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Improving branch distribution models in trees using X-ray computed tomography

Emmanuel Duchateau[1*], **David Auty**[1], **Frédéric Mothe**[2] and **Alexis Achim**[1]
[1]*Faculté de foresterie, géographie et géomatiques, Université Laval, 2405 rue de la Terrasse, Québec G1V 0A6, QC, Canada*
[2]*INRA, UMR1092 LERFoB, 54280 Champenoux, France*
**correspondence:* emmanuel.duchateau.1@ulaval.ca

Highlights: The use of external measurements to describe the distribution of branches on tree stems can induce imprecision and bias in estimates of both the number of annual growth units and the azimuthal distribution of branches. The scanning of logs using X-ray computed tomography yielded knot data that enabled more accurate identification of the limits of each growth unit. Such information, in conjunction with current models of tree architecture, can be incorporated into functional-structural models describing relationships between tree morphology and biological processes.

Keywords: X-ray computed tomography, tree architecture, black spruce, branch distribution

INTRODUCTION

Computer-based systems capable of simulating the 3D structure of plants, their metabolic processes and environmental interactions are increasingly being developed to increase our understanding of how plant architecture and biological processes interact (Fourcaud et al. 2008). In trees, such functional-structural models can be useful tools for understanding and predicting important wood quality attributes such as branch morphology and distribution. An underlying principle of these models is that plant structure can be described in terms of a hierarchical system of replicating 'architectural units' (Barthélémy et al. 1989). In temperate tree species, the 'growth unit' (GU) i.e. the annual elongation of the terminal shoot from the apical meristem (De Reffye et al. 1995), is the single most important component of existing branch distribution models (e.g. Colin and Houllier 1991).

Such models are normally parameterized using data from external measurements. This has the advantage that data collection is relatively straightforward and can be accomplished with limited equipment. However, this simplicity may come at the expense of accuracy for certain measurements, such as branch inclination and azimuthal orientation. More recently, X-ray computed tomography techniques have been developed that can generate high-precision internal information, which could lead to improved model accuracy.

Black spruce (*Picea mariana* (Mill.) BSP) is the dominant conifer in the North American boreal forest. It develops according to Rauh's model of monopodial, rhythmic growth and attains its final developmental stage after 10-15 years (Bégin and Filion, 1999). After this, the basic structure of first and second order axes (trunk and branches, respectively) and third and fourth order axes (twigs) is duplicated through a process known as reiteration. The high reiterative capacity of black spruce accounts for its characteristically high phenotypic plasticity. This leads to a complex and apparently disorganised branching structure that complicates the development of functional-structural models, since the precise delineation of annual growth units can be difficult. The objectives of this study were: 1) to develop a method based on selective filters to locate annual growth units on black spruce logs using data derived from X-ray computed tomography and 2) to examine the distribution of branches around black spruce stems at the stem and growth unit levels.

MATERIALS AND METHODS

Measurements were taken on 33 black spruce trees from unmanaged stands in Québec, Canada. First, branch and tree characteristics were recorded following the protocol established by Colin and Houllier (1991). Sample trees were then cut into successive 2.5 m logs for X-ray scanning. Each of the resulting 107 logs were scanned at 2 mm intervals along the longitudinal axis with a 2-mm-wide X-ray beam, so that the scanned segments were contiguous. This provided accurate internal profiles for 23,040 knots (Duchateau et al. 2013).

The total number of growth units in each 2.5-m section was determined from the difference in the number of annual growth rings between discs cut from each end of the log. However, the precise limits of each annual shoot were difficult to determine, even using the X-ray data (Fig. 1). We developed an empirical method based on two filters to select the most likely location of the limits of each GU, which should correspond to the location of nodal branches produced from subterminal buds. First, the basal area of each branch (i.e. cross-sectional surