in wood properties between these two regions in the tree. With MW properties being ideal for many industrial uses and being quite different than JW properties, which are not ideal for many industrial uses. Some research has focused on the effects of radial variation on wood utilization and in particular the size of the juvenile wood zone (Zobel and van Buijtenen, 1989; Zobel and Sprague, 1998; Larson *et al.,* 2001).

Juvenile wood displays lower quality than mature wood in conifers due in part to juvenile wood displaying shorter cells, high earlywood to latewood ratio, and generally thinner cell walls than mature wood, which will directly result in lower density in the juvenile wood zone. In addition, compared to mature wood, conifer juvenile wood displays greater cell wall microfibril angle, higher longitudinal shrinkage, more compression wood, higher lignin and hemicellulose content, and lower cellulose content (Panshin and de Zeeuw, 1980; Larson *et al.,* 2001). In black spruce, the transition from JW to MW is gradual rather than abrupt. With increased cambial age, a larger proportion of latewood and variation in earlywood density are major factors controlling variation in ring density (Koubaa *et al*., 2005; Alteyrac *et al.,* 2006).

A commonly used proxy for establishing wood density from pith to bark is cambial age as this is physiologically representative and can also be easily derived from rapid x-ray diffraction technology. Widely used automated x-ray densitometers allow acquisition of large amounts of data on radial density patterns at a relatively low cost and with relatively little effort. From pith to bark, the radial pattern of annual ring density can be classified into three general types: 1) the average ring density increases gradually from JW to MW; 2) the average ring density is high near the pith and decreases rapidly outwards, followed by a gradual increase; and 3) the average ring density decreases from pith to bark either as a straight line or a curve (Panshin and de Zeeuw, 1980).

Of these density patterns, type II pattern is a typical pattern for conifers growing in northern North America, e.g. five species or species groups of the conifers from the Pacific Northwest (Kennedy 1995), i.e. Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco; Lodgepole pine, *Pinus contorta* Dougl.; Western hemlock, *Tsuga heterophylla* (Raf.) Sarg.; Engelmann spruce, *Picea engelmanni* Parry ex Engelm; white spruce; sitka spruce; black spruce; alpine fir, *Abies lasiocarpa* (Hook.) Nutt; amabilis fir, *Abies amabilis* (Dougl.) Forbes; grand fir, *Abies grandis* (Dougl.) Lind; noble fir, *Abies nobilis* (Dougl.) Lind., and in many hard pines such as radiate pine (*Pinus radiate*) and loblolly pine (*Pinus taeda* L.) (Zobel and van Buijtenen, 1989; Lachenbruch et al., 2011).

Many studies have tried to elucidate the underlying reasons for JW patterns (Koubaa *et al.,* 2000; Alteyrac *et al.,* 2006). The invariably high density occurring in the rings adjacent to the pith, was concluded to be attributed to high earlywood specific gravity (Megraw, 1986; Koubaa *et al.,* 2005), which was causally observed in many conifers previously (Elliott, 1970). Interestingly there is little evidence supporting the idea of heritable impacts on earlywood cell diameter of these rings adjacent to the pith (Lenz *et al.,* 2010). Telewski (1989) termed the wood adjacent to the pith as ‘flexure wood’, which is thought, to be formed in response to complex loading patterns trees are subjected to at a young age. Variation in mechanical structure caused by distinct local conditions might be another trigger resulting in different initial density values. After the first few rings, both earlywood density and latewood proportion decline rapidly which explains the initial decline in ring density as rings move outward radially.

Additionally, instead of studying specific radial patterns of certain wood properties, phenotypic studies showed “genetically-formed” tissues from JW to MW can be found radially in *Pinus radiata* (Cato *et al*., 2006), as well as longitudinally in *Pinus pinaster* (Paiva *et al*., 2008). They both found genetic controls were greater apically in the tree than at the base in the JW, however the opposite situation was displayed in MW.

Density variation is known to be controlled, in large, by genetic and environmental controls, however it is sometimes hard to distinguish between genetic or environmental control. Genetically density is strongly correlated with cambial age but poorly correlated with diameter (Day *et al.,* 2002). Sometimes, the opposite correlations can be observed where density is strongly correlated with diameter and poorly correlated with cambial age (Lachenbruch *et al*., 2011). It is easy to understand the former, for the latter it can be interpreted by both genetic and environmental effects, especially in situations with strong environmental effects. For these cases, instead of cambial age, the variable "distance from the pith" is often used (Lundgren, 2004). This variable is particularly suitable when strong external interference, such as silvicultural practices, was involved (Lundgren, 2004) as it can be treated as a joint variable representing size and cambial age to some extent. However, on occasion these two variables, cambial age and distance from pith, are similar and exchangeable (Mäkinen *et al.,* 2002b).

Lachenbruch *et al.* (2011) believed that cambial age is a better predictor of the radial pattern than is stem diameter in both softwoods and hardwoods. His conclusion was inferred from analysis of a series of pre-set (genetic) or environmental changes in the xylem's structure and function. He also mentioned that, in reality, age and size are always strongly correlated, thus, we hardly know which variables can be a better predictor for a particular case. The radial variation of the average density was always accompanied with changes in ring width (Wimmer and Downes, 2003; Alteyrac *et al.,* 2006; Moore, 2011). For most spruce species, ring width is wide near the pith and increases quickly to the maximum value, thereafter, a gradual decrease until an asymptotic value is achieved. Graphically, in the radial pattern of ring width, the maximum value and the quasi-asymptotic decrease can partially reflect the mirrored variation pattern of density. Therefore, due to the unclear mechanism of the physiological process in response to environmental sources, the best choice is to include growth rate as a potential variable in research (Franceschini *et al*., 2010).

### Radial pattern in response to growth rate

The relationship between growth rate and density is a frequently discussed controversy in the literature (Larson, 2001; Bowyer *et al.*, 2003). In earlier studies, the prevailing thought was that slow-growing softwoods with narrow-rings had denser wood than fast-growing softwoods with wider-rings (Bowyer *et al.*, 2003). It is understandable this was the prevailing thought since most data sets were produced from natural stands in which wider rings were normally associated with the juvenile zone. After the middle of the twentieth century when increased silvicultural practices were occurring, the quality of fast-growing trees from wider initial spacing, were being investigated. It was found that the wider rings were not necessarily displaying the density found in the interior rings by the pith (Larson *et al*., 2001). Owing to increased concern on the wood quality of fast-growing/improved forests with shortened rotations (Bendtsen, 1978; Zobel & Van Buijten, 1989; Zhang & Morgenstern, 1995; Alteyrac *et al.*, 2005), the effect of growth rate on wood quality has drawn people's attention once again (Zhang *et al.*, 1993; Guilley *et al.*, 1999).

Most literature has found a negative but weak relationship between growth rate and wood quality e.g. Norway spruce (Franceschini *et al.,* 2010), Sitka spruce (Gardiner *et al.,* 2011). Also Simpson and Denne (1997) reported that the strength of this negative relationship increased from the stem base to the tree tip, for a given cambial age in Sitka spruce. In balsam fir, Koga and Zhang (2004) found a significant negative correlation between growth rate and density below 3 m in the stem, but there was no significant effect above this height. Wimmer and Downes (2003), on the other hand, reported a positive relationship between ring width and ring density in Norway spruce, which was associated with higher late-season rainfall. In Douglas-fir, Kennedy (1995) stated the effect of growth rate on density is much less compare to the age effect. However, a negative relationship was found when faster radial growth was a result of high early-season rainfall. Besides changes linked to climatic conditions, the relationship between ring width and wood density may also be altered by the application of fertilization (Mäkinen *et al*., 2002) and thinning (Jaakkola *et al.,* 2005).

In black spruce, studies have reported that ring width does not significantly affect wood density in mature wood (Risi and Zeller, 1960; Hall, 1984). On the other hand, negative correlations between wood density and growth-related traits (DBH, tree height and bole volume), were detected by Zhang and Morgenstern (1995). Zhang *et al.* (1996) reported moderate negative correlations between wood density and growth rate in 15-year-old black spruce trees, but these relationships could be reversed for given provenances, environmental conditions and geographical locations. More recently, Koubaa *et al.* (2000) observed the combined effect of cambial age and growth rate and concluded that the negative effect of ring width on wood density in black spruce was not significant beyond a cambial age of 25 years. Contrary to this Larson *et al.* (2001) concluded the effect of growth rate in the juvenile zone should be negligible and not significant for most end uses. Therefore, the major variable relating to variation in wood density comes from inherent variation which can be related to cambial age i.e. juvenile and mature.

Currently, wood density research is based on data at the ring level. Ring width and its related variables (i.e. rings per inch of radial growth) have been the most commonly used variables to formulate growth rate. When sampled at breast height, ring width was usually negatively correlated to the average ring density (Zhang *et al.,* 1996; Alteyrac *et al.,* 2005). This can be explained by the idea/observation of "constant latewood width" first introduced by Brazier (1970) in Sitka spruce. He observed that latewood width remains relatively constant between rings, so that variation in ring width is tightly related to earlywood width. Similar results have been found in black spruce (Zhang *et al.,* 1996), sitka spruce (Moore, 2011) and jack pine (Savva *et al*., 2010) as shown in Figure 2-1.

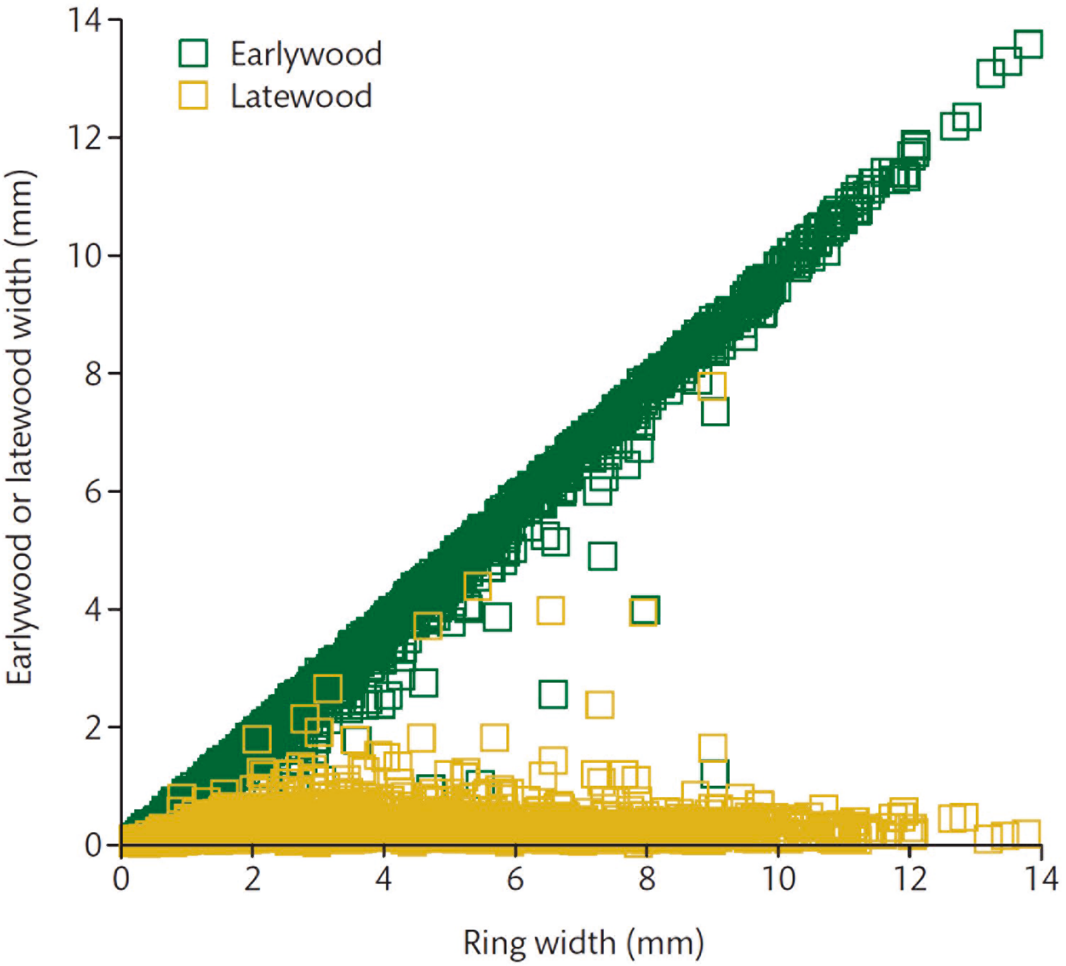

**Figure 2-1 Earlywood and latewood width to the total ring width in Sitka spruce (Moore, 2011)**

Despite having been investigated extensively, after reviewing the literature much confusion and contradiction exists as to which factor, cambial age or growth rate, has the most effect on density, as they are also often confounded. Although it is hard to separate these two sources independently, at least, we know the effects of cambial age and growth rate on wood density occur in combination and the effect of growth rate on wood density still has some controversy. In addition, the effect of growth rate may also be affected by social status in the stand. For example, the dominant tree may show one radial pattern while the neighbouring suppressed tree of the same species may show a different pattern. More details on this will be discussed in the inter-tree variation section.

### 2.1.3 Longitudinal variation along the stem length

Stem growth occurs in two directions: elongation increasing the stems length and radial expansion increasing the stems diameter or circumference. However, due to the time, budget limitations, convenience and practical reasons, many investigations only sample at breast height (e.g. Schweingruber *et al*., 1990; Zhang *et al.,* 1998). In addition to the simplicity of operation, the irregular expansion of the tree base was stabilized at breast height so climate-growth relationships could be investigated without including growth irregularities found in the tree base (Schweingruber *et al*., 1990). Moreover, Zobel and van Buijtenen, (1989) describe the intra-tree variation as generally more pronounced in the radial direction than longitudinally along the stem length of the same successive growth ring. Therefore, investigating density variation at breast height to avoid sampling from several height positions could provide reasonable accuracy with minimum cost and effort.

However, with improved technologies (e.g. X-ray film technique), the cost and effort of sampling are well reduced. And more and more studies found that to understand the longitudinal variation it is necessary and extremely valuable to help us understand whole tree variation. Indeed, limited information is available relating to the formation of the wood along the whole stem length. However, there are a few hypotheses recognised such as the important role of the tree crown in wood formation proposed by Larson *et al.* (1969). He proposed that as the tree crown recedes upward with increasing height growth annual rings from the lower stem of older trees will likely display a higher proportion of latewood due to the increased distance from the active growth in the crown. He also noted that earlywood-type cells with lower density were still formed in the crown (Larson, 1973). This leads to the proportion of earlywood decreasing from the apical meristem down the stem to the base and latewood decreasing from the base of the stem to the apical meristem. The different density values along the stem length can thus be expected as varied physiological age and crown effects at different stem heights. Panshin and de Zeeuw (1980) stated a general decreasing pattern can be found from base to the top of the merchantable trunk below the crown in most of the principal commercial softwoods.

An underlying assumption for radial density studies undertaken at breast height was that this sample height was able to represent the variation of the whole stem, which is not necessarily true. The axial pattern is not always consistent in conifers, which appears to interact with radial growth rate and other environmental sources such as social status. In cedar trees, the intermediate and suppressed trees were found to display few variations among stem heights (Panshin and de Zeeuw, 1980). In Norway spruce, Mäkinen *et al.* (2007) found no significant effect of height on ring density at a given cambial age, while Jyske *et al.* (2008) found a small positive height effect (3%-6%) at the same cambial age. In black spruce, Alteyrac *et al.* (2005) reported a large variation in density among stem heights, but the variation was smaller in mature wood than juvenile wood. Additionally, climate sensitivity of density among stem heights was not identical. It was found that climate sensitivity is decreasing from apical to basal regions of trees since it could be related to hydraulic limitations and downward carbon allocations during ring formation (Fritts, 1976; Kerhoulas and Kane, 2012).

In previous investigations, there are a few methods to study axial variation in wood density: 1) comparing the same cambial age annual rings counted from the pith to the bark (Alteyrac *et al.,* 2005; Alteyrac *et al.,* 2006); 2) comparing annual rings counted from the bark inwards to the pith, i.e. rings formed in the same calendar year (Splechtna *et al.,* 2000; Wimmer and Downes, 2003); and 3) comparing annual rings from axial cross-sectional sections, i.e., annual rings at the same distance from the pith are compared (Jyske *et al.,* 2008). These three methods have advantages and disadvantages depending on the objectives of the study.

## 2.2 Inter-tree variation

### 2.2.1 Tree to tree variability

In conifers, even within a species, the variability of wood density among trees growing under the same growing conditions can be quite large. In many species, such variability among the trees was much greater than site-to-site variability or among species. However, this large tree variation pattern is relatively consistent among provenances (Zobel and van Buijtenen, 1989). Individual tree genetics could contribute to the variation of density (e.g. Douglas-fir, Rozenberg *et al*., 2001; Norway spruce, Franceschini *et al*., 2010; black spruce, Zhang and Morgenstern, 1995), which is usually referred to as the genetic effect (Zobel and van Buijtenen, 1989; Jaakkola *et al.,* 2005; Schneider *et al*., 2008). This tree variation potentially masks some other sources and causes difficulties in predicting wood density as well as utilization of the resource. Normally, variation in juvenile wood is less than in mature wood (Larson *et al.,* 2001). Lenz *et al.* (2010) inferred the influence of genetic control becomes stronger with increasing cambial age. In previous investigations, foresters were attempting to reduce the tree effect by genetic improvement or silvicultural practices. Moreover, to sample sufficient trees is a helpful method to achieve valid density estimates for groups of trees.

In addition to genetic control, environmental effects also play an important role in the variation among trees. The impact of environmental sources on trees within a site (under similar growing conditions) is small, where the primary impact was assumed to be competition from the neighbouring trees (Zubizarreta Gerendiain *et al.,* 2007). Competition for limited resources (e.g. nutrients, water and light) directly impacts the growth and crown development of individual trees and the different carbon allocation leads to varied wood density along the stem. For example, different social status may have various light conditions enabling different amounts of photosynthate being available for the cambium and thus the rings with different density were produced. An example of social status would be a dominant tree displaying one radial pattern while the neighbouring suppressed tree of same species displaying a different pattern (Zobel and van Buijtenen, 1989). By comparing a group of cloned Norway spruce, researchers found that increasing competition among the neighbouring trees leads to increased wood density (Swenson *et al*., 2007; Zubizarreta Gerendiain *et al.,* 2009). A suppressed tree would display denser wood (Guilley *et al.,* 2004; Savva *et al.,* 2010), and accordingly the taller and faster growing trees (dominant tree) would have relatively low density (Alteyrac *et al.,* 2005). However, in traditional dendrochronological studies, sampling procedures have often been established to serve the purpose of minimizing non-climatic effects by selecting dominant trees not under strong competition (Fritts, 1976; Schweingruber, 1996). Obviously, this approach dismisses the effect of tree-size on sensitivity to climate. In fact, in coniferous species, a consistent result was found that small-diameter trees were more sensitive to drought (Pichler and Oberhuber, 2007; De Luis *et al*., 2009) while similar climate sensitivity among social status was found in cold climates by Chhin *et al*. (2008). Therefore, such size mediated climate sensitivity is complex and may be location-specific.

### 2.2.2 Site to site variability

Site-related sources such as moisture, availability of sunlight and nutrients, site quality, wind, slope and snow and ice can also contribute to density variation (Macdonald and Hubert, 2002; Bowyer e*t al*., 2003). These sources primarily depend on the microenvironment around the tree such as soil type, latitude, elevation, slope, aspect, stand composition and spacing, which lead to varied cell dimensions and cell wall thickness and therefore varied density. Different species can respond quite differently to each source (Bowyer *et al*., 2003). Therefore, some studies treat site factors as a comprehensive indicator instead of determining the effect of each source (Guilley *et al*., 1999; Jaakkola *et al.,* 2005; Schneider *et al.,* 2008).

Overall growth and wood formation have been related to site effects (Zobel and van Buijtenen 1989). Most investigations of commercial conifers were established on rich sites (or at least moderate sites), the difference in wood density derived from site effect therefore can be small to insignificant (Guilley *et al.,* 2004; Franceschini *et al.,* 2010). At a small regional scale, researchers often assume environmental sources i.e. site quality, will be the same for each tree within the site and these values will be constant over time. However, Zobel *et al.* (1960) presented highly significant differences between sites for all wood characteristics in loblolly pine (*Pinus taeda* L.). Rossi *et al.* (2007) compared two neighbouring sites located on a south and north-facing slope in the treeline ecozone of larches and pines. The authors found that due to the temperature of stems and soil in the later spring of the southern site, which was warmer than the opposite side, the difference in cambial activity between the two sides was elucidated. In jack pine, Schneider *et al.* (2008) reported considerable influence of site on earlywood density and latewood density.

Additionally, trees from sites with varied fertilizer treatments can produce wood with highly varied growth rates as well as quality characteristics (Zobel and van Buijtenen, 1989; Larson *et al*., 2001; Jaakkola *et al*., 2006; Mäkinen *et al*., 2007), which imply the natural stands with different nutrient supply may lead to similar variance. Thus, changes in growing conditions from one site to another could be taken into account in the study of variation in wood density.

### 2.2.3 Human interferences - silvicultural practices

Over the past several decades, forest management has tried to increase stem volume through increasing the proportion of intensively managed plantations and shortening rotation length with the end goal of higher volumes. However this approach raises another question: can such practical applications produce fast-growth forests with high quality?

Common silvicultural treatments include: thinning, pruning, fertilization, irrigation, initial spacing (planting), and cultivation with the first four frequently used. Normally, thinning often involves removing suppressed or undesirable trees to reduce competition among the rest of the trees, resulting in the growth rate of the forest to be accelerated due to increased availability of water, nutrients, solar radiation and increased spacing among individual trees (Wimmer & Downes, 2003). Pruning has been used to remove the lower branches at the base of the crown leading to wood with smaller knot sizes and producing a bole of knot free lumber when processed. Fertilization and irrigation have been used to provide extra nutrition and water supply to stimulate tree growth (usually after pre-commercial thinning) (Zobel and van Buijtenen, 1989; Smith *et al*., 1997). Currently many different effects of silvicultural practices on wood properties have been reported (Zhang *et al.*, 1996; Chui *et al.,* 1997; Downes *et al.,* 1999; Mäkinen *et al.,* 2002; Jaakkola *et al.*, 2005, 2006; Alteyrac *et al.*, 2005; Kantavichai *et al*., 2010). These silvicultural treatments impact tree growth by changing environmental stimulus and in particular increasing the size and shape of the crown through increased growing space around each tree (Zobel and van Buijtenen, 1989; Smith *et al*., 1997). A modified crown therefore produces wood grown under a different growth rate and therefore affects the final wood quality (Larson, 1969).

In balsam fir, Chui *et al.* (1997) and Koga *et al.* (2002) found pre-commercial thinning likely leads to decreased ring density due to reduced latewood proportion, however such a decrease was not found to be significant. Mäkinen *et al.* (2002) found in Norway spruce, that fertilization facilitated radial growth in earlywood width in particular, however it also lead to a reduced wood density in the lower stem due to a decrease in the proportion of latewood. Additionally, both earlywood density and latewood density were observed to be decreased but proportionately more in latewood (Mäkinen *et al.*, 2002). In relation to initial spacing, Robbins (2000) found little effect on wood density in several young Douglas-fir stands ranging from 309 to 18,730 trees/ha. Wider initial spacing in plantations tends to induce lower wood density in black spruce (Zhang *et al*., 2002). Jaakkola *et al.* (2005, 2006) observed fertilization and thinning treatments significantly increased radial growth rate of trees, however a slight to no significant effect was found on wood density in Finland. As mentioned previously, stand density management aims to accelerate the growth of trees and shorten rotation age as growth conditions were affected by crown development (Raulier *et al.*, 1996). However, Alteyrac *et al.* (2005) found stand density caused little variation in wood density and had more impact on ring width features than on ring density features in natural black spruce stands.

In general, it is accepted that trees with inferior properties can be found in intensively managed sites compared to natural forest trees (Chui *et al.,* 1997; Larson *et al*., 2001; Mäkinen *et al*., 2002; Jaakkola *et al.,* 2005). The main result of silvicultural effects is the enhancement of growth rate by promoting crown expansion at the cost of wood quality. Therefore, an optimal balance needs to be found between wood quality, stem growth rate and crown expansion.

### 2.3 Climatic effect on wood density variation

Many studies have displayed the existence of climatic impacts on cell size and cell wall thickness in conifers (Zobel and van Buijetenen, 1989; Larson *et al.,* 2001; Rossi *et al.,* 2008). Wood density has been proven to be closely related to wood anatomy (Zobel and van Buijetenen, 1989). Trees growing in boreal forests have the ability to adapt to different growing conditions with limited resources (Kozlowski *et al.,* 1991). Wood density displays a declining tendency with varied temperature and water availability northwards along latitudinal gradients (Zobel and van Buijetenen, 1989). Briffa *et al*. (1992) found a strong correlation between ring density and summer temperature on a large geographic scale across Western North America for a series of conifers species. Conkey (1986) proposed the climate-density relationship should be explained from a physiological perspective in red spruce (*Picea rubens*) of Eastern North America. In a later study, Conkey (1988) displayed a decreased relationship between spring temperature and maximum density over time; however such a relationship was not significant during certain time intervals (1965-1984). Larson *et al.* (2001) proposed that JW should be less sensitive than MW to climatic effects in plantations of the southern pines. In black spruce, anatomical structures and density characteristics were tested and correlated with summer temperature (Wang *et al*., 2002). St-Germain and Krause (2008) stated that varied anatomical structures were partly a result of different latitudes.

## Climatic effect on anatomical structures

In the following section, we refer to the effects of temperature and precipitation on anatomic structures during cell differentiation. Cell differentiation refers only to activity in the vascular cambium, a lateral meristem as compared to an apical meristem.

In boreal forests, trees are dormant in fall to avoid damage to the vulnerable cambium during the cold winter and reactivate later in the spring when environmental sources (temperature is the main essential condition) are appropriate. Thereafter, cambial activities (i.e. growth rate) increase rapidly to attain a maximum value around the date with the maximum day length (Rossi *et al.,* 2006), followed by a photoperiod-constrained decrease and cessation in the autumn, which is referred to as annual periodicity (Rossi *et al*., 2006; Begum *et al*., 2013). Another opinion suggested by Mäkinen *et al.* (2003) is that maximum growth rate is controlled by temperature. During each growth phase in xylem formation, several successive stages within the cell differentiation process need to occur before tracheids begin functioning physiologically (Deleuze and Houllier, 1998; Rossi *et al.,* 2008). Generally, in conifers, cell differentiation involves cell division, cell enlargement, secondary cell wall development followed by lignification and finally autolysis. These stages can be observed simultaneously in samples collected early in the growth season when the vascular cambium is most active. The level of activity depends on spring conditions of a particular year and on the position along the length of the main stem. The first two stages are related to tracheid diameter while the third stage involves cell wall thickening and the addition of lignin, which has been shown to be a very different physiological processes compared to the first two stages (Larson 1964). Cambial cell division and radial cell enlargement were stimulated by hormonal signals mainly produced in new shoots and needles of the uppermost crown while secondary cell wall thickening is dependent on availability of photosynthate produced in older needles located in the lower crown (Larson *et al*., 2001).

More specifically, during the late spring in boreal forest regions, a few closely spaced cells (cambial initials) in the dormant cambium start to divide quickly at first. The new cells are produced rapidly and the cambial zone widens, which visibly reveals the onset of cell division. The cells in this stage have been described as displaying radial diameters twice the size of the cambial initial cells (Begum *et al.,* 2008; Rossi *et al.,* 2008). Thereafter, these new cells enlarge radially in the next stage of differentiation. The radial size of the tracheid is essentially set during the enlargement phase (Deslauriers, 2003). During the subsequent maturation phase cellulose deposition occurs, increasing the secondary cell wall thickness and this is followed by lignification where lignin is infused into the cell corners first and then the rest of the cell wall (Panshin and de Zeeuw, 1980). The last stage of cell differentiation is protoplast or cell autolysis where all cell contents are flushed from the cell and the tracheid cell becomes functional for transport (Fritts, 1976; Deslauriers, 2003; Gričar *et al*., 2005; Rossi *et al*., 2008). Each stage plays a different role in determining the final anatomical structure of the cell. As mentioned previously tracheid size was determined during cell division and cell enlargement while the cell wall thickness was linked to the latter periods of growth during the growth season. Therefore, all aspects of cell development are also determined by the availability of hormones, nutrients and water but also on growing conditions such as temperature and sunlight, which will determine the amount of cells the cambium produces in a growing season.

Some research has occurred to formulate the effect of climate on the onset of growth and dormancy of cambial activity, growth rate during the growth season, length and width of the cell wall and associated variations in balsam fir (Deslauriers, 1999, 2003; Krause *et al*., 2010), Norway spruce (Mäkinen *et al.,* 2003), black spruce and some other conifers (Rossi *et al*., 2006, 2007, 2008). In temperate and cool climate zones, many researchers have highlighted the importance of temperature and whether reduced growth under cold temperatures blocks carbon assimilation or reduces carbon allocation (Körner, 1998). During the stage of cambial reactivation, the external environment needs to be at a certain temperature to provide suitable conditions for cambial reactivation (Gričar *et al.,* 2006; Rossi *et al*., 2006, 2008; Begum *et al.,* 2007, 2008) while water stress was rarely reported mainly because snowmelt and spring rains typically provide sufficient water early in the growth season (Körner, 2003; Rossi *et al*., 2011). Therefore, the availability water partially explains the observation that minimum daily temperature is more important than the maximum daily temperature during the on onset of cambial activity (Begum *et al*., 2008; Rossi *et al.,* 2008, 2011). During the cell enlargement stage, with increased atmospheric temperatures, the soil water reserve is reducing due to the vapor pressure deficit, inducing smaller tracheids through the control of turgor pressure (Ryan *et al.,* 1994). Thus water availability is the major limiting factor for growth at this stage (Bouriaud *et al.,* 2005a). Cell wall thickening is also regulated by climate, but detailed information is still lacking. During this stage, the availability of photosynthate is a very important determinant (Panshin and de Zeeuw, 1980, Larson *et al.,* 1964), which depends on two aspects: the supply of photosynthate and efficiency of its transport. These two aspects are considered to be related to temperature and water availability (Rossi *et al*., 2009; 2011). Water availability is a complex indicator, which cannot be measured directly. Precipitation has often been used to represent water availability in previous studies (Lebourgeois *et al.,* 2010). There are some other climatic sources (e.g. $CO_2$ concentration, nitrogen and sulphur deposition) also involved in contributing to the physiological process of cells within a growth ring, however only temperature and precipitation will be discussed in detail.

Therefore, the following general points on climate can be made relating to temperature and precipitation:

1) each stage in cell differentiation is more or less influenced by climate and consequently the variation of density can be inferred; and

2) the effect of each climatic variable might be different at each stage, however detailed information is still lacking and needs to be further investigated.

In the following paragraphs the effects of particular climatic variables, i.e. temperature and precipitation, on anatomical structures and density, are discussed separately in detail.

### 2.3.1 The effect of temperature

Under a global warming context, the response of forest ecosystems to increasing mean annual temperatures has drawn the attention of many researchers. A positive trend in annual mean air temperature – increase of 0.9 °C on average- was observed in southern Canada (south of 60 °N) over the last century, which is associated with a stronger increase in night temperatures (daily minimum temperature) than the increase in daily maximum temperatures (Zhang *et al.,* 2000). This warming has resulted in a deceased diurnal temperature range from 0.5 to 2.0 °C. Therefore, this dramatic effect of increasing growing-season temperatures can also be seen in growth ring formation changes (Lebourgeois, 2000; Franceschini *et al*., 2012).

It is widely known that temperature plays an important role in density of conifers at higher latitudes (Briffa *et al*., 1992a). Most studies on the relationship between temperature and density originated, in the field of dendrochronology. Instead of average ring density, the maximum density was the most frequently used density characteristic because of its tight correlation with summer temperature (Conkey, 1986;

D'Arrigo *et al.,* 1992; Larson, 1994; Splechtna *et al.,* 2000; Hughes, 2002; Wang *et al*., 2002). This is due to the fact that under strong summer temperature influences, maximum density was highly sensitive to temperature variation and often used for climate construction (Schweingruber *et al.,* 1991; Briffa *et al*., 1992a, 1992b). Few studies have been conducted on the effect of temperature on other density characteristics such as average ring density, earlywood density, latewood density, and minimum density. Generally, the positive effect of temperature was found in the mean ring density (D'Arrigo *et al*., 1992; Wimmer and Grabner, 2000). In Norway spruce, Wimmer and Grabner (2000) found average temperatures during May, August and September of the current year to be positively related to average ring density. The earlywood density was found to be positively correlated with average temperatures from March to September with the exception of July, whereas minimum density could be positively linked to March and April. In jack pine, Savva *et al.* (2010) displayed the average temperature of May positively related to mean ring density and earlywood density. The temperature of June was negatively related to earlywood density but positively related to latewood density (Savva *et al.,* 2010). Bouriaud *et al*. (2005a) also suggested a positive effect of temperature on wood density but this effect was more apparent later in the growth season. Kilpeläinen *et al*. (2007) conducted a 6-year elevated temperature treatment and found this increased earlywood and mean wood densities in Scot pine. Wang *et al.* (2002) mentioned the average temperature from May to September was positively linked to the *MxD*, earlywood density, and latewood density in black spruce.

Anatomically, in Scot pine, Antonova and Stasova (1993) found initial cell division and cell enlargement were positively related to increased temperatures mainly from May to June. In tree line Norway spruce, Gindl *et al.* (2000) revealed cell division and cell enlargement were positively related to the mean temperature from mid-July to August and maximum latewood density was positively correlated with the mean temperatures of August and September. Moreover, lignin content in the secondary cell wall layer of the last few latewood tracheids in tree rings was found to be positively related to the temperature from early September to the third week in October. Although a link between the duration of latewood lignification and maximum latewood density was not found, it is more information to attempt to elucidate the role and relationship between the three main polymer ingredients of the wood cell wall. Wimmer and Grabner (2000) conducted a similar study in Germany for Norway spruce where summer temperature (July to September) was highly related to cell-wall proportion of latewood, however a poor correlation was found between earlywood cell-wall proportion and temperature during the early part of the growth season. In black spruce, cell wall thickness of cells in the whole growth ring, cell wall thickness of latewood and the ratio of cell wall thickness to lumen diameter were all found to be positively correlated with temperature from May to September, however the relationship between these anatomical variables and temperatures during growth seasons can be inconsistent, for example cell wall thickness of latewood positively correlated to temperatures from the end of May to July and late August to early September. Cell wall radial diameter of earlywood tracheids was found to be related to temperatures during the first half of the growing season (Wang *et al.,* 2002).

Similar results were observed in other species at high latitudes of the northern hemisphere such as in balsam fir (Deslauriers *et al*., 2003, Krause *et al.,* 2010) and Siberian larch (*Larix sibirica* Ledeb) (Kirdyianov *et al.,* 2007). It appears that high temperatures are positively related to tracheid size during the early growth season and cell wall thickness during the later growth season. Basically, cell division and enlargement are positively related to temperature during the first half of the growth season from April to July, depending on location, species and climatic signals at that time, and cell wall thickening was related to temperatures in the second half of the growth season from July to September. Additionally, in order to test the hypothesises of tree response to climatic signals, there are some intensive studies that expose trees to artificial environments (chamber) under different growing conditions (elevated temperature or $CO_2$) and monitoring the response of the growth and any changes in anatomic structure. In Scots pine (*Pinus sylvestris* L.), Kilpeläinen *et al.* (2007) showed that increased temperatures resulted in decreased earlywood lumen diameter, increased tracheid width and increased tracheid wall thickness. They suggested that the smaller lumen might be a result of earlier cambial initial activity and faster radial growth rates. A similar study was carried out with Norway spruce by Kostiainen *et al.* (2009), where they found increased temperatures improved cell wall thickness of earlywood and wood density, but little impact was found on the radial or tangential size of tracheids.

In addition, some studies report a limit on the positive effect of temperature on cell production and anatomical dimensions. Once this limit is exceeded, the inversed impact of the temperature relationship was not linear e.g. *Pinus sylvestris* L. (Antonova and Stasova, 1993; Deleuze and Houllier, 1998), *Larix siberica* Ldb. (Antonova and Stasova, 1997), *Picea abies* (Deleuze and Houllier, 1998), *Eucalyptus grandis* (Thomas *et al.,* 2007).

Although a general positive relationship between temperature and wood density has been reported, such a relationship is not necessarily valid anymore with changes in the climate since 1960 (Briffa *et al.,* 1998). This phenomenon has been referred to as ‘divergence’ (D'Arrigo *et al.,* 2008). This relationship has been found to be decreasing broadly across the world and among many tree species. However, Weih and Karlsson (2001) suggested temperature effects on aboveground growth might not necessarily be related to whole-tree production, increasing wood density might be expected from increasing air and soil temperatures.

### 2.3.2 The effect of precipitation

Both temperature and precipitation are known to affect ring features, compared to temperature, the availability of water has received less attention. Conkey (1979) presented the maximum density was positively correlated to precipitation in May, negatively correlated to precipitation in August and September in red spruce. Ring widths were mainly dependent on precipitation and minimum density was weakly correlated with precipitation (Wimmer & Grabner, 1997, 2000). Additionally, Wimmer and Grabner (2000) reported August and September precipitation was negatively related to latewood density and maximum density. Summer precipitation, particularly June precipitation has been reported to be positively related to radial growth (Mäkinen *et al.,* 2000, 2001). Bouriaud *et al.* (2005a) used soil water deficit as a comprehensive indicator of low rainfall or high temperatures and found this resulted in the cambium producing latewood-like cells in the earlywood and then incomplete latewood (i.e. false ring), therefore increasing wood density. This is in agreement with Jyske *et al.* (2010) conclusion that droughts during the growth season might lead to increased earlywood or latewood. Büntgen *et al.* (2007) tested four conifer species (*Picea abies* (L.) Karst., *Larix decidua* Mill., *Abies alba* (L.) Karst., and *Pinus mugo* (L.)) in the Tatra region of Poland and Slovakia, showed maximum density to be negatively correlated with precipitation in July and August.

Anatomically, Wimmer and Grabner (2000) reported cell wall thickness in earlywood was poorly correlated with both temperature and precipitation. Earlywood tracheid length was negatively correlated to precipitation in April and July and cell wall thickness in latewood was negatively related to precipitation in August and September. Additionally the latewood proportion was found to increase with increased rainfall during the summer, which the authors proposed is a result of early cessation of earlywood formation and prolonged latewood growth. Yasue *et al.* (2000) reported low rainfall in August resulted in less cell wall material production thus less dense latewood was produced in Glehn's Spruce (*Picea glehnii* Mast.). In black spruce and balsam fir, Krause *et al.* (2010) found water conditions positively correlated with lumen area and radial cell diameter in earlywood, while no significant relationship was detected with cell wall thickness in the earlywood and anatomical features in latewood. Soil water content, is known to be tightly linked to precipitation and temperature to some extent (Ryan *et al*., 1994). Jyske *et al.* (2010) conducted drought experiments and found insufficient water supply during the growth season could lead to increased cell wall proportion within a growth ring therefore increasing in density.

To summarize the above two effects, precipitation affects soil water content and contributes to the variability of density, where sufficient water availability supports ring expansion and facilitates transportation of photosynthate while insufficient water combined with high temperatures might lead to increased density early in the growth season and decreased density later in the growth season.

## The effects of temperature and precipitation during xylogenesis

A series of climate-growth studies were conducted during the last several decades, some studies were simply investigating the correlation between ring features (ring width features and density features) and climate; others investigated the relationship between anatomical features and climate, which also leads to implied correlations between ring features and climate.

Although the information in the literature is quite fragmented and the general effects of climate are just that, general in many instances due to complex interacting biotic and abiotic sources affecting tree growth. This being said there are, however, certain patterns displayed at each differentiation phase as summarized below:

**Reactivation and cell division -** During the cold winter, the cambium is dormant and inactive. With increasing temperatures in the spring, triggered by external and internal signals, reactivation occurs. The onset of cell division, has been shown to be correlated mainly with temperature, e.g. minimum, mean and maximum daily temperature, which are all known to have a significant effect on cell division (Rossi *et al.,* 2008; Begum *et al.,* 2008). In order to precisely determine the accurate length of the growth season, the date of onset and end of cambial activity are needed. Recently, many physiological studies have developed methods to determine when cambial reactivation occurs such as critical temperature (Rossi *et al.*, 2008, 2011), or degree-days (Seo *et al.*, 2008; Begum *et al.*, 2008). Therefore, it may be beneficial to use climate data in order to gain more knowledge to determine the exact growth season.

**Cell enlargement -** In this phase, a large proportion of the variation within cell enlargement was explained by both temperature and precipitation (Krause *et al.,* 2010). Under the confounding effects of temperature and precipitation, soil water content is highly related to the size of the tracheids through turgor pressure (Ryan *et al.,* 1994).

**Secondary cell wall development and lignification -** In the later months of the growth season, cell division in the cambium is slowing down and supply of photosynthate is reserved more for activity in the cambium than in the crown and shoots. Temperature and water availability both have been shown to limit carbon allocation (Körner, 2003; Rossi *et al*., 2009, 2011; Lebourgeois et al. 2010). During this phrase, temperatures are high and freezing nights are rare, which leads to the most favourable thermal conditions during the growth season (Deslauriers *et al*., 2003; Krause *et al.,* 2010). Cambial activity culminates when maximum temperature occurs (1 or 2 weeks) (Rossi *et al*., 2006). At this time, temperature is not the most important determinant on cell wall thickening due to high soil evaporation, whereas water availability plays an important role, which may result in the cell wall thickness being poorly correlated with temperature and highly correlated with precipitation (Yasue *et al*., 2000; Wang *et al.,* 2002). Later in the growing season, a negative relationship was found between precipitation and cell wall thickness. Yasue *et al.* (2000) inferred the negative correlation might correspond to shorter day length. However, Büntgen *et al.* (2007) claimed that temperature and precipitation are negatively correlated during the summer thus positive correlations between temperatures and cell wall thickness leads to a reversed relationship between precipitation and cell wall thickness.

### 2.3.3 Climatic sensitivity of density indicators according to tree size

In dendroclimatology, most sampling protocol was established to minimize non-climatic effects by selecting dominant trees to mitigate severe competition (Fritts, 1976; Schweingruber, 1990). However, forests are also composed of suppressed trees which may be important as they are an important part of the final composition of mature stands and their access to resources (soil, light) is different. Many studies have shown that the hypothesis of the identical climate sensitivity was not necessarily validated among dominance levels. It has been shown that dominant trees of silver fir and Norway spruce were more sensitive to climatic variables than intermediate trees (Mérian and Lebourgeois 2011; Castagneri *et al*. 2012). However the opposite result was found when considering pine species (De Luis *et al*. 2009). This difference was interpreted as a variation of thermal stress and transpiration among dominance levels (Mérian and Lebourgeois 2011).

Additionally, previous studies have focused mostly on size mediated climate-growth relationships (Chhin *et al.,* 2005; De Luis *et al.,* 2009; Mérian and Lebourgeois, 2011). Fewer studies have investigated density-climate relationships. Moreover, most dendrochronological research was applied on a part of the annual ring density feature, e.g. latewood density or maximum density (D'Arrigo *et al*., 1992; Wang *et al.,* 2002; Buntgen *et al*., 2010; Franceschini *et al.,* 2012). However, little information was provided on the effects of climate on the profiles at the intra-annual time scale (e.g. on average ring density, minimum or earlywood density, and maximum or latewood density). Therefore, it is reasonable to hypothesize that black spruce trees from different dominance levels will have different wood density-climate relationships.

### 2.3.4 Climatic sensitivity of density indicators along the stem

In dendrochronological and densitometric studies, samples are traditionally taken from breast height (1.3 m aboveground) since growth irregularity (Schweingruber *et al.,* 1990) and growth ring anomalies (Schweingruber, 1996) at the tree base are stabilized here as well as the operational simplicity (Zhang *et al.,* 1996).

An underlying assumption for these studies undertaken at breast height was (1) radial density pattern at breast height is able to represent the variation of the whole stem and (2) its climate sensitivity was identical with other stem heights. Such assumptions confirmed the height effect was not ignorable; for the former one, the significant height effects had been identified on the density pattern in Norway spruce (*Picea abies* (L.) Karst.)) (Mäkinen et al. 2007) and black spruce (*Picea mariana* (Mill.) B.S.P.) (Alteyrac *et al.,* 2005; Xiang *et al.,* 2013a); for the latter one, growth-climate relationships were found to change according to disc height (Bouriaud *et al.,* 2005b; Chhin *et al.,* 2010; van der Maaten-Theunissen and Bouriaud, 2012; Kerhoulas and Kane, 2012). For example, Chhin *et al.* (2010) stated radial growth in the lower stem regions such as at breast height was likely regulated by climatic sources before the growth season while upper stem regions were likely affected by the conditions during the growth season. In black spruce, growing conditions correlated with growth rate (Xiang et al., 2013a; 2013b), and the hypothesis of co-varying density-climate relationships among disc heights along the stem could be reasonably proposed.

**The evolution of model**

To formulate the variation of wood density, modelling has been a powerful tool for a long time. However, previous research has only explained part of the variation of wood density by including some of the above variables (Zhang *et al.,* 1996; Guilley *et al*., 1999; Jyske *et al*., 2008; Franceschini *et al.,* 2010), which can be attributed to two major reasons: 1) wood density pattern is highly varied; 2) many sources are correlated.

To date, the mixed-effects model approach has been proposed which can efficiently handle hierarchical data structured as the categories (discs nested in trees and trees nested in sites) and are always treated as nested levels. It is an advanced method to inform researchers how much variation can be explained and which nested level the unexplained variations belong to, and therefore to identify potential variables to improve the interpretability of the model. However, the accuracy of mixed-effects models highly depends on the form of the basic model (Rathbun *et al*., 2011; Mclane *et al*., 2011). As wood density is highly variable throughout the tree a mixed-effects model might not be appropriate. Indeed, determining the confounding effects of cambial age, growth rate and height along the stem is recognised as one of the most difficult aspects of fitting wood density models (e.g. Alteyrac *et al.,* 2005; Gardiner *et al.,* 2011). The highly variable radial patterns among samples, particularly in the juvenile wood zone, prove difficult to incorporate into a single modelling step (Xiang *et al*., 2013).

Another modelling strategy, frequently called "parameter prediction models" in forestry (Clutter *et al*., 1983; Schabenberger and Pierce, 2002) or 'random coefficients modelling' in econometrics (Littell *et al*., 2006) as well as 'two-stage models' (Pinhero and Bates, 2000), have been applied for decades and proven to be an efficient method for such 'clustered data' (Achim *et al.,* 2006; Rathbun *et al.,* 2011; Mclane *et al.,* 2011) and assist us in understanding the mechanisms of density variability.

With respect to the growth-climate relationship, most statistical techniques are usually applied in dendrochronological studies for construction of past climate based on tree rings. For investigating the correlation between density and climate, the mechanisms of the inter-ring variability were explained by increased investigations, especially for the sites where trees are located around the limits of their ecological scope e.g. near treeline (Wang *et al*., 2002; Gruber *et al*., 2009). Although these studies were conducted at widely distributed locations, models on simulating the relationship between ring features and climate are still relatively simple (Fritts *et al.,* 1991; Hughes, 2002). Additionally, more recent studies are trying to explore nonlinear relationships between ring features and climate (Woodhouse, 1999; D'Odorico *et al.,* 2000). These studies have displayed that, compared to a linear relationship, the nonlinear correlation may be better to help disentangle multi climatic sources or formulate the extreme climatic impact; however in the nonlinear correlation it was found the explanation of the variability was not significantly improved (Hughes, 2002; Franceschini *et al*., 2013b).

## 2.4 Sources of variation of wood density summary

The literature provides informative data on aspects of wood density characteristics (e.g. average ring density, minimum ring density, maximum ring density), however the literature is still lacking a comprehensive explanation for the variation of wood density due mainly to differing patterns of wood formation resulting from genetic and environmental sources. Some general conclusions can be summarized:

1) Variation in wood density of an individual tree is related to intra-tree sources (early wood-latewood difference, cambial age, radial growth rate and stem height) and inter-tree sources (genetic, site and climate) as well as human factors;
2) The relationship between cambial age and wood density may help to further our understanding of physiological processes in the tree;
3) It is important to investigate the correlation between growth rate and wood density combined with cambial age as growth rate is impacted by aging;

4) To investigate relationships between ring density characteristics (i.e. *MnD*, early wood density, *RD*, *MxD* and latewood density) and climate, the climatic sensitivities along the stem height, based on tree size need to be determined; and

5) Although many different modelling approaches have been applied attempting to explain correlations, to date, few valid universal approaches have been produced.

Indeed informative results have been provided in previous studies, however the effect of temperature, precipitation and their interactions on anatomical features and thus density is still isolated and inconclusive. Therefore more studies need to be conducted to further our understanding and gain sufficient information to fully understand the physiological process and its associated response to external stimuli.

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# Chapter 3 Age- and growth-related trends in the wood density of black spruce (*Picea mariana* (Mill.) B.S.P.)

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## 3.1 Abstract

Wood density variation affects structural timber performance and is correlated with several potentially confounding factors, such as cambial age, position in the stem and growth rate. To date, these relationships have not been comprehensively quantified in black spruce (Picea mariana (Mill.) B.S.P.). This research aims to describe the variation in annual ring density in black spruce as a function of cambial age, stem height and growth rate. Radial density profiles from 107 black spruce trees were analysed using a two-stage modelling approach. First, the parameters of a nonlinear function were estimated separately for individual samples. Linear regression was then used to model the parameters obtained in the first stage as functions of internal and external tree descriptors. Annual ring density was high near the pith, declined rapidly in the first 15 annual rings, before increasing to more stable values between rings 25-60. However, just less than 25% of the samples showed a gradual decline towards the bark, typically after ring 60. Describing and quantifying and radial density patterns, including the decline close to the bark, will help further our understanding of the links between tree growth and ring density over the life of the tree.

## 3.2 Introduction

Black spruce (*Picea mariana* (Mill.) B.S.P.) is one of the most important and valuable species for both lumber and pulpwood production in Eastern and Central Canada, and an important commercial and reforestation species from the Atlantic coast to Manitoba (Boyle *et al.,* 1989; Zhang, 1998). In the boreal forest of Canada, black spruce is mainly harvested from natural stands. Consequently, with the importance of its wood and fiber to the forest industry, understanding the influence of natural forest dynamics on wood attributes is important in order to formulate appropriate management strategies for maximizing the value of the resource at harvest.

As demand for wood and wood products has increased in recent decades, research efforts have focused more intensively on wood and fibre quality attributes in addition to volume production (Jozsa and Middleton, 1994; Evans *et al*., 1994; Koubaa *et al*., 2000; Franceschini *et al*., 2012). Of these attributes, wood density is one of the most important and useful wood quality indicators (Panshin and de Zeeuw, 1980; Zhang *et al.,* 1996), and is closely correlated with the mechanical properties of wood (Zhang *et al*., 1993; Koga and Zhang, 2004) and with certain strength properties of paper (van Buijtenen, 1982). Furthermore, with growing interest in forest carbon sequestration, wood density can also be used in allometric equations as an essential component of aboveground biomass estimations (Ketterings *et al.,* 2001; De Vries *et al.,* 2006).

Previous studies have quantified the effects of the different sources i.e. internal variables such as cambial age, ring width and genetic origin (Alteyrac *et al.,* 2005; Jyske *et al.,* 2008; Savva *et al.,* 2010) and external variables such as position along the stem, site quality and climate (Wang *et al.,* 2002; Bouriaud *et al.,* 2004; Guilley *et al.,* 2004), on annual ring density. Within-stem variations in ring density may consequently be related to various intrinsic and extrinsic sources, which have potentially confounding effects. In this context, a modelling approach based on the observed effects of important variables, such as cambial age, annual growth rate and position along the stem, on annual ring density, can help further our understanding of these complex interrelationships.

In spruces, the radial pattern of variation in wood density typically shows a rapid decrease near the pith followed by a more gradual increase towards bark (Panshin and de Zeeuw, 1980), a trend that has been confirmed specifically for black spruce (Zhang *et al*., 2002; Alteyrac *et al.,* 2005). Despite having been investigated extensively, the reported correlation between growth rate and wood density is not consistent among studies. For example, a negative correlation between annual ring width and wood density has been reported in both Norway spruce (*Picea abies* (L.) Karst.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (Franceschini *et al.,* 2010, 2013; Gardiner *et al*., 2011). Also in Sitka spruce, Simpson and Denne (1997) reported that the strength of this negative correlation increased from the stem base to the tree tip, for a given cambial age. Conversely, in balsam fir (*Abies balsamea*), Koga and Zhang (2004) found a significant negative correlation between growth rate and density below 3 m in the stem, but there was no significant effect above this height. Wimmer and Downes (2003), on the other hand, reported a positive relationship between ring width and ring density in Norway spruce, which was associated with higher late-season rainfall. However, a negative relationship was found when faster radial growth was a result of high early-season rainfall. Besides changes linked to climatic conditions, the relationship between ring width and wood density may also be altered by the application of fertilization (Mäkinen *et al*., 2002) and thinning treatments (Jaakkola *et al.,* 2005).

In black spruce, some studies have reported that ring width is not significantly correlated with wood density in mature wood (Risi and Zeller, 1960; Hall, 1984). On the other hand negative correlations, between wood density and growth-related traits (DBH, tree height and bole volume) were detected by Zhang and Morgenstern (1995). Zhang *et al.* (1996) reported moderate negative correlations between wood density and growth rate in 15-year-old black spruce trees, but these could be reversed for given provenances, environmental conditions and geographical locations. More recently, Koubaa *et al.* (2000) observed the combined effects of cambial age and growth rate and concluded that the negative correlation between ring width and wood density in black spruce was not significant beyond a cambial age of 25 years.

The effect of height along the stem on the radial patterns of variation in wood density has received rather less attention. In Norway spruce, Mäkinen *et al.* (2007) found no significant effect of height on ring density, while Jyske *et al.* (2008) found a small positive height effect (3%-6%) for a given cambial age. In black spruce, Alteyrac *et al.* (2005) reported a large variation in density among stem heights, but the variation was smaller in mature wood than juvenile wood.

The aim of this study was to investigate the relationships between cambial age, growth rate, and height along the stem with annual wood density variation in black spruce trees. More specifically, we present the development of a model, which describes the general within-stem patterns of variation in average ring density in black spruce from naturally regenerated, unmanaged stands.

## 3.3 Materials and method

### 3.3.1 Sampling

Trees were sampled in an area 400 km northwest of Thunder Bay, Ontario, Canada. A total of 13 stands were sampled from natural forests located in the Lake St. Joseph Ecoregion, between 51° 42' N and 52° 6' N and between 90° 3' W and 94° 31' W, at an elevation of 400 m (Table 3-1). Mean annual temperature varied between -1.7° and 1.0° C, mean annual precipitation ranged between 613 mm and 787 mm, mean summer rainfall between 244 mm and 299 mm, and the mean length of the growing season between 162 and 179 days.

All sites were pre-selected based on species composition (dominated by black spruce), stand age (greater than 50 years old) and crown closure criteria (greater than 55 % crown closure). Three temporary sample plots (TSP) with a plot radius of 5.64 m (100 m$^2$) were established at each site.

**Table 3-1 Mean (SD) stand-, tree- and ring-level characteristics for each site.**

| Site No. | Latitude (north) | Longitude (west) | Elevation (m.a.s.l) | BA ($m^2\ ha^{-1}$) | Age (years) | DBH (cm) | Height (m) | RW (mm) | Ring density ($kg/m^3$) |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 51° 29' | 93° 46' | 410 | 37.13 | 107 | 16.1 | 16.4 | 0.8 (0.51) | 509.28 (67.26) |
| 2 | 51° 33' | 93° 52' | 390 | 33.11 | 60 | 14.8 | 14.3 | 1.6 (0.63) | 459.53 (51.41) |
| 3 | 51° 30' | 93° 48' | 430 | 30.05 | 100 | 14.0 | 14.4 | 0.9 (0.42) | 525.22 (51.67) |
| 4 | 51° 9' | 91° 24' | 380 | 40.33 | 78 | 15.6 | 16.0 | 1.1 (0.68) | 514.37 (62.44) |
| 5 | 51° 8' | 91° 25' | 380 | 45.33 | 83 | 13.6 | 14.7 | 0.9 (0.38) | 507.25 (56.02) |
| 6 | 51° 43' | 91° 43' | 400 | 41.97 | 136 | 19.4 | 19.0 | 0.8 (0.52) | 496.21 (57.57) |
| 7 | 51° 42' | 91° 47' | 400 | 41.22 | 127 | 19.5 | 18.4 | 0.8 (0.43) | 501.35 (69.84) |
| 8 | 51° 43' | 91° 46' | 400 | 35.47 | 138 | 19.1 | 18.0 | 0.9 (0.44) | 511.82 (62.52) |
| 9 | 51° 41' | 91° 50' | 400 | 40.23 | 78 | 14.1 | 14.6 | 1.0 (0.46) | 477.63 (57.38) |
| 10 | 51° 40' | 91° 52' | 400 | 43.48 | 74 | 13.0 | 13.1 | 0.9 (0.44) | 504.08 (63.07) |
| 11 | 51° 41' | 91° 51' | 400 | 39.26 | 125 | 19.7 | 20.2 | 0.9 (0.36) | 493.30 (66.80) |
| 12 | 51° 42' | 91° 44' | 400 | 41.19 | 90 | 15.7 | 15.7 | 0.9 (0.53) | 497.43 (62.23) |
| 13 | 51° 42' | 91° 49' | 400 | 33.51 | 80 | 22.1 | 19.1 | 1.5 (0.66) | 489.89 (56.84) |

m.a.s.l is meters above sea level; BA is the basal area of the living trees per hectare; RW is annual ring width

Three trees were selected for destructive sampling from each TSP. The selected trees were: 1) the tree with the largest diameter at breast height (DBH, measured 1.3 m above ground level), 2) the tree with the median DBH and 3) the tree with the DBH closest to the average of the quadratic mean DBH and the DBH of the smallest tree of the plot; hereafter described as dominant, codominant, and intermediate trees (Smith et al. 1997), respectively. These tree selection rules ensured that a large range of radial growth rates was represented in the dataset. Mean tree- and ring-level characteristics for each dominance level are given in Table 3-2. After felling, the total height of each sample tree was recorded, before 5-cm thick transverse discs were cut at predetermined heights. In the dominant and codominant trees, discs were taken at 0.5 m, 1.3 m, 1.75 m, the live crown base (LCB) and at two equidistant points between 1.75 m and LCB. Discs at successive heights from ground level were labelled M1, M2, M3, M4, M5, and M6, respectively. In the intermediate trees, only the M2 disc (1.3 m) was sampled, as discs beyond this height were generally very small. Sampling positions were adjusted to avoid branch whorls or obvious stem damage, and discs less than 8 cm in diameter were omitted from the study.

**Table 3-2 Mean (SD) tree- and ring-level characteristics for each dominance class.**

| Dominance class | Age (years) | DBH (cm) | Height (m) | No. of rings | RW (mm) | Ring density (kg/m$^3$) |
|---|---|---|---|---|---|---|
| Dominant | 96 | 20.2 | 18.3 | 17466 | 1.13(0.59) | 486.03(59.21) |
| Co-dominant | 95 | 14.7 | 15.9 | 15178 | 0.82(0.45) | 512.83(62.14) |
| Intermediate | 92 | 11.6 | 14.4 | 2483 | 0.62(0.32) | 535.19(65.98) |

RW is annual ring width

### 3.3.2 Wood density measurements

The discs were cut longitudinally through the pith and then into radial strips with a constant thickness of 2 mm in the longitudinal direction and a width of 25 mm tangentially. The samples were placed in a conditioning chamber set at 60% relative humidity and 20° C until they reached a constant mass, corresponding to an equilibrium moisture content of approximately 12%. The samples were then scanned with an X-ray beam at a resolution of 40 µm in a QTRS-01X Tree Ring Analyzer (Quintek Measurement Systems Inc., Knoxville, TN, USA). No extractions were carried out prior to scanning because the extractives content of black spruce wood is known to be very low (Lohrasebi *et al.,* 1999).

The X-ray densitometry values were calibrated using a gravimetrically determined target density for each specimen, calculated from the mass and volume derived from the thickness and scan area of the samples. After scanning, the transition point between successive annual rings was determined as the point of equidistance between the maximum value of the previous ring and the minimum value of the current ring. Any incomplete or false rings and rings with compression wood or branch traces were excluded from the dataset. All data where cambial age (*CA*) was less than or equal to 140 years was used for the development of the models, because only one tree had a higher *CA*. In total, density data from 35,127 annual rings in 450 radial strips from 107 trees sampled at 13 sites were analysed in this study.

Due to very slow radial growth in several samples, it proved impossible to delineate the limits of earlywood and latewood with consistent accuracy in the densitometry data. To examine the factors that influenced density in narrow rings, thin radial-transverse cuts were prepared for examination under a microscope. On each sample, the twenty rings closest to the bark were examined to determine ring width, earlywood width and latewood width. The limits between wood types were determined visually and width measurements were made using the Motic Images Plus 2.0 digital microscopy software. Eight pairs of high- and low-density ring series were compared in this way. A series of conditions were applied to ensure that each pair was directly comparable i.e. the two discs had to come from the same site, from trees of the same dominance class and age (maximum difference of 10 years), and from the same sampling height. The absence or presence of a density decline near the bark was used to determine whether discs represented either a high- or low-density ring series. The ring series were selected randomly from all those that met the specified conditions. One pair of representative ring series is shown in Figure 3-1.

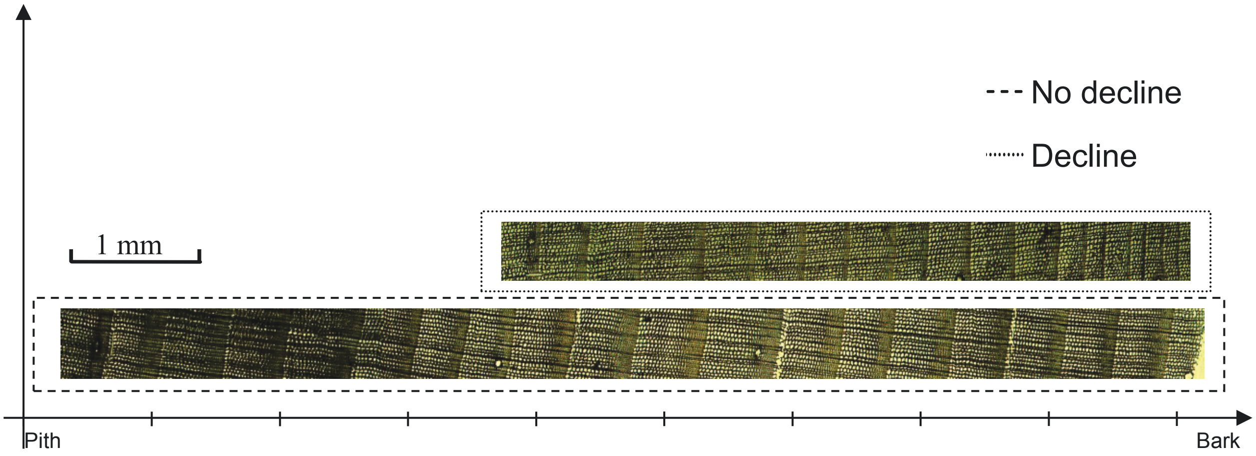

**Figure 3-1 Radial-tangential images from a pair of ring series examined under the microscope (16×).**

### 3.3.3 Model development

Due to the hierarchical structure of the data, with observations on annual rings nested within discs, themselves grouped in trees clustered within sites, nonlinear mixed-effects modelling techniques were first applied (Guilley *et al*., 2004; Franceschini *et al.,* 2010; Gardiner *et al*., 2011). However, in our initial modelling efforts, we found that the variation among individual discs followed many distinctive pith-to-bark patterns, which could not easily be described by a single equation. To circumvent this problem, a two-stage modelling strategy was used (Achim *et al*., 2006; McLane *et al.,* 2011; Duchateau *et al.,* 2013). First, the parameters of a nonlinear equation describing the pith-to-bark profiles of annual ring density were estimated for each disc separately. The parameter values obtained in the first stage were then modelled as functions of tree- and disc-level variables using linear regression.

#### 3.3.3.1 Stage 1: Fitting disc-level model forms to individual discs

Several nonlinear model forms used to model wood density in other species (Franceschini *et al.,* 2010; Gardiner *et al.,* 2011) were tested, but performed poorly due to a low rate of convergence among discs. This was attributed to a decline in wood density that was observed in the outerwood of a proportion of the samples, which those models could not account for. Instead, we found that the radial pattern of ring density could be more appropriately described using a *Michaelis–Menten* equation with the addition of two exponential terms:

$$RD = b_0 \cdot e^{-b_1 \cdot CA} + \frac{b_2 \cdot CA}{b_3 + CA} - e^{-b_4 \cdot CA} + \varepsilon \qquad (3\text{-}1)$$

where *RD* is the mean ring density of the ring (kg $m^{-3}$); *CA* is cambial age (years), and $b_0$, $b_1$, $b_2$, $b_3$, $b_4$ are empirically determined parameters. Parameter $b_0$ denotes the intercept when *CA* approaches a theoretical value of 0 and $b_1$ denotes the scale parameter of the early decrease in *RD*. The error term $\varepsilon$, was assumed to be normally distributed, with $N$ (0, $\sigma^2$). The first exponential term $b_0 \cdot e^{-b_1 \cdot CA}$ has a value, which decreases rapidly in the first few annual rings and then gradually approaches an asymptote close to zero.

The second part of the equation is a *Michaelis–Menten* function where $b_2$ reflects the pseudo-asymptotic *RD* of mature wood, and $b_3$ denotes the rate of progression between this asymptote and a minimum value reached in the juvenile period (Auty *et al.,* 2008, 2012). In the last part of the equation, the $b_4$ parameter allows for a decline in *RD* that can occur at high cambial ages, which can override the asymptotic value of $b_2$.

The *optim* function in the R statistical programming environment (R Development Core Team 2013) was used to search iteratively for the best combination of parameters in each disc i.e. those, which minimized the sum of squared residuals. The convergence of this iterative process towards a solution was highly dependent on finding suitable starting values for each parameter. Due to the high variation among radial profiles, one single set could not be used for all discs. An algorithm was hence used to approximate disc-specific start values. First, a third-degree polynomial model was fitted to provide an approximate representation of the *RD* vs *CA* profile. The predictions from this model were then used to find the start values of $b_0$, which corresponded to the *RD* in the first three annual rings from the pith. This variable was chosen based on a preliminary regression analysis, which showed that it was the best linear predictor of $b_0$. The start values of parameter $b_1$ were calculated as a function of the start value of $b_{0,}$ so that the first part of the model (i.e. $b_0 \cdot e^{-b_1 \cdot CA}$) approached 0 at *CA* 10 to 15. For $b_2$, the *RD* of mature wood (i.e. from *CA* 25 to 60) was used. Again, the choice of the period of 25 to 60 years to express the average density of mature wood was based on a preliminary analysis in which different periods were tested. A similar strategy was used for $b_3$, but in this case to allow $\frac{b_2 \cdot CA}{b_3 + CA}$ be equal to the mean predicted *RD* at *CA* 10 to 15.

A first iteration was executed on each radial profile to find optimal parameters, excluding $b_4$. Then, using the obtained set of parameter estimates, more stringent searching intervals were defined and estimates of all parameters were obtained, including $b_4$ when samples where the decline in *RD* was observed. Based on a visual inspection of each radial profile, the specific conditions for the inclusion of the exponential term containing the $b_4$ parameter were: 1) when a declining trend in *RD* was observed close to the bark in the mature wood zone (i.e. $CA > 25$) and 2) when the decline continued for a period of at least 20 years. Due to the exponential nature of the decline, the start value for $b_4$ was adjusted to account for discs of different ages. Convergence was achieved for 85% of the radial samples using the *optim* package, but for the remaining samples the starting values were entered manually, so that parameters were estimated for the entire dataset. Model fit was assessed through a combination of visual analysis of plots of residuals against fitted values and explanatory variables, fit indices ($R^2$) and selected model error statistics (Parresol, 1999):

$$ME = \frac{\sum y_i - \hat{y}_i}{n} \tag{2}$$

$$|ME| = \frac{\sum |y_i - \hat{y}_i|}{n} \tag{3}$$

$$RMSE = \sqrt{\frac{\sum y_i - \hat{y}_i}{n}} \tag{4}$$

$$ME\% = \frac{100}{n} \sum \frac{y_i - \hat{y}_i}{\hat{y}_i} \tag{5}$$

$$|ME|\% = \frac{100}{n} \sum \frac{|y_i - \hat{y}_i|}{\hat{y}_i} \tag{6}$$

which represent the mean error, mean absolute error, root mean square error, mean percentage error and mean absolute percentage error, respectively. In these equations, $y_i$ is the observed value, $\hat{y}_i$ the predicted value and $n$ is the number of observations.

#### 3.3.3.2 Stage 2: Linear models for each parameter of the disc-level profiles

Once the parameters of Eq. [3-1] had been estimated for each disc, linear mixed-effects models were fitted to each vector of parameter values in turn. The general form of the models can be expressed as:

$$Y_i = X_i\beta + Z_i b_i + \varepsilon_i \qquad (7)$$

where $Y_i$ represents parameters $b_0$, $b_1$, $b_2$, $b_3$, $b_4$ in Eq. [3-1], $X_i$ is the vector of fixed effects for the parameter of interest, $\beta$ the associated vector of fixed effects parameters; $Z_i$ is a vector of random effects groups, $b_i$ is the vector of random effects variables and $\varepsilon_i$ the residual error term. The random effects $b_i$ and within-group errors $\varepsilon_i$ are assumed to be independent for different groups and to be independent of each other for the same group and normally distributed, that is $\varepsilon_i$ follows $N(0, \sigma^2)$ and $b_i$ follows $N(0,\Psi)$ for each group, $\Psi$ being the variance-covariance matrix of random effects (Pinheiro and Bates, 2000).

In order to find the most representative set of predictor variables and avoid potential issues with multicollinearity, the potential explanatory variables were divided into two categories:

1) Tree-level descriptors: tree age at breast height (*Age*, yrs), total height of the tree ($H_t$, m) and mean ring width in the mature wood at 1.3 m ($RW_{BHm}$, mm);

2) Disc-level descriptors: disc position along the stem ($H_{disc}$, m from stem base), average ring width near the pith ($RW_p$, mm), average ring width in mature wood ($RW_m$, mm), average growth rate (diameter or ring area) for different ranges of cambial age close to the bark ($RW_b$, mm or $RA_b$, mm$^2$) and slope of the local regression of the annual ring width close to bark ($Sl_b$, mm yr$^{-1}$). Definitions of the abbreviations used for the explanatory variables in this study are given in Table 3-3.

Considering the logical link between the selected variables and the behaviour of each parameter in Eq. [3-1], we hypothesized that $RW_{pi}$ was likely to be included in the $b_0$ and $b_1$ models. Similarly, $RW_{BHm[i,j]}$ was hypothesized to be related to $b_2$. In addition, parameter $b_4$, was thought to be related to the age of the sample and the growth rate either close to the bark or in the mature wood zone. Thus *Age*, $RW_{bi}$ or $RA_{bi}$, and $RW_{m[i,j]}$ were candidate variables that described the competitive status of the tree at each height in the stem. In addition, $Sl_{bi}$ was also considered since it is also closely related to tree vigour (Bigler and Bugmann, 2003, 2004).

**Table 3-3 Definitions of the abbreviations for the candidate explanatory variables used in this study**

| Abbreviations | Description (unit) |
|---|---|
| $Age$ | tree age at breast height (years) |
| $H_t$ | total height of the tree (m) |
| $H_{disc}$ | disc position along the stem from stem base(m) |
| $RW_p$ | average ring width near the pith (mm) |
| $RW_{pi}$ | average ring width of the first 1, 2, 3, 4 or 5 rings near the pith (mm) |
| $RW_m$ | mean ring width in mature wood (mm) |
| $RW_{m[i,j]}$ | mean ring width from cambial age $i$ to $j$, $i$=20, 25, 30; $j$=55, 60 (mm) |
| $RW_b$ | average growth rate (diameter) for different ranges of cambial age close to the bark (mm) |
| $RW_{bi}$ | average growth rate (diameter) at the last 10, 15, 20, 25 or 30 rings (mm) |
| $RA_b$ | average growth rate (ring area) for different ranges of cambial age close to the bark ($mm^2$) |
| $RA_{bi}$ | average growth rate (ring area) at the last 10, 15, 20, 25 or 30 rings ($mm^2$) |
| $Sl_b$ | slope of the local regression of the annual ring width close to bark ($mm\ yr^{-1}$) |
| $Sl_{bi}$ | slope of the local regression of the annual ring width of the last 10, 15, 20, 25 or 30 rings ($mm\ yr^{-1}$) |
| $RW_{BHm}$ | mean ring width in the mature wood at 1.3 m (mm) |
| $RW_{BHm[i,j]}$ | $RW_{BHm}$ with a series of the time ranges, where $i$=20, 25, 30; $j$=55, 60 |

However, after the mixed-effects models were fitted for parameters $b_0$, $b_1$, $b_2$, and $b_3$, a correlation analysis revealed that the parameters obtained at the disc level were not independent of each other. Therefore, for those parameters, seemingly unrelated regression (SUR) was used for parameter estimation. SUR accounts for correlated error terms among different equations by estimating the parameters of the equations simultaneously (Lei *et al.,* 2005). Additionally, since parameters $b_1$ and $b_3$ did not follow a Gaussian distribution, models were fitted to their natural log-transformed values.

In samples where there was no observed decline in *RD* near to the bark, the second exponential term in Eq. [3-1] was omitted from the model. Logistic regression was therefore used to predict the occurrence of the $b_4$ parameter as a function of $Age$, $RW_{bi}$, $RA_{bi}$, $RW_{m[i,j]}$ or $Sl_{bi}$. The predicted probabilities take values between 0 and 1, and were categorized into binary outcomes using a cutpoint analysis (Hein and

Weiskittel, 2010). The sensitivity and specificity of all potential threshold values (from 0 to 1 with an interval of 0.001) were calculated and the optimum was defined as the value giving the highest sum of sensitivity (true positives) and specificity (true negatives). Then, a linear mixed-effects model (Eq. 3-7) was fitted to the $b_4$ values for the instances where a decline was observed. The estimated parameters were then combined with results from the logistic model so that the last term of Eq. [3-1] was only present when the predicted value was above the cut-point threshold.

Once models for all parameters were fitted, these were then substituted back into Eq. [3-1] for the prediction of wood density. The performance of the full model was then evaluated using the error statistics given by Eqs. [3-2] - [3-6], and from fit indices, calculated from the fixed effects of the model. Simulated wood density profiles were finally constructed using predictions from the full model. As some explanatory variables were related to more than one parameter in Eq. [3-7], the simulations were based on the mean values of the explanatory variables in the dominant, co-dominant and intermediate diameter classes. Predictions were then plotted to give a visual representation of the correlations between the explanatory variables and wood density profiles. To show the correlations of within-tree characteristics with wood density, different percentiles of the measured data were used for selected explanatory variables, while the remaining tree-level variables were fixed to their mean values within each dominance class. Disc-level variables were fixed to selected values (e.g. mean quartile values) within each disc level and dominance class combination.

A potential issue with the use of an exponential function in Eq. [3-1] to model the decline near the bark is that predictions cannot be extrapolated beyond the range of the data, since they would approach zero very quickly. Therefore, we attempted to estimate a limit beyond which the predictions of the decline are no longer valid. For all discs in which the decline was observed, we calculated a relative rate of decline for which our reference was the average ring density of rings 25 to 60 ($RD_{m2560}$). For each disc where the decline occurred, the difference between $RD_{m2560}$ and the minimum ring density ($RD_{min}$) at the bark was calculated. The 95th percentile of the observed ratios of ($RD_{m2560}$-$RD_{min}$)/ $RD_{m2560}$ was 27.2%, which we used in the simulations as a limit of applicability of our model.

## 3. Results

Annual ring width for ranged from 0.1 mm to 4.8 mm, with a mean value of 1.0 mm, and *RD* ranged from 250.2 kg $m^{-3}$ to 839.5 kg $m^{-3}$, with a mean value of 501.1 kg $m^{-3}$ (not shown). When averaging the pith-to-bark profiles for all discs, *RD* was high near the pith and decreased rapidly in the first 12 growth rings i.e. declined from 591.0 kg $m^{-3}$ to a minimum of 473.8 kg $m^{-3}$ between rings 10 and 15. This was followed by a slow increase until a more constant value was reached between rings 25 and 60. Based on the criteria described above, the dataset was separated into two groups. It was observed that 106 out of a total of 450 radial samples displayed a gradual decline in *RD* near the bark and therefore required the inclusion of parameter $b_4$. The rest of the samples showed more of an asymptotic pattern where high densities were maintained towards the bark (Figure 3-2).

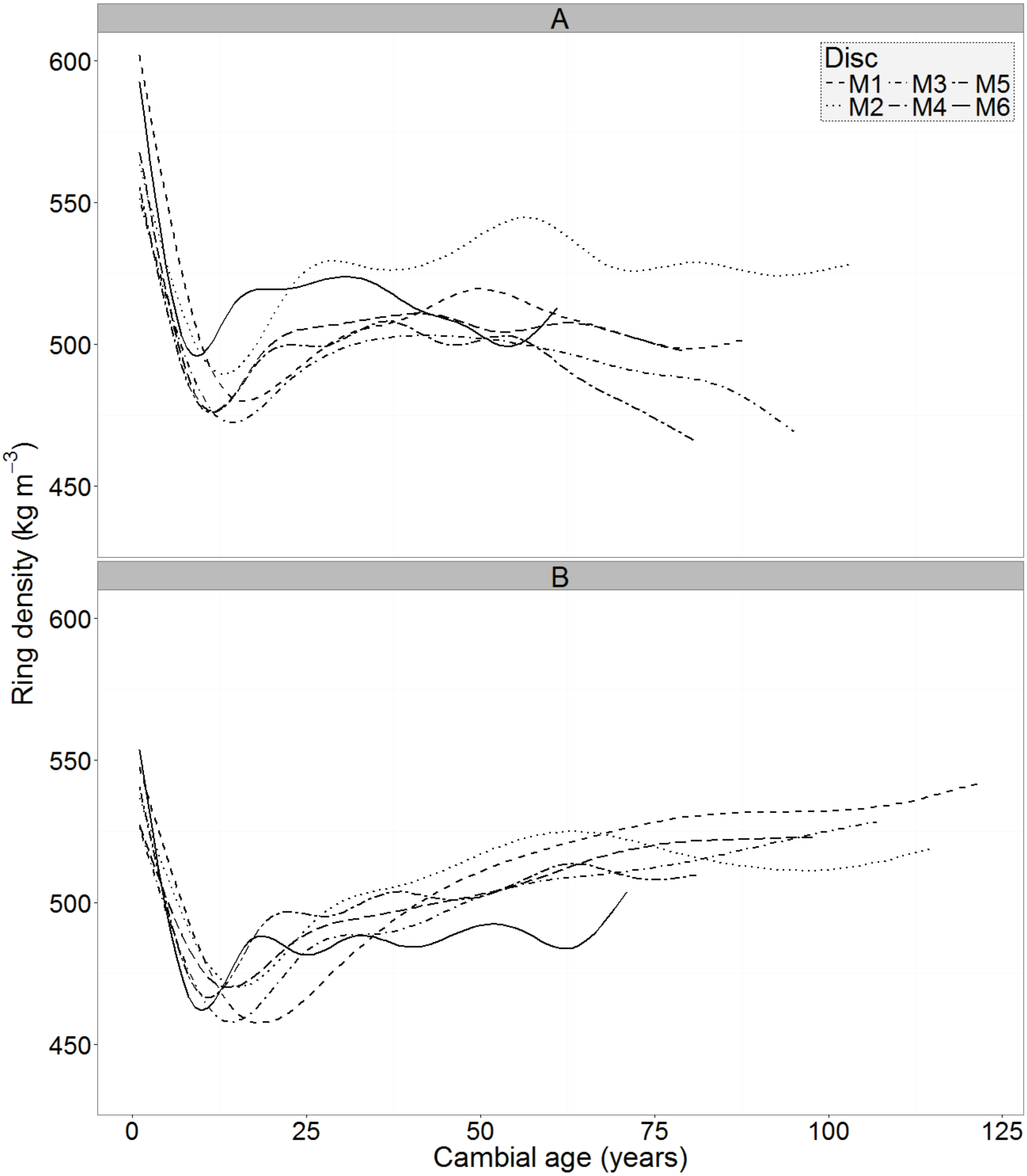

**Figure 3-2 Ring density vs. cambial age for the 107 black spruce sample trees. Lines represent smoothing splines fitted to the data at each sampling height. A) Discs with a density decline close to the bark; B) Discs with no density decline close to the bark.**

A summary of the parameter values obtained in Stage 1 of the model fitting process (Eq. 3-1) can be found in Table 3-4.

**Table 3-4 Descriptive statistics for parameters $b_0$, $b_1$, $b_2$, $b_3$, $b_4$ obtained by fitting Eq. [3-1] to samples from individual discs**

| Parameter | Min. | Mean | Max. |
|---|---|---|---|
| $b_0$ | 373.0 | 589.3 | 808.5 |
| $b_1$ | 0.010 | 0.259 | 2.188 |
| $b_2$ | 402.2 | 560.9 | 779.6 |
| $b_3$ | 0.005 | 5.764 | 77.960 |
| $b_4$ ($b_4>0$) | -0.098 | -0.050 | -0.020 |

For the individual parameter models in Stage 2, various combinations of just 6 explanatory variables were found to be significantly correlated with the variation of the parameters estimated using Eq. [3-7] (Table 3-5 and Table 3-6).

**Table 3-5 Coefficients and associated SEs for each explanatory variable for the $b_0$, $b_1$, $b_2$, $b_3$ parameter models, and adjusted $R^2$ values**

| | | Variables | | | | |
|---|---|---|---|---|---|---|
| | | Tree Level | | Disc Level | | Adjusted $R^2$ |
| Parameter | Intercept | $H_t$ | $RW_{BHm2560}$ | $H_{disc}$ | $RW_{p3}$ | |
| $b_0$ | 683.31*** | -3.93*** | | 6.79*** | -38.21*** | 0.14 |
| | ± 16.18 | ± 1.01 | | ± 1.30 | ± 6.03 | |
| $\ln(b_1)$ | -0.96*** | -0.05*** | | 0.06*** | | 0.09 |
| | ± 0.15 | ± 0.01 | | ± 0.01 | | |
| $b_2$ | 643.70*** | | -70.54*** | -5.00*** | | 0.25 |
| | ± 6.80 | | ± 6.17 | ± 0.92 | | |
| $\ln(b_3)$ | 0.71** | 0.06*** | | -0.11*** | | 0.08 |
| | ± 0.24 | ± 0.01 | | ± 0.02 | | |

Note: significance codes: 0.05 '*'; 0.01 '**'; 0.001 '***'. $H_t$: total height of the tree; $RW_{DBH2560}$: mean ring width from cambial age 25 to 60 of the disc at breast height; $H_{disc}$: disc position along the stem; $RW_{p3}$: average ring width of the first 3 rings

The occurrence of parameter $b_4$ was found to be significantly related to *Age* and $RW_{m2560}$, but was not related to $Sl_b$, $RW_{bi}$ or $RA_{bi}$. A predicted value threshold of 0.104 was used as the cutpoint in the logistic model, above which a decline in *RD* near the bark was considered to be present (sensitivity = 0.63, specificity = 0.77). Then, in the model fitted to the observed occurrences of $b_4$, the linear mixed-effects model showed significant effects of *Age* and $H_{disc}$, but no relationship with growth rate was detected (Table 3-6).

**Table 3-6 Coefficients and associated SEs for each explanatory variable for the $b_4$ parameter model and adjusted $R^2$ values calculated from the fixed effects**

| | | Variables | | | |
|---|---|---|---|---|---|
| | | Tree Level | Disc Level | | Adjusted $R^2$ |
| Parameter | Intercept | *Age* | $H_{disc}$ | $RW_{m2560}$ | |
| $b_4^{\#}$ | -5.14***<br>± 1.32 | 0.05***<br>± 0.01 | | -2.15**<br>± 0.73 | |
| $b_4$>0 | -8.62e-2***<br>± 0.01 | 4.48e-4***<br>± 0.00 | -2.97e-3***<br>± 0.00 | | 0.68 |

Note: $^{\#}$ denotes the binary logistic model for testing the occurrence of the decline. Significance codes: 0.05 '*'; 0.01 '**'; 0.001 '***'. *Age*: tree age at breast height; $H_{disc}$: disc position along the stem; $RW_{m2560}$: mean ring width from cambial age 25 to 60 of each disc

Disc-level models from Stage 1 had good fit (mean $R^2$ of 0.37) and were generally unbiased, despite the large variability in the radial profiles of *RD* (Figure 3-3, Table 3-7).

**Table 3-7 Fit indices and error statistics calculated from the fixed effects of the disc-level models and full model given by Eq. [3-1]**

| **Disc-level models** | $R^2$ | *ME* | \|*ME*\| | *RMSE* | *ME*% | \|*ME*\|% |
|---|---|---|---|---|---|---|
| Min. | 0.00 | -26.1 | 13.8 | 17.6 | -6.4 | 2.8 |
| 1st Qu. | 0.20 | -0.3 | 23.2 | 29.4 | 0.0 | 4.7 |
| Median | 0.38 | 0.9 | 26.4 | 33.8 | 0.2 | 5.4 |
| Mean | 0.37 | 0.9 | 27.7 | 35.6 | 0.3 | 5.5 |
| 3rd Qu. | 0.54 | 2.1 | 31.6 | 40.3 | 0.4 | 6.2 |
| Max. | 0.86 | 23.2 | 54.4 | 75.0 | 4.8 | 10.3 |
| **Full model** | | | | | | |
| Mean | 0.17 | 0.1 | 44.9 | 58.1 | 0.2 | 9.0 |

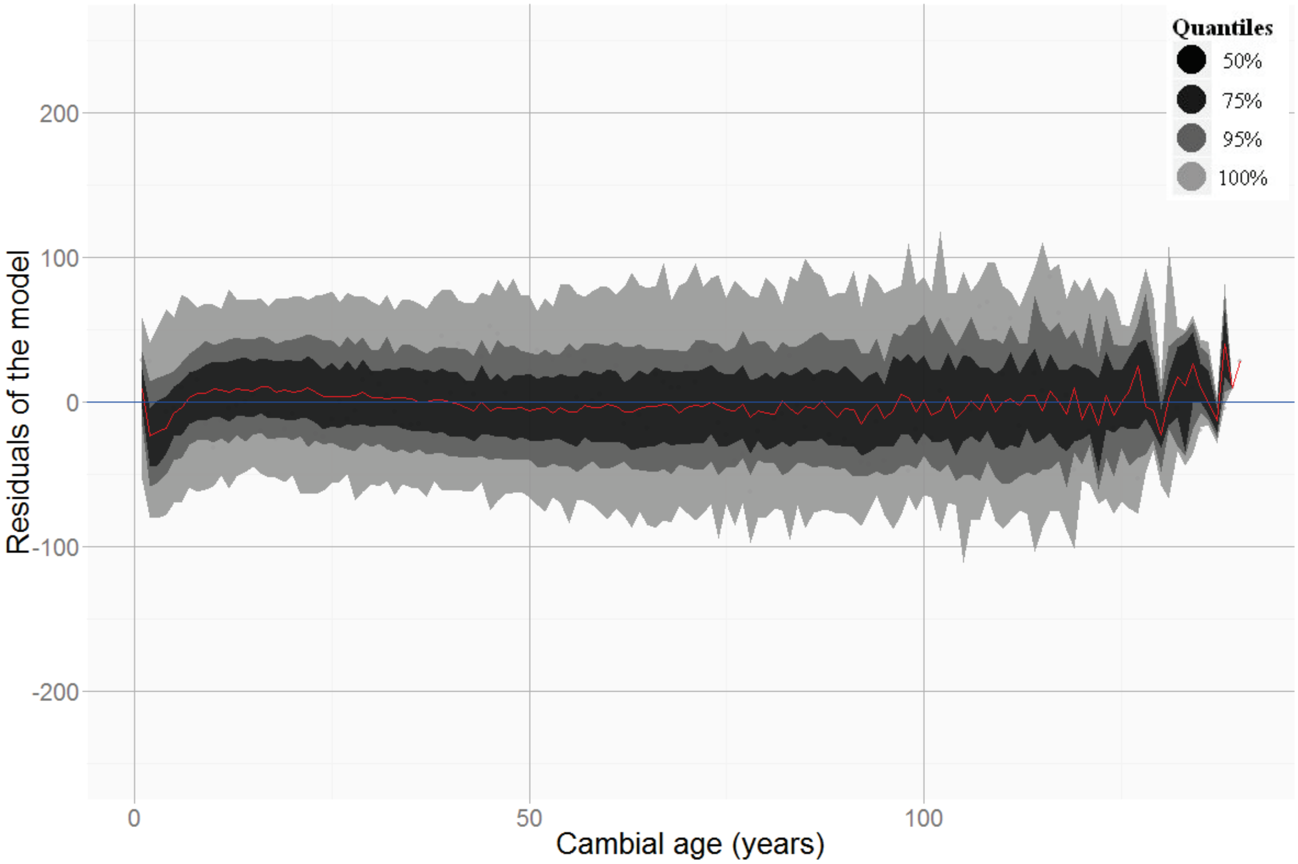

**Figure 3-3 Model residuals of the stage 1 predictions vs. cambial age. Percentiles of the residuals are represented by the different shades of grey. The red line represents the median value of the residuals for a given cambial age.**

When predictions were calculated from the full model, the $R^2$ decreased to 0.17, although the mean error and mean percentage error (0.2 kg $m^{-3}$ remained very low at 0.1 kg $m^{-3}$ and 0.2%, respectively (Figure 3-4, Table 3-7).

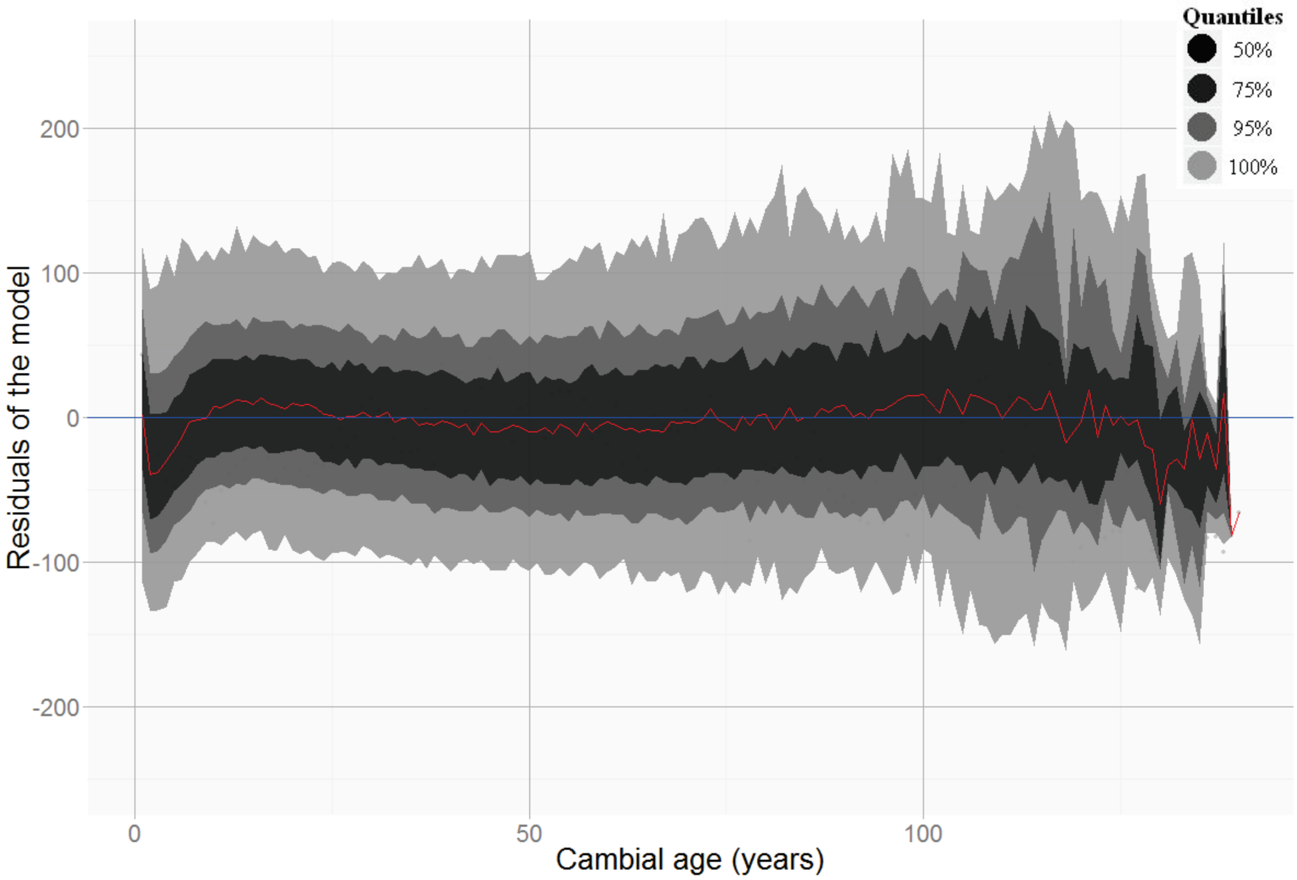

**Figure 3-4 Residuals of the stage 2 predictions against cambial age. Percentiles of the residuals are represented by the different shades of grey. The red line represents the median value of the residuals for a given cambial age.**

In general, lower minimum values of *RD* around the 15th annual ring and higher maximum values near the bark were attained in the lower stem (Figure 3-5).

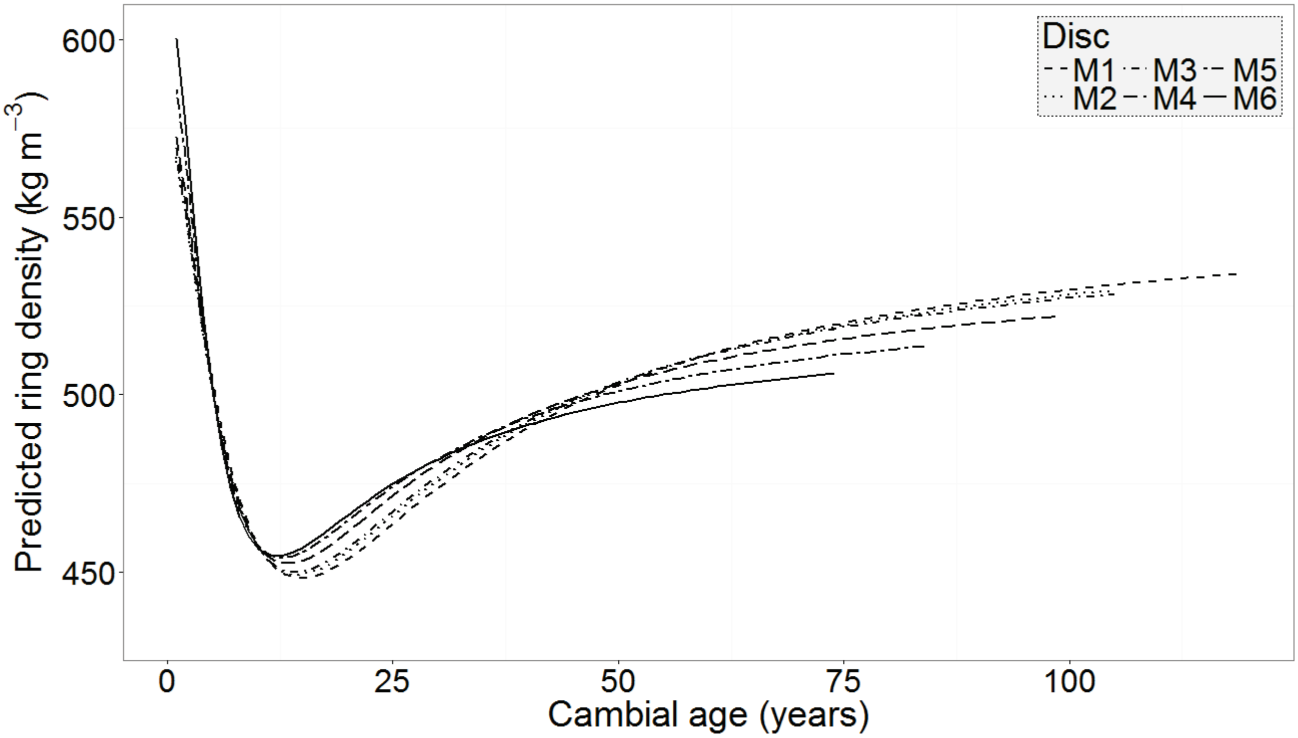

**Figure 3-5 Simulated radial density profiles with cambial age at different sampling heights ($H_{disc}$) for a typical dominant tree. Tree-level variables (i.e. *Ht, Age and* $RW_{BHm2560}$) were set to their mean values for dominant trees, while disc-level variables (i.e. $H_{disc}$, $RW_{p3}$, $RW_{m2560}$) were set at their mean values for each disc height in a dominant tree. Lines represent the mean predictions at successive disc heights (M1 to M6) from the stem base.**

For a given cambial age, the *RD* of a slower-grown (i.e. lower value of $RW_{BHm2560}$) intermediate tree was generally higher than for the other dominance classes, although the decline in wood density near the bark was more likely to occur (Figure 3-6). However, even the *RD* profiles of dominant trees could also show a declining trend beyond a certain age (not shown).

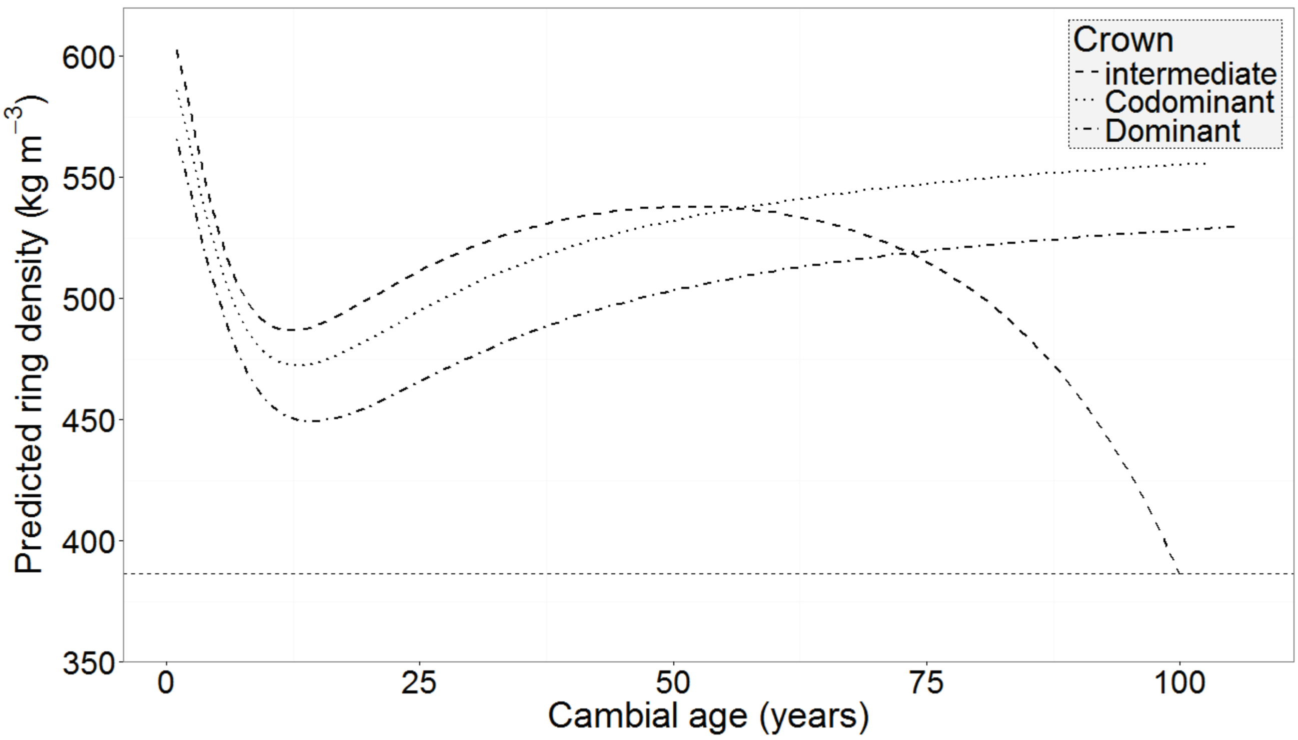

**Figure 3-6 Simulated radial density profiles with cambial age at breast height (*$H_{disc}$* = 1.3m) for trees in each dominance class. The horizontal line denotes the proposed limit of application of our model. Tree-level variables (i.e. *Ht, Age and $RW_{BHm2560}$*) were set to their mean values within each dominance class, while disc-level variables (i.e. *$RW_{p3}$, $RW_{m2560}$*) were set at their mean values at breast height within each dominance class.**

The more detailed analysis of ring series close to the bark did not reveal any relationship between the occurrence of a decline and annual ring width. However, the proportion of latewood was lower on average in discs showing the density decline (Figure 3-7).

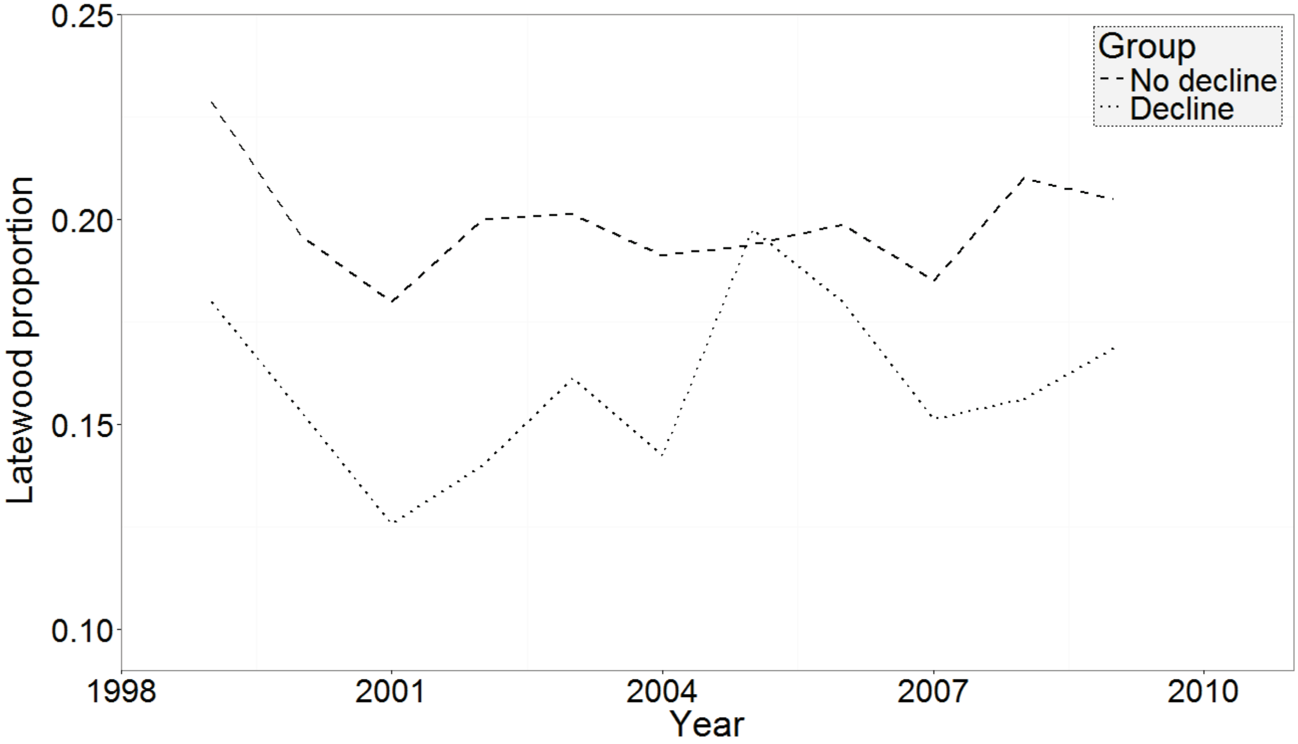

**Figure 3-7 Latewood proportion of the two groups of ring series analysed using observations under a microscope.**

## 3.4 Discussion

The wood density data in our study showed the typical radial pattern found in spruces that has also been observed in other studies (Alteyrac *et al.,* 2005; Gardiner *et al.,* 2011). Average ring density was high near the pith and decreased rapidly outwards, followed by a slow increase until values stabilised between growth rings 25 and 60. This pattern corresponds to the type II pith-to-bark profile described by Panshin and de Zeeuw (1980).

Investigating the complex interrelationships between cambial age, growth rate and height along the stem is recognised as one of the most difficult aspects of wood density studies (e.g. Alteyrac *et al.,* 2005; Gardiner *et al.,* 2011). The highly variable radial patterns among samples, particularly in the juvenile wood zone, proved difficult to incorporate into a single analysis. However, modelling individual profiles in a first stage, and then constructing linear models for those parameters in a second, proved to be a robust solution. The choice of an equation containing three separate components allowed enough flexibility to represent the large variation in density profiles. The first two terms in the equation are capable of describing the type II density pattern previously described, while the final exponential term was included when it was necessary to model a decline close to the bark.

The relatively poor fit of the full model in this study could be explained by the fact that, despite its classification as a type II species, wood density profiles in black spruce are, in reality, extremely variable. This variability will inevitably increase the absolute magnitude of the model errors by increasing the deviation between observed and predicted ring density. However, the sampling strategy in this study was designed to capture the natural variability found in black spruce unmanaged stands by sampling across a range of tree ages and sizes. By modelling the parameters of the individual density profiles, we were able to reduce these errors when compared with initial model fits to the pooled dataset. The low fit indices for the $b_1$ and $b_3$ parameters were probably due to the large variability in the initial decline near the pith. The high density of wood adjacent to the pith in black spruce has been attributed to high earlywood density and low earlywood proportion (Alteyrac *et al.,* 2005; Koubaa *et al.,* 2005). Both earlywood density and latewood proportion tend to decline rapidly in the first few rings, which is reflected in the decline in ring density. The wood adjacent to the pith, termed 'flexure wood' by Telewski (1989), is thought to be formed in response to complex loading patterns to which trees are subjected at a young age. This high-density wood also has steeply oriented microfibrils that confer low stiffness, and together these characteristics ensure that trees are flexible enough to withstand high stresses without breaking. Differences in local conditions between individual trees may lead to different initial values of density and therefore different rates of decline.

As expected, ring density was negatively correlated to the average ring width of the mature wood. In our analysis, the best predictions were obtained between rings 25 and 60. However, these must not be taken as precise limits. Rather, they are indicative of an overall negative relationship between radial growth rate and wood density in the part of the profile described by the second term of our equation. Accordingly, dominant trees tended to have lower density rings in the period preceding the decline than the trees in other dominance classes. This is in accordance with observations in Sitka spruce that, for a large range of ring widths, latewood width remains relatively constant between rings, so that variation in ring width is closely related to earlywood width (Brazier, 1970). Similar results have been found in black spruce (Zhang *et al.,* 1996), and jack pine (*Pinus banksiana* Lamb.) (Savva *et al.,* 2010).

However, a gradual decrease in ring density after approximately 60 years was observed in around 24% of the samples, which, to our knowledge, has been reported in very few studies (e.g. Schär and Schweingruber, 1987). The latter study reported a similar density decline in subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). This was associated with a reduction in latewood density after approximately 50 years, while earlywood density remained relatively constant. Elsewhere, evidence of a positive correlation between growth rate and wood properties has been reported, but such correlations appear to be mainly related to water availability. For example, in young loblolly pine (*Pinus taeda* L.), higher ring density associated with faster radial growth was related to the increased growth of latewood in wetter growing seasons (Cregg *et al.,* 1988). Conversely, a simultaneous decrease in ring width and wood density in Norway spruce coincided with increased early season rainfall, which resulted in the increased production of earlywood (Wimmer and Downes, 2003).

The decline in wood density in the current study was observed in only a proportion of trees, but typically spanned several years, during which the rate of decrease progressively increased. For these reasons, it is highly unlikely that it was related to water availability. The decline in wood density near the bark was associated with higher cambial ages and slower growth rates in the mature wood i.e. in the period before the onset of the decline. Comparable studies of black spruce wood density have tended to sample either young or dominant trees (e.g. Zhang *et al.,* 1996; Alteyrac *et al.,* 2005). Measures of mean growth rate and the slope of mean growth rate (‘growth level’ and ‘growth trend’, respectively), have been used to predict tree mortality in Norway spruce (Bigler and Bugman, 2003, 2004), although in our study, growth trend was not significantly correlated with the decline in wood density. Trees with little or no latewood—

a phenomenon referred to as ‘starvation wood’ by Brazier (1977)—have also been reported growing in poor stands in Scandinavia. Examination of the microscopy samples in our study, tended to confirm the existence of a similar type of wood, because of the low proportion of latewood in the samples with a density decline. It is possible that, in situations where resources are severely limited, trees can only maintain radial growth by producing lower density wood in the annual rings (Swenson and Enquist, 2007). The observed decline in wood density may therefore imply a reduction in aboveground maintenance costs. Such a change in resource allocation may help increase the longevity of old, declining trees (Robichaud and Methven, 1993).

Although height along the stem had a significant influence on all the parameters of Eq. [3-7], its overall effect varied with cambial age. Other studies on Norway spruce have found a weak or insignificant pattern of variation in wood density with position in the stem (Mäkinen *et al.,* 2007; Jyske *et al.,* 2008). In the current study, wood density tended to increase with height in the stem up to a cambial age of approximately 45 years, which is in agreement with the findings of Alteyrac *et al.* (2005). It has been suggested that this is due to the physiological ageing of the cambium, so that juvenile wood formed higher up the stem has more mature traits than wood produced at young cambial ages lower down the stem (Larson, 1969; Alteyrac *et al.,* 2005). However, the fact that the trend was reversed beyond ring number 45 suggests that more work is necessary to fully understand the factors driving the variations in wood density with height along the stem.

## 3.5 Conclusions

This study investigated wood density variations in black spruce stems growing in unmanaged stands. Use of a two-stage modelling approach was justified in this case since it helped to separate the interrelated effects of cambial age, growth rate and height along the stem on wood density. In mature wood, radial growth rate, was found to be negatively correlated with wood density. However, declining trends in annual ring density near the bark were observed, which were found to be more common in old and slow-growing trees. We hypothesise that such trends reflect a gradual reduction in tree vigour over the life of the tree.

The observed decline in wood density has implications for forest management because silvicultural interventions designed to reduce the effects of the decline by promoting vigorous growth, such as commercial thinning, may need to be considered. An appropriate rotation age may also be used as a means of avoiding the decline in wood density. In addition to any considerations about its possible effect on end-product properties, the occurrence of the decline could also have implications for aboveground biomass estimations, which could be improved by including the conditions for when a decline might occur. Future work should be conducted to investigate the possible impacts of this penomenon on carbon allocation to other parts of the tree.

## 3.6 Acknowledgements

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# Chapter 4 Size related density-climate relationships in Black spruce (*Picea mariana* (Mill.) B.S.P.)

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## 4.1 Abstract

Wood density indicators such as mean ring density (*RD*), minimum ring density (*MnD*) and maximum ring density (*MxD*) of dominant trees are influenced by climate-related factors and growth rate. However, the effects of stand competition on the relationship between climatic factors and *RD*, *MnD* or *MxD* are unclear. Utilizing black spruce (*Picea mariana* (Mill.) B.S.P.) from northwestern Ontario, Canada, the aim of this study was to (i) identify the effects of climatic factors and growth rate on *MnD* and *MxD, and* (ii) quantify these relationships for different dominance levels. Densitometric data from 72 trees of various dominance levels (dominant, co-dominant and intermediate) were analysed using mixed-effect models. For each dominance level, models including ring width and pith to bark variations were built. Monthly climatic variables (mean temperature and precipitation, minimum and maximum temperature) were then integrated into these preliminary models. The effect of growth rate and cambial age were detrending by the separated models for each density indicator. The addition of climatic factors significantly improved the performance of the model. The warm early summer nights (May), and warm summer nights (July), which are associated with drought in the early summer (May-June) promote high *MnD*; While *MxD* increased with warmer late spring and early summer (April-June) and mild extreme late summer temperatures (August) along with drought in the late summer (July-August). However, for each density indicator, different responses to climatic variables were observed between dominance levels. Our approach will help further our understanding of the effects of growth rate, climatic effects and crown level on the variation of intra-ring density.

## 4.2 Introduction

Over the past several decades, forest biomass productivity has been found to be strongly influenced by global climate change (Cook *et al*., 1987; Boisvenue and Running, 2006). In the boreal forest zone, increases in forest biomass productivity were observed in response to increasing temperatures (Boisvenue and Running, 2006). In this context, as an essential part of forest biomass productivity, the annual biomass increment was often investigated and estimated considering climate-related ring width (Hogg *et al*., 2008). Ring width of conifers was shown to vary with temperature (D'Arrigo and Jacoby, 1993; Mäkinen *et al*., 2003), water availability (Savva *et al*., 2010; Jyske *et al*., 2010; Kantavichai *et al*., 2010), and atmospheric carbon dioxide (Kilpelainen *et al*., 2003, 2005).

However, the computation of annual biomass increments also involves wood density, which is often introduced as a constant value (Ketterings *et al*., 2001; Pussinen *et al*., 2009). This is an incorrect assumption in these studies, as wood density is known to vary significantly according to stand conditions, genetics and climate (Zobel and van Buijtenen, 1989).

Wood density of conifers is a macroscopic representation of the wood structure. As a consequence of a transition from large and thin-walled earlywood tracheids to small and thick-walled latewood tracheids, the ring density increases from earlywood to latewood (Decoux *et al*., 2004). These anatomical characteristics result from variation in cambial activity (Fritts *et al*., 1991; Larson *et al*., 2001; Begum *et al*., 2008), which is under strong climatic influence for its onset of growth (Rossi *et al*., 2008; Begum *et al*., 2008; Lenz *et al*., 2012) and the onset of dormancy (Rossi *et al*., 2008; Begum *et al*., 2008).

Therefore, wood density indicators were under the influence of climatic determinism. Intra-annual wood density variations of Norway spruce (*Picea abies* (L.) Karst.) were related to fluctuations in soil moisture deficit (Bouriaud *et al*., 2005b). On the same species, Wimmer and Grabner (2000) stated that the minimum ring density (*MnD*) was poorly related to both temperature and precipitation, while maximum ring density (*MxD*) was related to summer temperatures and late summer precipitation. In red spruce (*Picea rubens*) growing in the boreal forest, Conkey (1988) displayed a general positive relationship between spring temperature and *MxD*. Wang *et al*. (2002) found that *MxD* displayed a strong positive relationship to summer temperatures from May-September while the relationship between earlywood density and summer temperature was moderate. As a consequence of this climatic determinism, *MxD* series were frequently used in dendroclimatic studies (Briffa *et al.,* 1998; Schweingruber *et al.,* 1993), while *MnD* is rarely used in climatic reconstructions, although it may be under climatic control as it is the result of climatic controlled cambial activity (Schweingruber *et al.,* 1993).

Additionally, previous studies typically focussed on dominant or co-dominant trees. However, forests also contain intermediate trees which may be important as (i) they are an important part of the final composition of mature stands and (ii) their access to resources (soil, light) is different. In addition, it has been showed that dominant trees of silver fir and Norway spruce are more sensitive to climatic variables than intermediate trees (Mérian and Lebourgeois 2011; Castagneri *et al*., 2012). In contrast to this the opposite result has been reported in pine species (De Luis *et al*., 2009). This difference was interpreted as a variation of thermal stress and transpiration among dominance levels (Mérian and Lebourgeois, 2011). Therefore, it is reasonable to hypothesize that black spruce trees from different dominance levels will have different wood density-climate relationships.

For black spruce growing in northwestern Ontario (Canada) this study aimed to (i) identify the relationship between climatic factors and minimum, maximum and mean ring density, and (ii) determine the effects of different dominance levels on the wood density-climate relationship. These objectives will be achieved through a quantitative method to determine climatic effects on wood density indicators.

## 4.3 Materials and method

### 4.3.1 Sampling and climate data

We sampled 13 stands from old natural forests (greater than 50 years old) in the Lake St. Joseph Ecoregion, 400 km northwest of Thunder Bay, Ontario, between 51° 42' N and 52° 6' N and between 90° 3' W and 94° 31' W, at an elevation of 400 m. Mean annual temperature varied between -1.7° and 1.0° C, mean annual precipitation ranged between 613 mm and 787 mm, mean summer rainfall between 244 mm and 299 mm, and the mean length of the growing season between 162 and 179 days. More information on this region is available in the Ecoregions Working Group publication (1989). Three temporary sample plots with a plot radius of 5.64 m (100 $m^2$) were established at each site. From each plot, three trees with no visible signs of damage were collected: (i) a large dominant tree (with largest diameter at breast height (DBH)), (ii) a medium co-dominant tree (DBH close to the average of the quadratic mean DBH) and (iii) a small intermediate tree. A 5 cm thick transversal disc was cut at breast height from each tree after felling. In addition after felling, the total height of each sample tree was recorded.

Monthly temperature (mean, minimum and maximum) and precipitation were obtained from the nearest weather stations (Sioux Lookout at 50°07' N, 91°54' W) to the study locations according to Environment Canada’s website *(http://www.climate.weatheroffice.gc.ca/)*. A few missing meteorological data points were substituted by using data from a neighbouring station (Kenora at 49°48' N, 94°32' W).

**Ring width and ring density measurements**

One strip of a 2-mm thick (longitudinally), 25 mm wide (tangentially) and the length of pith to bark sample per disk was taken. The strips were set into a conditioning chamber set at 60% relative humidity and 20° C until they reached a constant mass, corresponding to an equilibrium moisture content of 12%. The wood density was scanned from these samples on a QTRS-01X Tree Ring Analyzer (Quintek Measurement Systems Inc., Knoxville, TN, USA) with an X-ray beam at a resolution of 40 µm as described in Xiang *et al*. (2013). From these measurements, mean ring density (*RD*), *MnD* and *MxD* were recorded (abbreviations see Table 4-1).

**Table 4-1 Abbreviations**

| Abbreviations | Description (unit) |
|---|---|
| ***RD*** | Ring density (kg $m^{-3}$) |
| ***MxD*** | Maximum ring density (kg $m^{-3}$) |
| ***MnD*** | Minimum ring density (kg $m^{-3}$) |
| ***RW*** | Ring width (mm) |
| ***CA*** | Cambial age (years) |
| ***Tmean.**** | Mean daily temperature at month * of current year (°C) |
| ***Tmin.**** | Average minimum daily temperature at month * of current year (°C) |
| ***Tmax.**** | Average maximum daily temperature at month * of current year (°C) |
| ***ExTmax.**** | Extreme maximum daily temperature at month * of current year (°C) |
| ***Prec.**** | Precipitation at month * of current year (mm) |
| ***Tmean.*p*** | Mean daily temperature at month * of previous year (°C) |
| ***Tmin.*p*** | Average minimum daily temperature at month * of previous year (°C) |
| ***Tmax.*p*** | Average maximum daily temperature at month * of previous year (°C) |
| ***Prec.*p*** | Precipitation at month * of previous year (mm) |
| ***T.Mean*** | Mean annual temperature (°C) |
| ***P.Mean*** | Mean annual precipitation (mm) |
| ***T.G*** | Mean temperature during growth season Apr - Sep (°C) |
| ***P. G*** | Mean precipitation during growth season Apr - Sep (mm) |
| ***T.G1*** | Mean temperature during first half growth season Apr - Jun (°C) |
| ***P. G1*** | Mean precipitation during first half growth season Apr - Jun (mm) |
| ***T.G2*** | Mean temperature during second half growth season Jul - Sep (°C) |
| ***P. G2*** | Mean precipitation during second half growth season Jul - Sep (mm) |

Following a highly variable radial pattern in the juvenile zone (Xiang *et al*. 2013), ring density was found to remain relatively constant after a cambial age (*CA*) of 25 years. In addition, a decline close to bark was detected for rings with *CA* higher than 60 years. Therefore, only the rings from CA 25-60 years were included in the dataset. As no climatic data was available before 1915 in this area, the rings formed during that period were eliminated from the dataset.

Tree-ring series were cross-dated by the software COFECHA (Holmes, 1983). Some discs were found (mostly from intermediate trees) to contain extremely narrow rings, especially at late stage of growth, which meant that they could not be cross-dated reliably. Those were discarded from the analysis. Additionally, all discs smaller than 8 cm in diameter were omitted from the study. Therefore, the final dataset was composed of 30 dominant trees, 28 co-dominant trees and 14 intermediate trees totalling 2455 rings.

Details of ring width, *RD*, *MnD*, *MxD* and other values for each dominance level are shown in Table 4-2, along with the results of the t-test to identify the difference between dominance levels.

**Table 4-2 Mean (SD) ring-level characteristics for each dominance level. Different letters indicate significantly different values between dominance levels.**

| Dominance level | Age (years) | DBH (cm) | Height (m) | No. of rings | RW (mm) | Mean ring density ($kg/m^3$) | Minimum ring density ($kg/m^3$) | Maximum ring density ($kg/m^3$) |
|---|---|---|---|---|---|---|---|---|
| Dominant | 84 | $19.7^a$ | $17.6^a$ | 1015 | $1.16 (0.48)^a$ | $481.76 (58.59)^a$ | $348.25 (45.51)^a$ | 776.96 (101.44) |
| Co-dominant | 81 | $13.3^b$ | 14.7 | 968 | $0.78 (0.35)^b$ | $529.68 (66.53)^b$ | $384.35 (61.72)^b$ | $784.16 (86.44)^b$ |
| intermediate | 79 | 11.5 | 14.5 | 472 | 0.64 (0.24) | 535.07 (65.53) | 396.38 (64.81) | 750.28 (81.51) |

Note: Tree age (Age) and number of rings (Nb of rings) were not used in the comparison. Significant differences were found in all comparisons between dominant level and intermediate level trees. Therefore, 'a' denotes significant difference between dominant level and co-dominant level; 'b' denotes significant difference between co-dominant level and intermediate level (P-value < 0.05).

### 4.3.2 Data analysis

To display the effect of climate on wood density, the *RD* was standardized per site plot against mean annual temperatures and precipitation from 1915 to 2008 (Figure 4-1 and Figure 4-2). Recently, statistical models have proven useful in removing the long-term trends in tree ring series, leading to similar results obtained from the traditional dendrochronological techniques (Bontemps and Esper, 2011). Therefore, we intend to establish a model of *RD*, *MnD* and *MxD*.

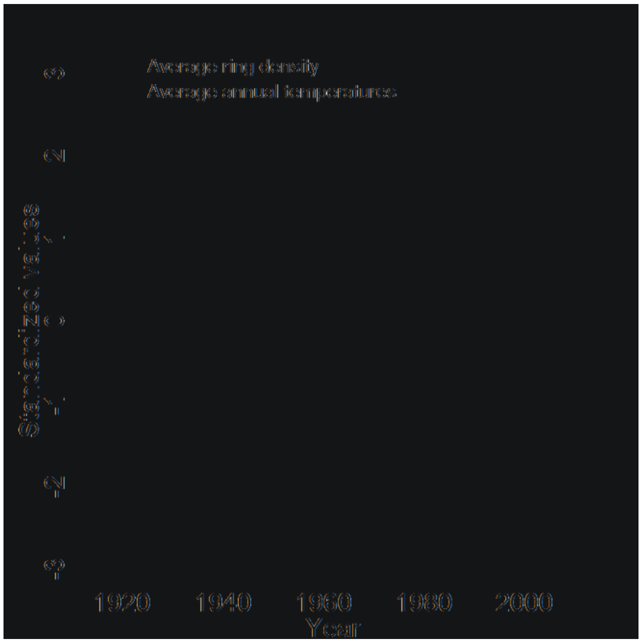

**Figure 4-1 Standardized (mean and lowess lines) variations in mean ring density and mean annual temperatures. Mean ring density was standardized per site without detrending non-climatic effects.**

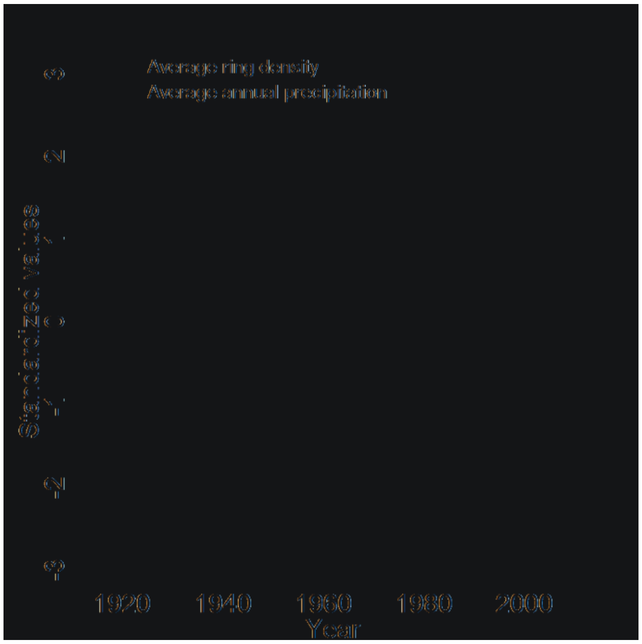

**Figure 4-2 Standardized (mean and lowess lines) variations in mean ring density and mean annual precipitation. Mean ring density was standardized per site without detrending non-climatic effects.**

As our data is longitudinal (i.e. a series of repeated measurements), we developed mixed effects-models of wood density indicators that could take into account the effects of ring width (*RW*) and *CA* (Figure 4-3 to Figure 4-5). Different mathematical forms of ring width and cambial age effects were tested. The analysis was made using the *lme* function of package *nlme* (Pinheiro *et al*., 2009) in the R statistical programming environment (2.11.0) (R Development Core Team, 2013). Models were selected according to the Akaike's information criterion (AIC) (Akaike, 1974) and likelihood ratio test for nested models (Pinheiro *et al*., 2009).

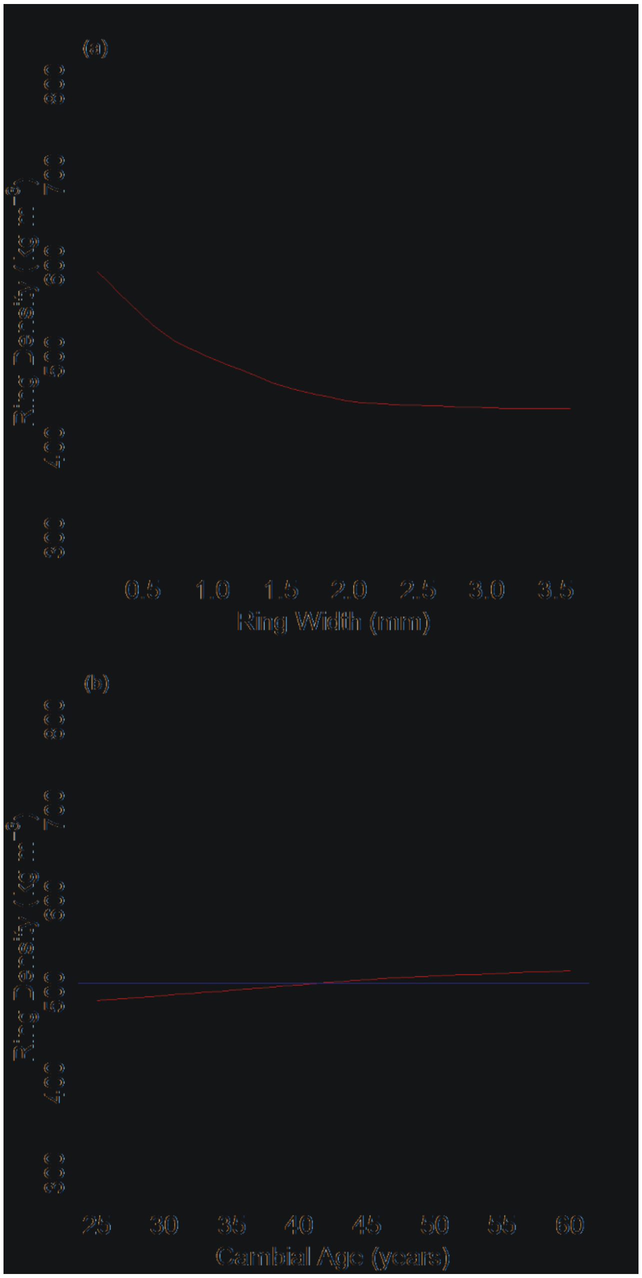

**Figure 4-3 Ring density against ring width (a) and cambial age (b). Horizontal line denotes average ring density and the curves were lowess lines**

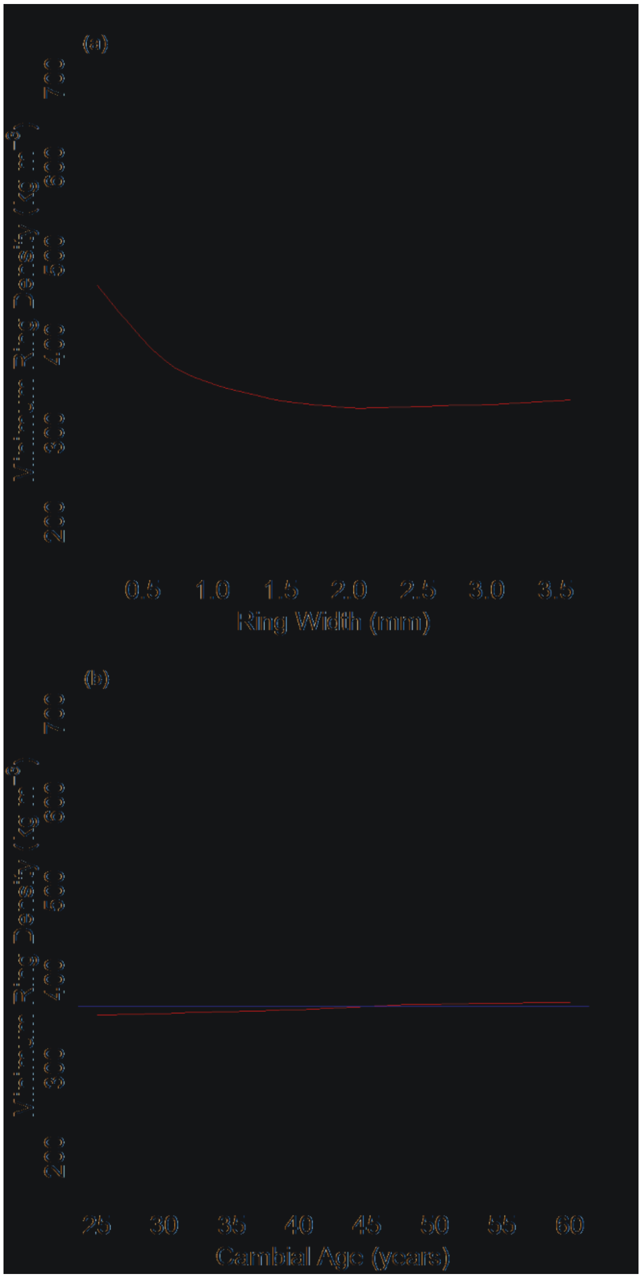

**Figure 4-4 Minimum ring density against ring width (a) and cambial age (b). Horizontal line denotes average ring density and the curves were lowess lines**

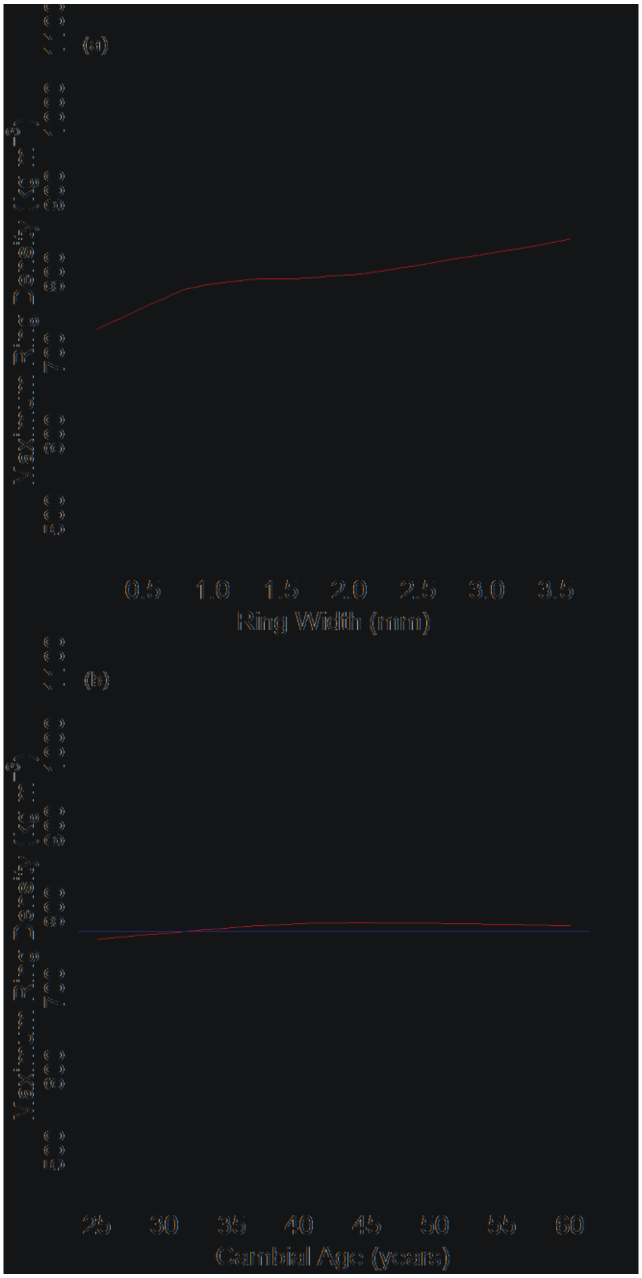

**Figure 4-5 Maximum ring density against ring width (a) and cambial age (b). Horizontal line denotes average ring density and the curves were lowess lines**

Since the main purpose of this step was to de-trend the effects of ring width and cambial age, the site and tree random effects were introduced for the intercept only without further partitioning the sources of within-group errors for each parameter. An autoregressive model of order 1, AR(1) (Pinheiro and Bates,

2000) was introduced and was found to be significant in all cases. After testing, the fixed effects for the wood density indicators were provided:

$$WD_i = f_i(CA, RW) = \begin{cases} RD: \quad \beta_0 + \dfrac{\beta_1}{1+\sqrt{RW}} + \dfrac{\beta_2}{1+\sqrt{CA}} \\ MnD: \beta_0 + \dfrac{\beta_1}{\sqrt{RW}} \\ MxD: \beta_0 + \dfrac{\beta_1}{RW} + \dfrac{\beta_2}{1+\sqrt{CA}} \end{cases} \qquad (4\text{–}1)$$

where $WD_i$ represents $RD$, $MnD$, or $MxD$, $f_i(CA, RW)$ a function of $CA$ and $RW$, $\beta_i$ denotes the associated parameters of fixed effects.

In a second step, the residuals from each model (4–1) were correlated to climatic variables. The correlation coefficients of the residuals of each wood density indicator against monthly climatic variables - previous January to current October as cambial activities often cease in October in the boreal forest (Rossi *et al.*, 2008) and carry-over effects of the previous year was identified (Fritts, 1976; Briffa *et al.,* 2002) - were used in order to identify the most influential climatic variables (p-value < 0.05). These variables were then further introduced in the models constructed and were tested. The general equation of the fixed effects was therefore:

$$WD_i = f_i(CA, RW) + g_i(climate) \qquad (2)$$

where $g_i(climate)$ is the effect of a given climate variable on a given density indicator.

Given our objective to investigate the effect of dominance level, once fixed effects for the pooled data were fitted, separate models for given dominance levels were assessed.

## 4.4 Results

### 4.4.1 Relationship between wood density indicators and climate

The historical trends of annual temperature, precipitation and ring density were shown in Figure 4-1 and Figure 4-2. A minor decrease of *RD* was found from 1915-1940 while the increase trends were found in annual temperature and precipitation during this period. A slight increase was found in *RD* since 1970 and annual temperature was also found to have a synchronous but steeper increasing trend; while annual precipitation displayed similar increase but start at 1980.

The correlation coefficients (Figure 4-6) of standardized wood density indicators against monthly climatic data show general information of each indicator related to the climatic factors when the interacting effect of ring width and cambial age were removed. *MnD* was negatively related to the average temperature during the second half of the growing season (Jul-Sep) as well as precipitation for May and June. *MxD* was positively related to the average temperature during the first half of the growing season (May-June), but negatively impacted by precipitation in July and August.

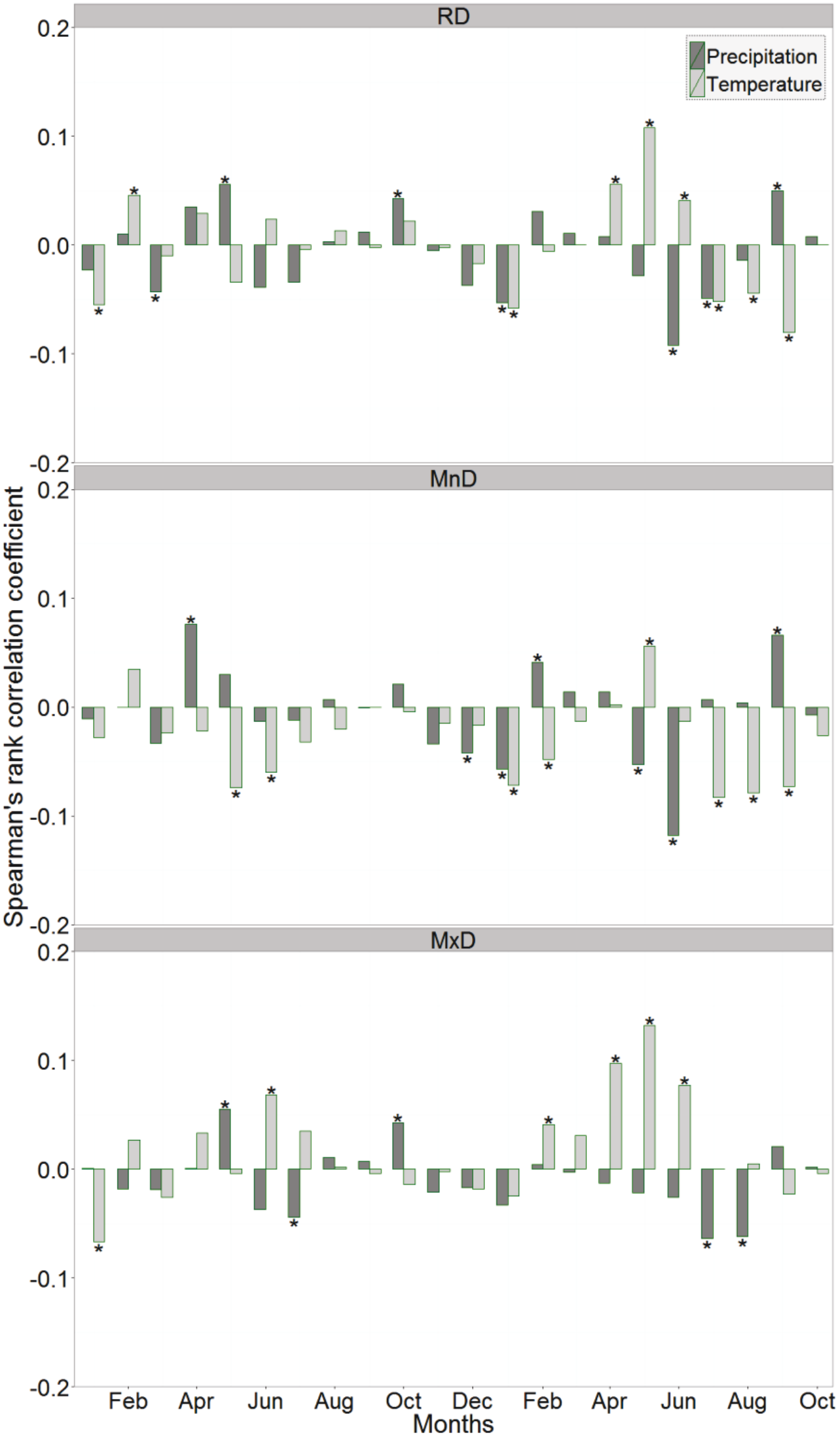

**Figure 4-6 Correlation coefficients between standardized average ring density, standardized minimum ring density, and standardized maximum ring density and monthly precipitation, temperature from January of previous year to October of current year. Note: * indicate correlation coefficient is significant ($p < 0.05$)**

### 4.4.2 Modelling effects of cambial age and ring width on density indicators (Model 1)

The non-climatic model (Model 1) was generally unbiased, despite the moderately high root mean square error in the radial profiles (Table 4-3 to Table 4-5). The largest $R^2$ of fixed effects was 0.22 in *MnD* compared to 0.07 in *RD* and 0.01 in *MxD*. With respect to random effects, a large portion of variability for all density indicators was attributable to the tree-to-tree variability i.e. 51%, 41% and 52% for *RD*, *MnD* and *MxD*, respectively. In addition, a small but significant site effect was also identified.

Varying effects of cambial age and varying mathematical forms of ring width on density indicators were detected (Table 4-3 to Table 4-5). A small positive CA effect was found for density indicators *RD* and *MxD*. Additionally, a negative effect of ring width was found on *RD* and *MnD*, although it was positively related to *MxD*.

**Table 4-3 Coefficients and associated SEs for ring density at different dominance levels**

| Ring density | **Pooled** | | | | **Dominant** | | **codominant** | | **intermediate** | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Model 1 | | Model 2 | | Model 2 | | Model 2 | | Model 2 | |
| | Est. | S.E. | Est. | S.E. | Est. | S.E. | Est. | S.E. | Est. | S.E. |
| (Intercept) | 556.6*** | 21.5 | 570.6*** | 23.7 | 506.2*** | 34.2 | 571.8*** | 38.5 | 636.0*** | 31.7 |
| $RW_1$ | 68.4** | 26.3 | 88.4*** | 25.4 | 79.5* | 39.1 | 106.7* | 41.9 | | |
| $CA_1$ | -617.0*** | 77.8 | -626.3*** | 75.4 | -338.7*** | 112.3 | -663.7*** | 121.7 | -1069.2*** | 183.5 |
| *Tmax.1* | | | -0.8*** | 0.2 | -0.7* | 0.3 | -0.7* | 0.3 | -1.5*** | 0.5 |
| *Tmean.4* | | | 0.8* | 0.3 | 1.2*** | 0.4 | | | | |
| *Tmean.5* | | | 2.8*** | 0.3 | 2.5*** | 0.4 | 3.0*** | 0.5 | 3.2*** | 0.7 |
| *Tmin.7* | | | -1.7*** | 0.5 | -1.5* | 0.7 | | | | |
| *Tmean.9* | | | -1.8*** | 0.5 | -2.0*** | 0.6 | -2.9*** | 0.8 | | |
| *Prec.4* | | | 0.1* | 0.0 | | | | | 0.2*** | 0.1 |
| *Prec.6* | | | -0.1*** | 0.0 | -0.1*** | 0.0 | -0.1*** | 0.0 | | |
| *Prec.8* | | | -0.1*** | 0.0 | -0.1*** | 0.0 | -0.1** | 0.0 | -0.1* | 0.0 |
| *Prec.3.p* | | | -0.1** | 0.0 | -0.1* | 0.1 | | | | |
| *Prec.5.p* | | | 0.1*** | 0.0 | 0.1* | 0.0 | 0.2*** | 0.0 | | |
| *Prec.8.p* | | | -0.1*** | 0.0 | | | -0.1*** | 0.0 | | |
| *Prec.12.p* | | | -0.1* | 0.0 | | | | | -0.2* | 0.1 |
| **Fit statistics** | | | | | | | | | | |
| AIC | 24806.7 | | 24573.9 | | | | | | | |
| **Coefficients of determination** | | | | | | | | | | |
| Fixed | 0.07 | | 0.11 | | 0.08 | | 0.12 | | 0.1 | |
| Site | 0.19 | | 0.23 | | 0.48 | | 0.25 | | 0.41 | |
| Tree | 0.7 | | 0.73 | | 0.72 | | 0.69 | | 0.65 | |
| **Error statistics calculated from the fixed effects** | | | | | | | | | | |
| RMSE | 65.5 | | 63.8 | | | | | | | |
| ME% | 0.4 | | 0.3 | | | | | | | |
| \|ME\|% | 9.9 | | 9.6 | | | | | | | |

Mathematical forms for cambial age and ring width: $CA_1 = \frac{1}{1+\sqrt{CA}}$ ; $RW_1 = \frac{1}{1+\sqrt{RW}}$ ; $RW_2 = \frac{1}{RW}$ ; $RW_3 = \frac{1}{\sqrt{RW}}$ ; Note: RMSE, ME%, and |ME|% which represent root mean square error, mean percentage error and mean absolute percentage error, respectively. *** p value < 0.001; ** p value < 0.01; * p value < 0.05.

**Table 4-4 Coefficients and associated SEs for minimum ring density at different dominance levels**

| Minimum density | **Pooled** | | | | **Dominant** | | **codominant** | | **intermediate** | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Model 1 | | Model 2 | | Model 2 | | Model 2 | | Model 2 | |
| | Est. | S.E. | Est. | S.E. | Est. | S.E. | Est. | S.E. | Est. | S.E. |
| (Intercept) | 277.2*** | 7.8 | 291.7*** | 10.2 | 302.8*** | 14.1 | 273.8*** | 14.0 | 291.8*** | 21.9 |
| $RW_3$ | 81.8*** | 4.2 | 83.3*** | 4.1 | 59.5*** | 6.6 | 84.9*** | 6.2 | 100.5*** | 9.1 |
| *Tmin.1* | | | -0.7*** | 0.1 | -0.7*** | 0.2 | -0.8** | 0.3 | | |
| *Tmin.5* | | | 2.4*** | 0.2 | 2.2*** | 0.3 | 2.3*** | 0.5 | 1.8*** | 0.6 |
| *Tmin.7* | | | -1.7*** | 0.4 | -1.9*** | 0.5 | | | -2.1* | 1.1 |
| *Prec.5* | | | -0.1*** | 0.0 | -0.1*** | 0.0 | -0.1*** | 0.0 | | |
| *Prec.6* | | | -0.1*** | 0.0 | -0.1*** | 0.0 | -0.1*** | 0.0 | -0.1* | 0.0 |
| *Prec.3p* | | | -0.2*** | 0.0 | -0.2*** | 0.0 | -0.2** | 0.1 | | |
| *Prec.10p* | | | 0.0* | 0.0 | | | 0.1* | 0.0 | | |
| **Fit statistics** | | | | | | | | | | |
| AIC | 23963.8 | | 23778.4 | | | | | | | |
| **Coefficients of determination** | | | | | | | | | | |
| Fixed | 0.22 | | 0.24 | | 0.05 | | 0.25 | | 0.14 | |
| Site | 0.31 | | 0.33 | | 0.51 | | 0.36 | | 0.25 | |
| Tree | 0.72 | | 0.73 | | 0.72 | | 0.73 | | 0.62 | |
| **Error statistics calculated from the fixed effects** | | | | | | | | | | |
| RMSE | 52.7 | | 52.1 | | | | | | | |
| ME% | 0.2 | | 0.2 | | | | | | | |
| \|ME\|% | 10.3 | | 10.1 | | | | | | | |

**Table 4-5 Coefficients and associated SEs for maximum ring density at different dominance levels**

| Maximum density | Pooled | | | | Dominant | | codominant | | intermediate | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Model 1 | | Model 2 | | Model 2 | | Model 2 | | Model 2 | |
| | Est. | S.E. | Est. | S.E. | Est. | S.E. | Est. | S.E. | Est. | S.E. |
| (Intercept) | 945.6*** | 20.1 | 928.8*** | 29.4 | 753.5*** | 25.2 | 961.3*** | 32.6 | 1077.8*** | 53.8 |
| $RW_2$ | -45.9*** | 3.1 | -45.4*** | 3.1 | -53.9*** | 8.0 | -47.2*** | 4.3 | -39.1*** | 4.5 |
| $CA_1$ | -802.4*** | 123.9 | -638.8*** | 122.3 | | | -1033*** | 180.9 | -1161.4*** | 228.4 |
| *Tmean.4* | | | 2.0*** | 0.6 | | | | | 3.2** | 1.2 |
| *Tmean.5* | | | 3.8*** | 0.5 | 4.5*** | 0.8 | 4.8*** | 0.8 | 3.8*** | 1.1 |
| *Tmean.6* | | | 1.8* | 0.7 | 2.8** | 1.1 | | | | |
| *ExTmax.8* | | | -1.8*** | 0.6 | | | | | -3.4*** | 1.1 |
| *Prec.7* | | | -0.1*** | 0.0 | | | -0.1* | 0.1 | -0.2*** | 0.1 |
| *Prec.8* | | | -0.2*** | 0.0 | -0.2*** | 0.0 | -0.1*** | 0.0 | -0.2*** | 0.1 |
| *Prec.5.p* | | | 0.1*** | 0.0 | | | 0.2*** | 0.1 | | |
| **Fit statistics** | | | | | | | | | | |
| AIC | 27448.2 | | 27294.3 | | | | | | | |
| **Coefficients of determination** | | | | | | | | | | |
| Fixed | 0.01 | | 0.03 | | 0.03 | | 0.04 | | 0.07 | |
| Site | n.s. | | n.s. | | 0.21 | | n.s. | | 0.41 | |
| Tree | 0.53 | | 0.56 | | 0.61 | | 0.49 | | 0.54 | |
| **Error statistics calculated from the fixed effects** | | | | | | | | | | |
| RMSE | 93.3 | | 91.5 | | | | | | | |
| ME% | 0.3 | | 0.3 | | | | | | | |
| \|ME\|% | 9.4 | | 9.2 | | | | | | | |

### 4.4.3 Modelling effects of climate combine with non-climatic effects (Model 2)

#### Effects of climate based on pooled data

By including climatic variables, the full model (Model 2) resulted in lower AIC values and improved error statistics (Table 4-3 to Table 4-5). This displayed that climate helped explain part of the variability of our wood density indicators. The climatic variables slightly improved the contribution of fixed effects by 4%, 2% and 2% for the total variability of the pooled data *RD*, *MnD* and *MxD*, respectively. In addition, the parameter estimates of non-climatic variables remained comparable between Models 1 and 2, thus confirming the existence of an effect of climate over and above that of *CA* and *RW*.

Generally, *MnD* was found to decrease with lower minimum temperatures in May, while *MnD* increased with lower minimum temperatures in January and July. Precipitation in May, June, and the previous March were found to negatively influence *MnD*, while the opposite effect was found in the previous October. Temperature in the early growing season (April to June) was positively correlated with *MxD*. In addition, extreme temperatures in August, were found to be negatively correlated with *MxD*, while the higher precipitation in July and August associated with less rainfall in May of the previous year lead to a lower *MxD*.

### Effect of climate according to dominance levels

Different non-climatic variables were included in Model 2 for each dominance level. Similar to the pooled data, the effect of cambial age was presented but only significant in models for *RD* and *MxD* (Table 4-3 to Table 4-5). The magnitude of *RW* and *CA* were slightly varied among different dominance levels.

The different occurrences of climatic variables in the models were observed among dominance levels. With respect to *MnD*, the negative effect of minimum temperature in January was absent in intermediate trees; the minimum temperature in May positively related to all dominance levels; the negative effect of minimum temperatures in July was absent in co-dominant trees; *MnD* of intermediate trees were less sensitive to the variables of precipitation, except for precipitation in June. The precipitation of the previous March was found significant for the dominant and co-dominant trees, however, precipitation of the previous October was only significant for the co-dominant trees.

The positive effect of the mean May temperature on *MxD* was found to be significant across all dominance levels, while mean temperatures in April and June were only significant in intermediate and dominant trees respectively; extreme temperatures in August were negatively correlated with *MxD* in intermediate trees; the influence of precipitation in July was not included into the *MxD* model for the dominant trees. Additionally, the precipitation of the previous May was only significant in the co-dominant trees for *MxD*.

## 4.5 Discussion

The growth-climate relationships have frequently been studied in dominant trees under different site conditions, elevations (Splechtna *et al*., 2000), latitudes (D'Arrigo *et al*., 1992, Briffa *et al*., 1998), but have also been found to be mediated according to dominance levels (Martín-Benito *et al*., 2008; De Luis *et al*., 2009; Mérian and Lebourgeois, 2011; Castagneri *et al*., 2012; Zang *et al*., 2012). However, the density-climate relationships were comparatively less studied, particularly in exploring their difference among dominance levels. Using statistical analysis for observed data under different dominance levels showed significant non-climatic effect including cambial age and ring width on density indicators of black spruce; and various climatic effects among dominance levels.

### 4.5.1 Effect of cambial age and ring width on density indicators

For the density indicators, we only detected a weak positive ageing trend for *MxD* in co-dominant and intermediate trees and the ageing effect was not significant for *MnD* while Franceschini *et al*. (2013) also found little ageing effect on *MnD*. Although, the dataset was set on a given period cambial age for minimizing age effect, a moderate positive relationship was identified between *MxD* and cambial age, similar relationship was also displayed by Jyske *et al*. (2008)

The negative relationship between ring width and *RD* was observed consistently in previous studies on conifers (Koubaa *et al*., 2000; Mäkinen *et al*., 2007; Gardiner *et al*., 2011). Less frequently reported is the moderate negative relationship observed between *MnD* and *RW* (Schweingruber *et al*., 1993; Mäkinen *et al*., 2002).

Unlike *MnD*, which is mainly under the determinism of internal factors (such as genetics and ontogeny), the *MxD* is more under the influence of external factors (e.g. climate) (Franceschini *et al*., 2013). Both *RW* and *MxD* were positively affected by summer temperature (D'Arrigo *et al*., 1992, Briffa *et al*., 1998), which lead to a positive correlation between ring width and *MxD* (Gindl *et al*., 2000). In addition, *MnD* was fitted by non-climatic factors with a better fit index suggested *MnD* could mainly under the influence of internal stimuli.

### 4.5.2 Effect of climate on *MnD* and *MxD* based on pooled data

The climatic effect on *RD* has been displayed in long term. This effect was confirmed in the modelling procedure. By including climatic variables, the error statistics and fit index of the models were improved for each density indicator, therefore suggesting a weak but significant climatic determinism on the chosen density indicators. Additionally, correlating strongly (0.82) with *MnD* and moderately (0.47) with *MxD,* the *RD* was significantly related to the climatic variables, which mostly could be found in the *MnD* and *MxD* models. Although in the past density-climate studies, the earlywood density or *MnD* was not studied as intensively as *MxD* as it is less sensitive to climate fluctuations, earlywood density or *MnD* still observed to be influenced by climate (Wimmer and Grabner, 2000; Savva *et al*., 2010, Franceschini *et al*., 2012). Therefore, in present study, we will focus on the significant climatic effects observed for *MnD* as well as *MxD* in the following lines.

In boreal and temperate forests, the importance of temperature is highlighted during cell differentiation (Gričar *et al*., 2006; Rossi *et al*., 2006, 2008; Begum *et al*., 2007, 2008). Previous research suggested that minimum daily temperatures are critical for the onset of cambial activity (Schrader *et al*., 2003; Begum *et al*., 2008; Rossi *et al*., 2008, 2011b). Similarly, we found a positive relationship between average minimum daily temperature in May and *MnD*, suggesting that the higher minimum temperature during night time resulted in higher *MnD* (Schweingruber *et al*., 1993). The relationship between *MnD* and climatic variables late in the growing season (July) was also found by Franceschini *et al.* (2013), and was interpreted as a result of the prolongation of the maturation of earlywood tracheids. Another reason is that most tracheids are known to be divided and enlarged during the warmest period of the growing season (Wang *et al*., 2002), which represents increased daytime temperatures and fewer cold nights, while increased night temperatures could improve cell production rate significantly (Deslauriers and Morin, 2005). Therefore, larger rings were produced, thus inducing lower *MnD* (Mäkinen *et al*., 2002; Franceschini *et al*., 2013).

We also observed a negative effect of minimum temperature in winter (January) on *MnD*. This is in accordance with other findings on conifers at the tree line (Grace and Norton, 1990; Pederson *et al*., 2004; Savva *et al*., 2010). The photosynthetic capacity can be reduced by exposure to cold temperatures in winter, through the massive loss of needles (Grace and Norton, 1990). Additionally, in order to balance the increased mechanical loading, as trees were anchored in the frozen soil during the cold winter, lower stem promotes the growth (Lundqvist and Valinger, 1996) likely along with higher density wood to support the whole structure.

Moreover, at the cell enlargement stage, the vapor pressure deficit is elevated with increased May temperatures and reduced precipitation in May and June, thus inducing smaller tracheids via control of turgor pressure (Ryan *et al*., 1994). This could explain the negative relationship between May and June precipitation and *MnD*.

It has been shown that *MxD* is positively related to summer temperatures for black spruce (Wang *et al*., 2002), a result that was the basis of temperature reconstruction models (Fritts, 1976; Schweingruber *et al*., 1993; D'Arrigo, 1992; Hughes, 2002). Our results are in accordance with these findings. The effects of the early growing season climate on *MxD* could be explained by ideal temperatures that prompted growth of new needles and increased accumulation of carbohydrates in the crown (Körner, 1998; Grace *et al*., 2002). Therefore, more photosynthate would be available for stem wood formation following the production of new needles. In addition, the negative effect of precipitation in the summer (August) on *MxD* was pronounced. The lower precipitation associated with high transpiration water loss during the summer was shown to be a result of low soil water reserves (Ryan *et al*., 1994; Yasue *et al.,* 1997; Lebourgeois *et al*., 1998; Durre *et al*., 2000), which could impact *MxD*.

### 4.5.3 Differences according to the dominance level

A negative effect of minimum temperatures in the winter (January) on *MnD* was found for dominant and co-dominant trees, but not for intermediate trees. It is well known that distribution of growth could be impacted by the mechanical load (bending, flexing) (Larson, 1963; Telewski, 1990), and radial growth of lower stem can be promoted with increased mechanical load applied during the dormant period as usually in boreal forests, trees are firmly anchored in the ground after the winter temperature below freezing (Lundqvist and Valinger, 1995). Therefore, the possible explanation is that, under the low winter temperature, the dominant and co-dominant trees would bear more loading capacity, and more stem radial growth was applied at breast height thus lower *MnD*. In addition, the negative effect of May precipitation on *MnD* was not significant in intermediate trees. Overlapped by the neighbouring crowns, intermediate trees experience less radiation and wind velocity, which might decrease transpiration (Kimmins, 1997; Bréda *et al.,* 2006). Therefore, the sensitivity to precipitation could be reduced in intermediate trees for the *MnD* (Pichler and Oberhuber, 2007).

Contrary to the lower response to May precipitation of the intermediate trees for *MnD*, *MxD* was observed to be negatively related to precipitation in July (except for dominant trees) and August (all dominance levels), indicating that the effect of precipitation at later growth season can be important for *MxD* of intermediate trees (Martín-Benito *et al.*, 2008). Droughts and dry weather in July and August have been associated with the production of latewood cells with thicker walls, and thus higher *MxD* (Jyske *et al*., 2010, Splechtna *et al*., 2000). In this case, the thicker latewood cell walls result from reduced soil water content (Yasue *et al*., 1997). Compared to the dominant and co-dominant trees, intermediate trees display less developed root systems (Van Lear and Kapeluck, 1995), which can increase their sensitivity to precipitation. Up to this point, the different influence of precipitation on *MnD* and *MxD* for intermediate trees could be explained. In the early growing season with abundant rain, the intermediate trees need less soil water due to their inferior transpiration (Olivar *et al*., 2012), consequently likely displayed less sensitivity to precipitation; while at later growing season, associated with increased temperature, less soil water could accessed by the intermediate trees as their underdeveloped root systems, therefore the higher sensitivity to precipitation was more likely occurred.

Temperature effects were found to be positively related to *MxD* in intermediate trees (April and May), co-dominant trees (May) and dominant trees (May and June) suggesting that the influence of temperature on *MxD* were significant in intermediate trees, co-dominant trees and dominant trees at successive months. For several coniferous species, it has been stated that soil water deficit in favor of latewood initiation such as loblolly pine (Cregg *et al*., 1988) and Norway spruce (Bouriaud *et al*., 2005). It thus can be presumed that, with the elevated upper soil layers temperature, the increased evapotranspiration associated with different ability of acquiring water among dominance levels, creating various initiations for latewood growth (Martín-Benito *et al.*, 2008). And such conditions could be favourable to form the higher maximum latewood density (Jyske *et al*., 2010).

In addition, the negative effect of extreme August temperatures on *MxD* was more pronounced in intermediate trees. Under great competitive stress, the intermediate trees tend to form a larger proportion of heterotrophic to autotrophic tissue with relatively higher respiratory costs (Naidu *et al.,* 1998). Reduced resource availability likely induces respiration to exceed photosynthesis during high temperature events (Martín-Benito *et al.,* 2008), which would leave less photosynthate available for cell wall construction.

We also observed a carry-over effect of precipitation from the previous March and October for *MnD*, as well as the previous May for *MxD* (Wimmer and Grabner, 2000; Goldblum and Rigg, 2005). This fact might be related to soil temperature and soil water reserves, which affected by the understory cover (e.g. moss, lichens). For example, Bonan and Shugart (1989) stated that a deep snowpack could protect lichens under cold winter and a thicker lichen layer could reduce evapotranspiration. Therefore, more soil water reserves might be available for the following growing season. Interestingly, the carry-over precipitation effect was not significant in the intermediate trees which could be explained, as mentioned previously, by the lower evapotranspiration and therefore leads to lower water requirements of intermediate trees compared to dominant and co-dominant trees.

### 4.5.4 Insufficient parts of the model

Although only a small amount of variability was explained by climatic variables, a significant improvement of the fit indexes was observed when they were introduced into the model. In addition, it should be noted that since ring width was already included in the model, it might already include some indirect effects of climate. Furthermore, the high variation of the density indicators could be another possible reason leading to the relatively small part of the variation explained. Despite the $R^2$ were slightly low, the predictions were unbiased, so that the general patterns of those indicators could be captured.

Also, when we tested the random effect of dominance levels for the pooled model, a relatively low contribution of dominance levels was found in the *MnD* and *MxD,* while a large portion of *RD* variability could be attributed to the dominance levels. We inferred that mean ring density depends on the highly varied latewood proportion instead of the less varied *MnD* and *MxD*. This is similar to the results from Splechtna *et al*. (2000), and it indicates that dominance levels can partially explain the variance at the tree level and its significance on *RD* via latewood proportion, as found previously (Xiang *et al*., 2013). However, the models were developed based on samples from a restricted area and advance validation is necessary.

## 4.6 Conclusions

Our study identified different climatic sensitivities related to dominance levels for selected density indicators (i.e. *MnD* and *MxD*) of black spruce in the boreal forest. In particular, *MnD*, dominant trees were more related to climatic variables, especially for precipitation related variables, than intermediate trees. On the contrary, *MxD* was influenced by temperature in intermediate trees, co-dominant trees and dominant trees at successive months at early growing season. These differences could be explained by variation from spring to summer in the photo-thermal stress stratification, transpiration rate, developmental level of root system, and respiratory maintenance costs. It should although be noted that there is still a lack of evidence to clearly identify the exact causes of such a phenomenon.

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# Chapter 5 Density-climate relationships vary according to disc height along the stem in black spruce (*Picea mariana* (Mill.) B.S.P.)

Adapted from the publication: Xiang W, Achim A, Franceschini T, Leitch M (2013) Density-climate relationships vary according to disc height along the stem in black spruce (*Picea mariana* (Mill.) B.S.P.). CJFR (to be submitted).

## 5.1 Abstract

Wood density indicators such as mean ring density (*RD*), minimum ring density (*MnD*) and maximum ring density (*MxD*) are known to be influenced by climate-related factors and growth rate. However, the effects of disc height on the relationship between climatic factors and *RD*, *MnD* or *MxD* to date have seldom been considered. Considering black spruce (*Picea mariana* (Mill.) B.S.P.) from northwest of Ontario, Canada, the aim of this work was to quantify the density-climate relationships for different disc heights. Densitometric data from 68 trees of six disc heights (M1-M6) were analysed using mixed-effect models. For each disc height, models including ring width and pith to bark variations were built. Then, monthly climatic variables were plotted against residuals from previous models. Generally, climate sensitivity among disc heights was similar during the growth season for each density indicator; however, the strength of the sensitivity was not constant. For *MnD*, we found: (i) an increased sensitivity to the early growing season temperature in the upper disc heights; to precipitation in May and June, and to both temperature and precipitation in September; (ii) a significant influence of the June temperature detected only in the top disc (M6); and (iii) a higher sensitivity to temperature in July and August in the mid stem disc (M2-M5). With respect to *MxD*, we identified (i) sensitivity to temperature early in the growing season, which was higher on average in the lower discs (M1-M3); and (ii) only the lowest disc (M1) was positively correlated with temperature in July and August, while it was inversely related to temperature in August at higher locations along the stem. This study will

help further our understanding of the effect disc height on density-climate relationships, and of the underlying implications for annual carbon allocation along the stem.

## 5.2 Introduction

Traditionally, dendrochronological and densitometric studies sample tree stems at breast height (1.3 m aboveground), since the irregular expansion of the tree base is stabilized here as well as for the operational simplicity (Schweingruber *et al.,* 1990a, 1990b; Zhang *et al.,* 1996). An underlying assumption for radial density studies conducted at breast height is that this height could represent the variation of the whole stem, which implies that the measured sensitivity to climate is constant all along the stem. Such an assumption was not necessarily validated. Significant effects of height on density patterns were reported in black spruce (*Picea mariana* (Mill.) B.S.P.) (Alteyrac *et al.,* 2005; Xiang *et al.,* 2013a). In addition, studies on growth-climate relationships conducted in different site conditions and elevations (Splechtna *et al*., 2000), latitude along the tree line (D'Arrigo *et al*., 1992, Briffa *et al*., 1998), and also disc heights (Chhin and Wang, 2005; Chhin *et al.,* 2010; van der Maaten-Theunissen and Bouriaud, 2012; Kerhoulas and Kane, 2012), all of which were found to have different results when compared to breast height sampling.

In conifers and especially in the *Picea* genus, negative correlations between density and growth rate have been identified (Koubaa *et al*., 2000; Franceschini *et al*., 2010) and the assumption of co-varying density-climate relationships among disc heights along stem could be reasonably proposed. However, considering the time lag between cell growth and cell wall thickening stages (Bouriaud *et al.,* 2005a), it could be expected that the density-climate relationships might not be identical with the reversed growth-climate relationships. Additionally, with the increasing interest in tree stem carbon sink and its fluctuations, a more accurate estimation of the density-climate relationship along the stem was required to get a more reliable estimation on annual biomass increment (Bouriaud *et al.,* 2005b) for a better understanding of biomass allocation within the tree. However, previous studies based on allometric equations from ring series often ignored inter-annual variations in wood density introduced it as a constant value (Graumlich *et al*., 1989; Ketterings *et al*., 2001).

From previous studies in which the samples were collected at breast height, wood density in the northern conifers was strongly affected by climatic factors as their effects on cambial activity lead to different allocations of growth requiring substances during ring formation (Fritts *et al.,* 1991; Lenz *et al*., 2012). The growth allocation response to climate for the rest of the stem was assumed to follow a trend where climate sensitivity is decreasing from top to base of tree, since it could be related to hydraulic limitations and downward carbon allocation during ring formation (Fritts, 1976; Kerhoulas and Kane, 2012). Chhin *et al.* (2010) suggested that a lag effect of climate in the growth of the upper stem is primarily affected by climatic factors during ring formation, while in the lower stem (breast height) it is more affected by climatic factors which precede ring formation. However, reduced climate sensitivity in the upper stem was shown for Norway spruce (*Picea abies* (L.) Karst.)) (Bouriaud *et al.,* 2005a), which contradicted the hypothesis of Chhin *et al.* (2010). The underlying explanation could be that growth allocation in response to climate along the stem is also affected by other sources. For example, high stand density (Gea-Izquierdo *et al.,* 2009) would likely smooth the extreme climatic effects through increased competition among individual trees, thus, leads to reduced sensitivity to climate. Cescatti and Piutti (1998) observed that high competition leads to trees that are more sensitive to water balance, while low competition results in more temperature-constrained growth. Additionally, average growth rate (i.e. tree size) was proven to mediate the sensitivity of density to climate (Xiang *et al.,* 2013b), but whether this difference results from overall growth or from inter-annual ring width level needs to be considered.

In addition to upper stem heights, Chhin and Wang (2005) presented samples from stump height that could be included into tree-ring chronologies with maintained climate sensitivity to maximum length of the sequences as the growth period prior to reaching breast height would be dismissed.

Black spruce is widely distributed in Eastern and Central Canada as an important commercial and reforestation species (Boyle *et al.,* 1988). There is rising concern of growth responses of boreal forests to recent climate change, particular for increased temperature scenarios (Schneider *et al.,* 2009). The fluctuation of growth allocation in black spruce needs to be recorded based on its essential role in the boreal forest. Therefore, the present study aims to compare radial density patterns in response to climate at different sampling heights in black spruce.

## 5.3 Materials and methods

### 5.3.1 Sampling and Climate data

In the Lake St. Joseph Ecoregion approximately 400 km northwest of Thunder Bay, Ontario, Canada, between 51° 42' N and 52° 6' N and between 90° 3' W and 94° 31' W, 13 stands from black spruce dominated natural forests were sampled. Three temporary sample plots (TSP) with a plot radius of 5.64 m (100 $m^2$) were established at each site. In each TSP, stem discs of two trees i) a dominant tree with the largest diameter at breast height (DBH), and ii) a co-dominant tree with a median DBH with no visible signs of damage were collected. Stem discs were sampled at 0.5 m, 1.3 m, 1.75 m, live crown base (LCB) and at two equidistant points between 1.75 m and LCB. Discs at successive heights from ground level up were hereafter referred to as M1, M2, M3, M4, M5, and M6, respectively.

Monthly mean temperature and monthly total precipitation were collected from the nearest meteorological stations (Sioux Lookout at 50°07' N, 91°54' W) of the study locations according to Environment Canada’s website *(http://www.climate.weatheroffice.gc.ca/).* A few missing meteorological data were replaced by using data from neighbouring stations.

### 5.3.2 Ring width and ring density measurements

The sampled discs were sawn at a constant thickness of 2 mm longitudinally and width of 25 mm tangentially for X-Ray densitometry analysis on a QTRS-01X Tree Ring Analyzer (Quintek Measurement Systems Inc., Knoxville, TN, USA). Measurements were made after the samples had been conditioned to an equilibrium moisture content of 12% with an X-ray beam at a resolution of 40 µm as described in Xiang *et al*. (2013). The density indictors: mean ring density (*RD*), minimum ring density (*MnD*) and maximum ring density (*MxD*) were available from the above measurement.

Following a highly variable radial pattern in the juvenile zone (Xiang *et al*., 2013), ring density was found to be invariant after a cambial age (*CA*) of 25 years. In addition, a decline close to the bark was detected for rings with *CA* greater than 60 years. As no climatic data was available prior to 1915 in this area, the rings formed prior to that period were eliminated from dataset.

Tree-ring series were cross-dated by the software COFECHA (Holmes, 1983). Some discs were found to contain extremely narrow rings especially at later stages of growth and could not be cross-dated reliably and were therefore not included in the analysis. Additionally, a few discs from bottom regions of the tree stem were excluded due to rot and discs less than 8 cm in diameter were omitted from the study. Therefore, the final dataset was composed of 35 dominant trees, and 33 co-dominant trees totalling 9816 rings. In Table 5-1, details of density, ring width, mean ring density, *MnD*, *MxD* and other values for each disc height are shown.

**Table 5-1 Characteristics of the samples per disc height**

| Disc level | Disc diameter (cm) | Disc height (m) | No of rings | RW (mm) | Mean ring density ($kg/m^3$) | Minimum density ($kg/m^3$) | Maximum density ($kg/m^3$) |
|---|---|---|---|---|---|---|---|
| M1 | 18.24(4.98) | 0.5(0) | 1811 | 1.04(0.5) | 495.89(60.08) | 359.04(51.97) | 763.31(98.98) |
| M2 | 16.55(4.97) | 1.3(0) | 1987 | 0.97(0.46) | 505.05(67.15) | 365.26(58.52) | 780.39(94.46) |
| M3 | 16.71(4.85) | 1.75(0) | 2074 | 0.89(0.37) | 497.36(56.77) | 361.05(50.58) | 771.8(99.53) |
| M4 | 15.94(4.4) | 3.8(0.64) | 1734 | 0.9(0.39) | 493.9(55.45) | 361.8(48.41) | 764.57(111.96) |
| M5 | 14.91(3.82) | 5.78(1.35) | 1249 | 0.86(0.39) | 497.64(54.25) | 368.51(50.05) | 753.73(107.5) |
| M6 | 13.98(4.17) | 7.44(2.04) | 961 | 0.9(0.41) | 491.93(49.93) | 363.64(49.87) | 747.97(110.01) |
| Tree level | Age (years) | Height (m) | No of rings | RW (mm) | Mean ring density ($kg/m^3$) | Minimum density ($kg/m^3$) | Maximum density ($kg/m^3$) |
| Total | 88(22) | 16.8(3.0) | 9816 | 0.93(0.43) | 497.54(58.62) | 362.87(52.12) | 766.06(103.3) |

### 5.3.3 Effect of cambial age and ring width on density indicators (stage 1)

The climatic sensitivities of density indictors can be assessed after accounting for the effects of cambial age and growth rate. The traditional de-trending technique was applied for ring chronologies in the past dendrochronological studies, using a selected time span cubic smoothing spline with a 50% frequency response (Cook and Peters, 1981) in the program ARSTAN (Cook, 1985) to remove the long-term trend and local disturbance (Cook *et al.,* 1990). Such a step of removing the non-climatic effects in dendrochronology is called ‘standardization’. The dimensionless and homoscedastic indices created from standardization could serve to amplify the climatic signal (high frequency or inter-annual variation) with low frequency or long-term variation controlled (Fritts, 1976).

Recently, statistical models have proven useful to remove the long-term trend in tree ring series, leading to similar results obtained from traditional dendrochronological techniques (Bontemps and Esper, 2011).

As our data was longitudinal, we built mixed effects-models of wood density indicators in order to take into account the effects of ring width (*RW*) and *CA*. Both site and tree effects were detected in the data (Xiang *et al.,* 2013), assumed to be Gaussian, and were introduced as a random effect into the model. Additionally, as the density indicators could be related to *CA* and *RW* differently along stem height (Xiang *et al.,* 2013; Franceschini *et al.,* 2013), various mathematical forms of *CA* and *RW* were tested for each disc height.

All analysis was made using the *lme* function of package *nlme* (Pinheiro *et al*., 2009) in the R statistical programming environment (3.0.1) (R Development Core Team, 2013). Models were selected according the Akaike's information criterion (AIC) (Akaike, 1974) and likelihood ratio test for nested models (Pinheiro *et al*., 2009). The site and tree random effects were introduced for the intercept only as this may remove differences of the effect of climate site by site according to the disc height. Therefore, only the intercept part was included in the two random effects of tree and site. An autoregressive model of order 1 AR(1) (Pinheiro and Bates, 2000) was introduced and was always found significant. After testing, the fixed effects for the mean ring density indicators were provided. These separated fitted models for each disc height to de-trend non-climatic effects (*CA* and *RW*) were described as stage 1.

### 5.3.4 Effects of climatic variables on the density indicators for each disc height (stage 2)

The residuals obtained from fixed-effects of models in stage 1 were used to correlate with climatic variables, namely, stage 2. In this stage, the Spearman's rank correlation coefficients were tested for the available monthly climatic variables. Based on the growing season for black spruce in the boreal forest (Rossi *et al.,* 2008), we only assessed the months from January of the previous year to October of current year.

## 5.4 Results

### 5.4.1 Effect of cambial age and ring width on the density indicators for each disc height (stage 1)

From the scatterplot, *RD*, *MnD* and *MxD* were correlated with *CA* (not shown) and *RW* (Figure 5-1 to Figure 5-3). The linear mixed effects models as a function of *CA* and *RW* for each disc height were therefore established (Table 5-2). Different mathematical forms of *CA* and *RW* were detected, generally, *RD* and *MxD* were found to have a significant positive correlation with *RW* in the lower stem (M1-M4) whereas a significant negative correlation at higher stem locations (M5-M6) was found for *MnD* and *MxD*. *RD* and *MnD* were negatively related to *RW* at all disc heights while *MxD* was positively correlated with *RW*. In total, 18 models were established for de-trending the non-climatic effects (*CA* and *RW*), the corresponding RMSE, mean percentage error and mean absolute percentage error, which are shown in Table 5-2. The *RD*, *MnD* and *MxD* chronologies were therefore established from the residuals based on the fixed-effects of these models in stage 1.

**Table 5-2 Coefficients and associated SEs for ring density, minimum ring density, and maximum ring density at different disc heights, and error statistics of these models**

| | | | **Parameter estimations** | | | | | | **Error statistics** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Disc | Formulas | $b_0$ Value (S.E.) | $b_1$ Value (S.E.) | b2 Value (S.E.) | b3 Value (S.E.) | b4 Value (S.E.) | b5 Value (S.E.) | RMSE | E% | \|E\|% |
| **RD** | M1 | $RD = b_0 + \frac{b_3}{\sqrt{RW}} + \frac{b_5}{1+\sqrt{CA}}$ | 574.5***<br>(16.26) | | | 32.1***<br>(5.96) | | -845.3***<br>(96.71) | 38.24 | -0.06 | 5.84 |
| | M2 | $RD = b_0 + \frac{b_1}{1+\sqrt{RW}} + \frac{b_5}{1+\sqrt{CA}}$ | 522.3***<br>(23.94) | 91.1**<br>(29.77) | | | | -487.5***<br>(85.03) | 36.37 | -0.04 | 5.38 |
| | M3 | $RD = b_0 + \frac{b_3}{\sqrt{RW}} + \frac{b_5}{1+\sqrt{CA}}$ | 520.4***<br>(12.50) | | | 18.8***<br>(4.60) | | -337.0***<br>(59.44) | 31.72 | -0.02 | 5.07 |
| | M4 | $RD = b_0 + b4 \cdot \sqrt{RW} + \frac{b_5}{1+\sqrt{CA}}$ | 530.4***<br>(11.58) | | | | 21.7**<br>(7.85) | -420.1***<br>(73.12) | 32.09 | -0.01 | 5.08 |
| | M5 | $RD = b_0 + b4 \cdot \sqrt{RW}$ | 469.8***<br>(10.51) | | | | 26.5**<br>(8.14) | | 32.18 | -0.02 | 5.03 |
| | M6 | $RD = b_0 + \frac{b_2}{RW} + b4 \cdot \sqrt{RW}$ | 397.4***<br>(18.61) | | 13.5**<br>(3.19) | | 73.0***<br>(4.81) | | 31.80 | -0.07 | 4.90 |
| **MnD** | M1 | $MnD = b_0 + \frac{b_1}{1+\sqrt{RW}} + \frac{b_3}{\sqrt{RW}}$ | 323.2***<br>(26.21) | -210.5*<br>(86.94) | | 134.3***<br>(18.25) | | | 29.92 | -0.04 | 5.86 |
| | M2 | $MnD = b_0 + \frac{b_3}{\sqrt{RW}}$ | 279.5***<br>(8.25) | | | 77.7***<br>(4.83) | | | 31.67 | -0.04 | 5.92 |
| | M3 | $MnD = b_0 + \frac{b_2}{RW}$ | 319.8***<br>(6.06) | | 29.3***<br>(1.28) | | | | 26.72 | -0.03 | 5.32 |
| | M4 | $MnD = b_0 + \frac{b_2}{RW}$ | 329.8***<br>(4.96) | | 22.7***<br>(1.51) | | | | 26.90 | -0.02 | 5.33 |
| | M5 | $MnD = b_0 + \frac{b_2}{RW} + \frac{b_5}{1+\sqrt{CA}}$ | 275.1***<br>(16.09) | | 23.8***<br>(2.09) | | | 405.1***<br>(101.13) | 30.68 | -0.08 | 5.58 |
| | M6 | $MnD = b_0 + \frac{b_2}{RW} + \frac{b_5}{1+\sqrt{CA}}$ | 253.0***<br>(15.62) | | 25.2***<br>(2.41) | | | 487.5***<br>(82.78) | 28.34 | -0.05 | 5.29 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **MxD** | M1 | $MxD = b_0 + \frac{b_1}{1+\sqrt{RW}} + \frac{b_5}{1+\sqrt{CA}}$ | 1267.8***<br>(35.88) | -605.7***<br>(45.88) | | | | -1485.3***<br>(148.26) | 60.45 | -0.04 | 6.33 |
| | M2 | $MxD = b_0 + \frac{b_3}{\sqrt{RW}} + \frac{b_5}{1+\sqrt{CA}}$ | 1034.1***<br>(28.33) | | | -132.0***<br>(10.71) | | -815.1***<br>(147.00) | 64.42 | -0.02 | 6.54 |
| | M3 | $MxD = b_0 + \frac{b_3}{\sqrt{RW}} + \frac{b_5}{1+\sqrt{CA}}$ | 994.7***<br>(24.30) | | | -150.4***<br>(9.19) | | -402.5**<br>(121.71) | 62.72 | -0.04 | 6.53 |
| | M4 | $MxD = b_0 + \frac{b_3}{\sqrt{RW}} + \frac{b_5}{1+\sqrt{CA}}$ | 1031.0***<br>(28.99) | | | -176.4***<br>(10.82) | | -497.2***<br>(141.39) | 62.77 | -0.02 | 6.67 |
| | M5 | $MxD = b_0 + \frac{b_3}{\sqrt{RW}} + \frac{b_5}{1+\sqrt{CA}}$ | 900.7***<br>(35.02) | | | -171.8***<br>(12.97) | | 375.3*<br>(176.06) | 64.90 | -0.04 | 6.78 |
| | M6 | $MxD = b_0 + \frac{b_1}{1+\sqrt{RW}} + \frac{b_5}{1+\sqrt{CA}}$ | 1071.8***<br>(59.00) | -818.7***<br>(76.44) | | | | 712.8**<br>(211.41) | 64.86 | -0.01 | 6.91 |

Note: *** p value < 0.001; ** p value < 0.01; * p value < 0.05; RMSE, ME%, and |ME|% which represent root mean square error, mean percentage error and mean absolute percentage error, respectively.

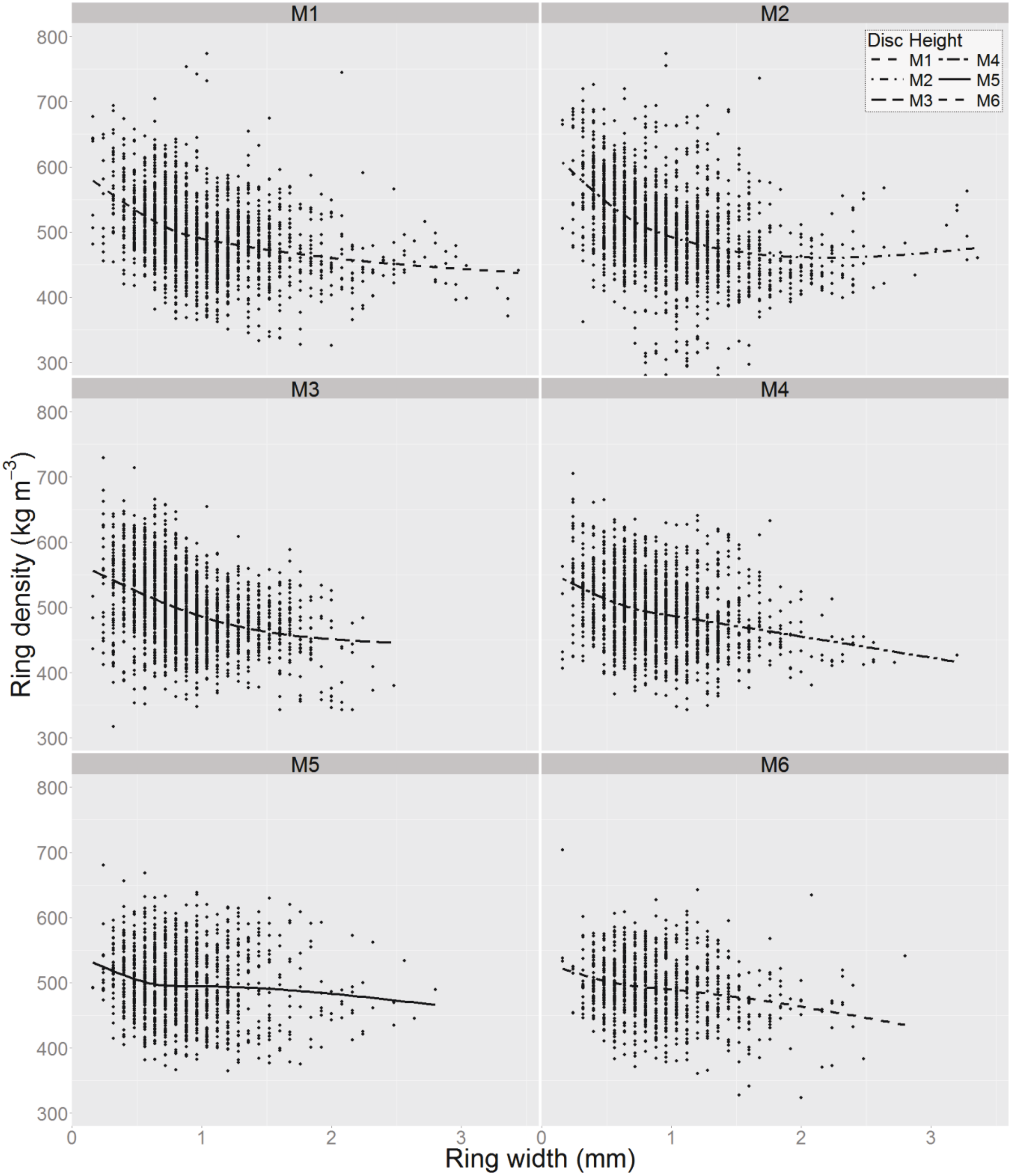

**Figure 5-1 Ring density against ring width at each disc height (M1-M6)**

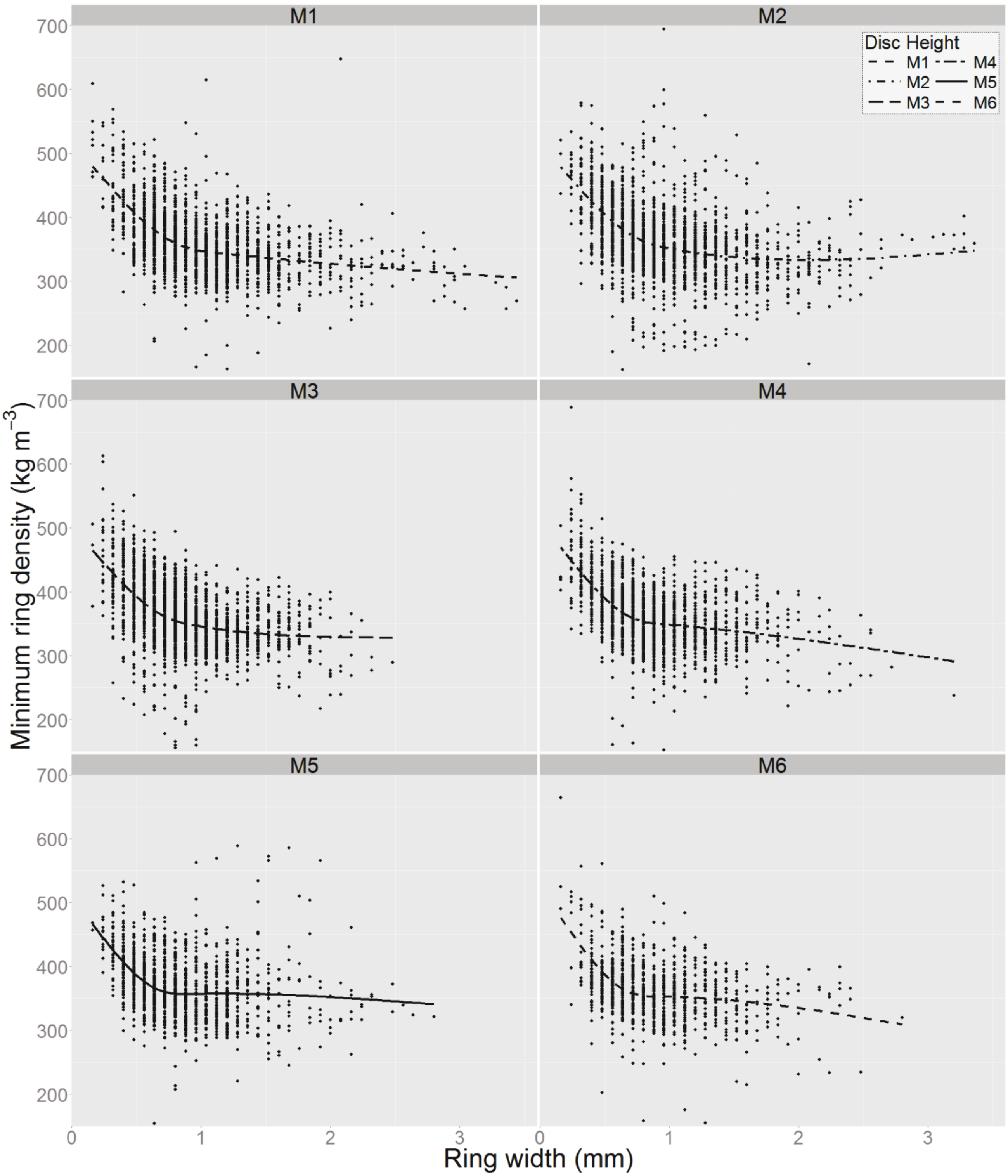

**Figure 5-2 Minimum ring density against ring width at each disc height (M1-M6)**

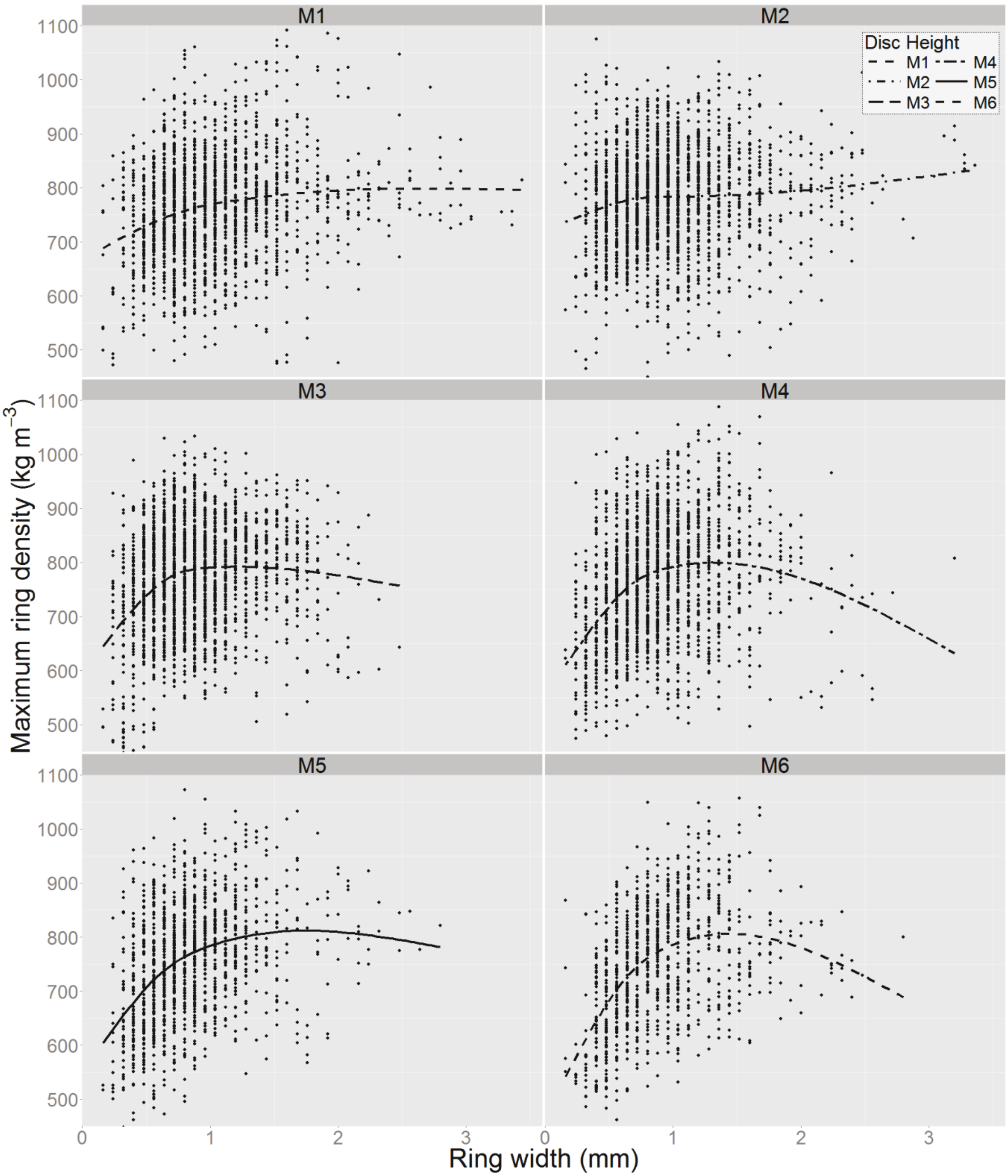

Figure 5-3 Maximum ring density against ring width at each disc height (M1-M6)

### 5.4.2 Effect of climatic variables on the density indicators for each disc height (stage 2)

The chronologies mentioned above were used to plot against monthly climatic variables, i.e. mean monthly temperature (Figure 5-4) and precipitation (Figure 5-5). Response of *MnD* sequence to temperature were found to be positively significant early in the growth season (April and May) for all discs but less temperature sensitivity was shown from lower discs compare to higher discs. A significant negative relationship was found late in the growth season i.e. only highest disc M6 in June and most discs from July to October. Additionally, many of the higher discs were negatively correlated with winter temperature (previous October to current February), however, a positive relationship was found at lower discs for the previous September. Moreover, the temperature of the previous February, May and June were found to be influential factors on *MnD*.

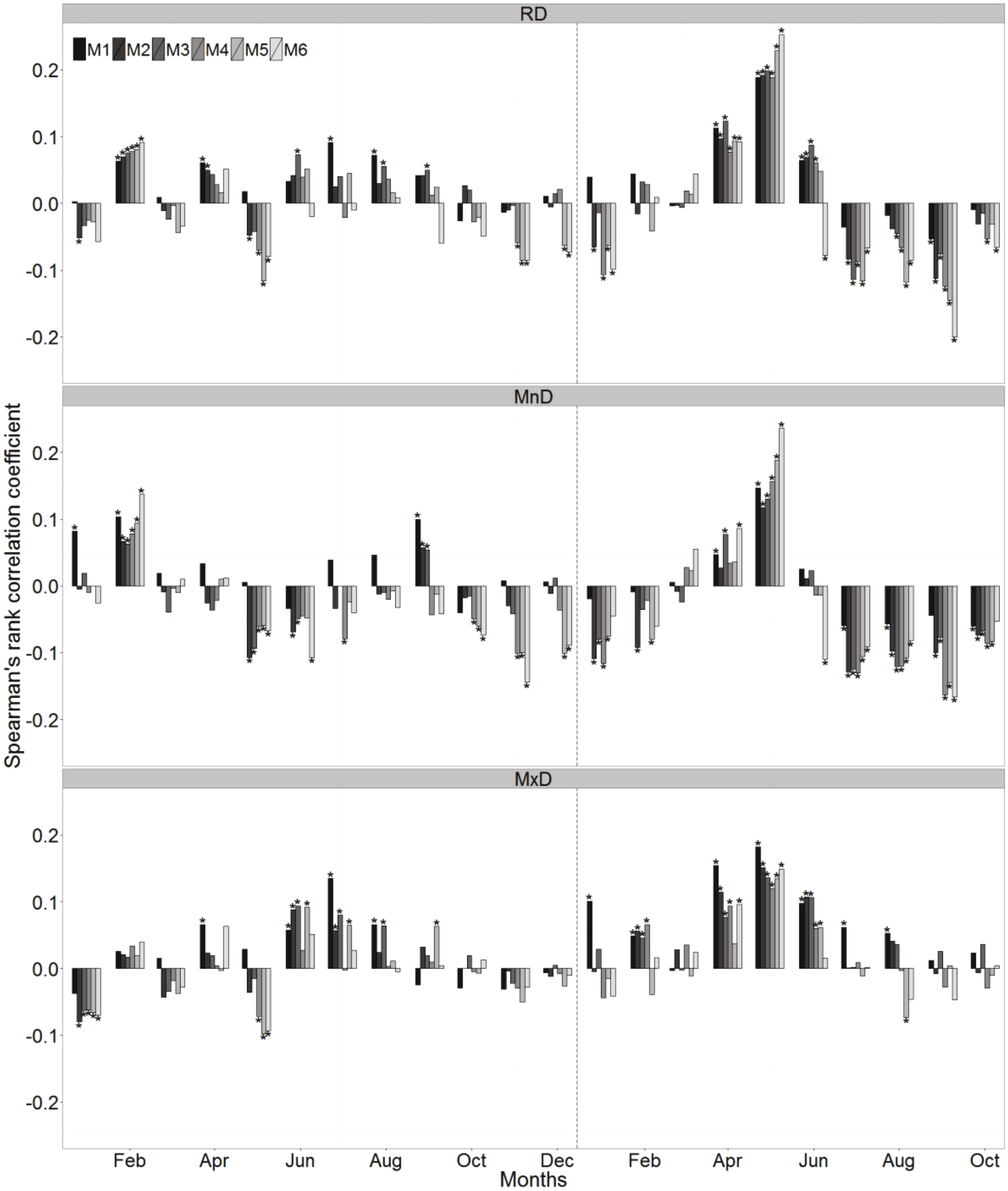

**Figure 5-4 Correlation coefficients between standardized average ring density, standardized minimum ring density, and standardized maximum ring density and monthly mean temperatures from January of the previous year to October of the current year. Note: * indicate correlation coefficient is significant (p < 0.05)**

*MnD* was found to be negatively correlated with precipitation in May and June and positively correlated in September for all discs; the higher discs showed slightly higher precipitation sensitivity in general though (Figure 5-5). The top disc M6 in March and bottom disc M1 in April were found to be negatively correlated to *MnD*. In addition, the *MnD* from lower discs (M1-M3) were negatively correlated with winter precipitation from the previous November to current January but positively correlated with precipitation in February in the higher discs (M4-M6). The significant effects of precipitation from the previous January to previous July were identified at various disc heights.

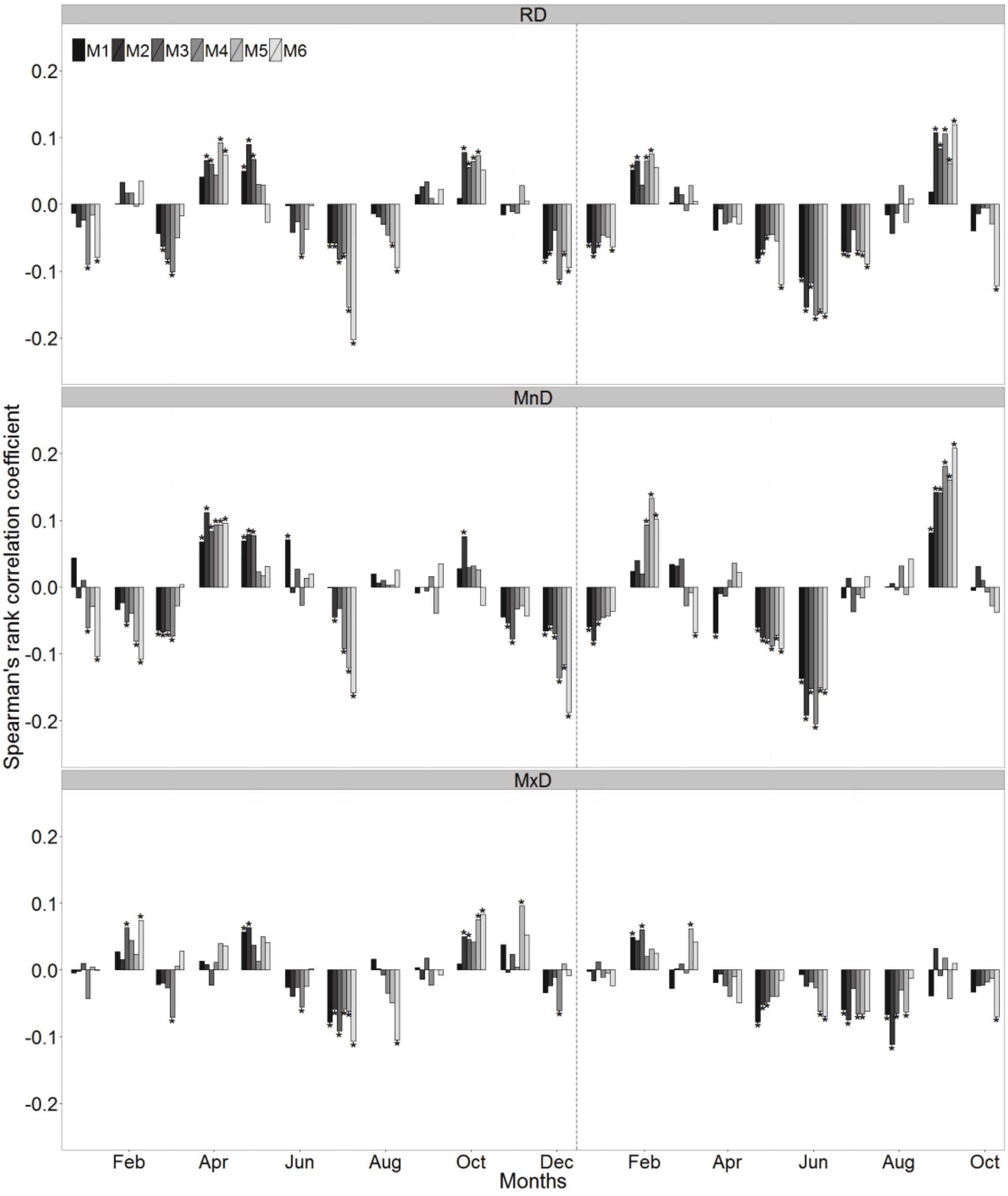

Figure 5-5 Correlation coefficients between standardized average ring density, standardized minimum ring density, and standardized maximum ring density and monthly precipitation from January of the previous year to October of the current year. Note: * indicate correlation coefficient is significant ($p < 0.05$)

For correlations between *MxD* and temperature (Figure 5-4) during the growth season, significant positive correlations were found early in the growth season (April to June) for most discs, a relatively high temperature sensitivity was found in lower discs; and significant positive correlations were displayed in July and August for disc M1, but an opposite negative relationship was found in August for M5. Additionally, *MxD* was positively related to winter temperature i.e. January for M1 and February for M1-M4. In addition, *MxD* was significantly correlated with temperature from the previous growth season, more specifically, *MxD* was negatively related to the previous May at higher discs (M4-M6) and positively correlated with the previous June, July and August at lower disc heights. Furthermore, expect disc M1, *MxD* value was also found to be negatively related to temperature in the previous January.

Figure 5-5 also displays correlations between *MxD* and precipitation. A negative relationship was found between *MxD* and precipitation during the growth season (May-August). However, different significances were displayed for each disc height, where negative correlations were significant mostly in the lower discs in May, July and August while in June there was significance at M5-M6, July at M4-M5; August at M5 along with October at M6. Additionally, significant effects of precipitation in winter were found (positively in October for M2-M6 and November for M5 and February for M1-M3, negatively in December for M4). The significant effects of precipitation were also found from the previous February to August except April at various disc heights.

## 5.5 Discussion

To compare the difference in density-climate relationships along the stem is an essential requirement to elucidate if density-climate patterns at breast height can be treated as representative of the annual carbon allocation and its associated variation in the whole stem (Bouriaud *et al.,* 2005a; Kerhoulas and Kane, 2012). In the present study, the density-climate relationships among disc heights displayed different strength and the direction of the sensitivity of annual density indicators to the monthly temperature and precipitation in the mature wood of old-growth black spruce. These results could assist researchers to further our understanding of carbon allocation within trees.

### 5.5.1 Effect of cambial age and ring width on density indicators

For the sampled dominant and co-dominant trees, at lower disc heights, the positive relationship between *MxD* and *CA* was inconsistent with the results presented by Jyske *et al*. (2008); and an insignificant ageing effect on *MnD* was also displayed by Franceschini *et al*. (2013). The negative relationship between *MnD*, *MxD* and aging at higher discs could be explained by the potential decline close to the bark as described by Xiang *et al.* (2013).

Additionally, the negative relationship between ring width and *RD* was confirmed in many previous studies based on samples from breast height (Koubaa *et al*., 2000, Mäkinen *et al*., 2007) and other heights within mature wood (Alteyrac *et al.,* 2005; Xiang *et al.,* 2013). In addition, a negative relationship was observed between *MnD* and *RW* (Schweingruber *et al*., 1993, Mäkinen *et al*., 2002). Moreover, since *RW* and *MxD* were both positively related to the summer temperature (D'Arrigo *et al*., 1992, Briffa *et al*., 1998), the positive relationship between *RW* and *MxD* would be observed (Gindl *et al*., 2000). Compared to the relationship between *RW* and density indicators at breast height, a similar relationship within mature wood can therefore be extrapolated for other disc heights in black spruce (Alteyrac *et al*., 2005; Xiang *et al.,* 2013).

### 5.5.2 Effect of climatic variables on *MnD* and *MxD*

*RD* correlated with *MnD* strongly (0.78) and *MxD* moderately (0.51). In the current study, we therefore are only going to present the significant variables for *MnD* and *MxD*.

The positive relationship between *MnD* and average temperature in the early growth season (May-June) was found to be related to the auxin-driven onset of cambial activity (Schrader *et al*., 2003; Rossi *et al*., 2008) suggesting that the higher minimum temperature resulted in a higher *MnD* (Schweingruber *et al*., 1993; Xiang *et al.,* 2013b). Additionally, the negative relationship between *MnD* and climate in the later part of the growth season (temperature: July-October;

precipitation: September) is in accordance with Franceschini *et al.* (2013), who suggested this finding is a result of an extended maturation of earlywood tracheids. Moreover, through turgor pressure (Ryan *et al*., 1994), the decreased vapor pressure deficit might be modified by elevated precipitation in May and June and lower May temperatures lead to a higher *MnD*.

A negative effect of temperature and precipitation in winter was also found for *MnD*. This has been suggested to be related to the following in a previous study by Xiang *et al.* (2013) (i) increased photosynthetic capacity and accumulation (Grace and Norton, 1990); (ii) hydraulic efficiency due to winter xylem embolisms (Pederson *et al*., 2004); and (iii) earlier initiation of cambial activity resulting from warmer winters associated with less snowpack (Goldblum and Rigg, 2005).

*MxD* was positively related to summer temperatures, which has been presented in the literature for black spruce previously (Wang *et al*., 2002). The positive effect of warmer temperatures (April-June) early in the growth season could lead to accelerated growth of new needles and higher photosynthetic accumulation in the crown (Körner, 1998; Grace *et al*., 2002). Both would result in more available photosynthate utilized during the secondary wall thickening phase (Fritts, 1976). Moreover, a negative effect of precipitation on *MxD* was identified throughout almost all of the growth season (May-August). This could be explained by high transpiration water loss and a corresponding low soil water reserve (Ryan *et al*., 1994; Yasue *et al.,* 1997), which is also in accordance with the results that drought leads to an enhanced secondary cell wall thickening of latewood (Splechtna *et al*., 2000; Jyske *et al*., 2010).

### 5.5.3 Density-climate relationships vary according to disc heights

In general, the density-climate relationships among different disc heights are similar during the growth season (van der Maaten-Theunissen and Bouriaud, 2012). However, the strength of the sensitivity differed not only with carbon allocation (i.e. top-down time lag effect) (Fritts, 1976;

Chhin *et al*., 2008, 2010), but also with the hydraulic effect according to different heights (Ryan and Yoder, 1997).

The strength of the sensitivity between *MnD* and temperature early in the growth season (April and May) consistently increased with height. Such an increased sensitivity with height during the early growth season indicates a time lag due to basipetal distribution of auxins within stem during the onset of cambial activity (Larson, 2001; Rossi *et al*., 2008). During the cell enlargement phase, only the top disc (M6) showed a significant correlation between *MnD* and temperature in June associated with the general elevated sensitivity with height to the precipitation in May and June, which likely resulted from hydraulic limitations due to the distance between the disc and the ground and gravitational effects (Ryan and Yoder, 1997; Koch *et al.,* 2004). During the late part of the growth season, the relationship between *MnD* and temperature are higher at the mid stem disc than both the top and bottom discs. This observation suggests differences in maturation of earlywood tracheids among discs could be interpreted as (i) the top-down allocation of newly fixed carbon is rendered less sensitive at higher discs (Fritts, 1976; Kozlowski, 1997; Kerhoulas and Kane, 2012); and (ii) a growth irregularity (Schweingruber *et al*., 1990b) and growth ring anomalies (Schweingruber, 1996) near the bottom regions of the tree would weaken the sensitivity to temperature. The increased sensitivity with height of *MnD* to both temperature and precipitation in September suggests hydraulic effects could be important at this stage.

The sensitivity of *MxD* was observed to be positively affected by temperature early in the growth season and *MxD* sensitivities were higher on average in lower discs than in higher discs. It is reasonable to expect that top-down carbon allocation and upward progression of latewood formation (Larson, 2001) might increase climate sensitivity to temperature in the lower discs compared to upper discs. Additionally the significant positive effect of temperature in July and August at the base disc (M1) could be a result of the time lag effect of top-down carbon allocation. Interestingly, the opposite effect of temperature in August was found in higher discs. This might be linked with greater respiration rates exceeding photosynthesis under high temperatures

(Martín-Benito *et al*., 2008) and reduced resource availability at the end of the growth season (Gower *et al.,* 1995), especially in the more vigorous growth regions found in the higher disc locations (Damesin *et al*., 2001).

The carry-over effects of precipitation and temperature before the growth season displayed moderate differences among disc heights. This result was likely explained by the accumulation of carbohydrates from the previous growth season as an important factor affecting growth in the following season (Fritts, 1976; Grace and Norton, 1990; Wimmer and Grabner, 2000; Chhin *et al.,* 2008). In the present study, the higher temperatures during winter likely resulted in lower *MnD* at higher stem locations. Minimal loss of needles in warmer winters (Grace and Norton, 1990) would render more available photosynthate in the following growth season for the higher discs, eventually increasing the growth rate of earlywood thus lower *MnD*. However this phenomenon might not be enough for the lower portions of the stem and latewood development (i.e. no effect on *MxD*). In addition, a negative correlation between *MnD* and the previous winters precipitation was pronounced at lower discs (significant only for previous December at higher discs), however it was positively related to precipitation in February for the higher discs. This might associated with deep snowpack in the winter, which would lead to delayed cambial reactivation in the spring (Goldblum and Rigg, 2005) and could possibly lead to a shortened duration of earlywood cell thickening, however this hypothesis requires further research to have it applied to all disc heights. For the rest of the carry-over effects, there is no obvious difference among disc heights, which indicates this effect is more at a tree level than individual disc level. Similar results were described in a previous study (Xiang *et al.,* 2013b).

## 5.6 Conclusions

Our study indicated direction similar but strength different sensitivity to climatic among disc heights for selected density indicators (i.e. *MnD* and *MxD*) of black spruce in the natural boreal forest. Nevertheless, it was confirmed that it need to be validated using density-climate relationship at breast height as a representative for other stem position as both radial density patterns and sensitivity to climate were different between stems.

For this case study, in general, the various climatic sensitivities were appeared in both density indicators, which were explained by the height related factors such as, auxin and carbon distribution, hydraulic effects and respiration rate. However, these factors are play different role for each density indicators during the growing season, therefore, the general pattern of the sensitivity to climate for both density indicators were hard to be concluded.

The present results can contribute towards our furthering our understanding of density indicators in respond to climate along the stem. This also has implications to understand carbon allocation along the stem where density has traditionally been treated as a constant value.

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# Chapter 6 CONCLUSIONS AND FUTURE WORKS

## 6.1 Conclusions

The modelling process is an efficient method to handle the interactive sources relating to wood density, allowing us to further our understanding of separating these interrelated effects, as well possibly helping to predict density trends under the influence of detected sources avoiding costly and sometimes impractical direct measurements. In the present study, we have tried to provide informative data on aspects of wood density characteristics (e.g. *RD*, *MnD*, *MxD*), whereas some detailed knowledge is still lacking a comprehensive explanation for the variation of wood density is due mainly to differing patterns of wood formation resulting from genetic and environmental sources.

A series of conclusions can be extracted from the current work:

1. The first work piece established a two-stage modelling approach as ring level, which separated the interrelated effects of cambial age, growth rate and height along the stem on *RD*. A small amount of site effects along with prominent tree effects were identified in the data-set. Importantly, declining trends in *RD* near the bark were observed and occur in old and slow-growing trees, which were hypothesised to be correlated with a decrease in tree vigour over the trees life. Therefore, the observed decline leads to some potential implications for (1) forest management as silvicultural interventions (e.g. commercial thinning) could reduce the effects of the decline by maintaining vigorous growth; and (2) aboveground biomass estimations could be overestimated for the old growth black spruce forest when density is introduced as a constant value in allometric equations.
2. In addition, the sources of variation of wood density were conducted by considering biotic factors (cambial age, growth rate, and disc height). On the other hand, wood density of conifers is a macroscopic representation of the wood anatomical characteristics, which were under climatic influence affecting cambial activity. Therefore, the

correlations between wood density indicators (i.e. *RD*, *MnD*, and *MxD*) and potential climatic determinisms were examined. Moreover, the density-climate relationships could be different among different dominance levels as cambial activity was affected by the variation of thermal stress and transpiration among dominance levels. Our study identified different climatic sensitivities related to dominance levels for selected density indicators of black spruce in the boreal forest.

3. Furthermore, for a better understanding of biomass allocation within the tree, more accurate estimations of the density-climate relationship along the stem was required to get a more reliable estimation on annual biomass increment. This various climatic sensitivity of the density indicators affected by disc height was hypothesised to be associated with auxin and carbon distribution, hydraulic effects and respiration rate. It was also confirmed that radial density patterns at breast height cannot be used as a robust representative as both radial density patterns and associated climate sensitivity were different between stems.

## 6.2 Future work

The above work provides informative knowledge to disentangle the confounding sources and clarifies the density-climate relationships among dominance levels and along the stem. However, there are still several sources that are not fully understood. In order to help us to get a better understanding of the relationship between wood physiological processes and wood density, more effort needs to be made in future as suggested below:

1. The declining trend of *RD* close to the bark was dectected in the main stem. Furture studies should be conducted to investigate the possible impacts of this phenomenon on carbon allocation to other parts of the tree.

2. Silvicultural practices were found to be significantly correlated with variation of wood density. Furture studies should foucus on intra-tree wood density variation under the influence of silvicultural practices (e.g. relased growth).
3. The present work on density-climate relationships were established at given cambial ages (25-60) to minimize the effect of cambial age, which suggests these relationships may be specific to this certain period of growth and this relationships might not be applicable in a long historical scope particularly in the context of recent global warming. The relationships should be validated by using the data with wider time frames.
4. Although the density-climate relationships were relatively weak compare to the growth-climate relationship, it can not justfy the breast height of the dominant trees to serve as a robust representative. Our results provide a feasible way to approach more accurate estimation of stem biomass increment, e.g. a new ‘constant’ density value could be calculated from our model and introduced in the allometric equation, however, more works were need to make it could be practically applied.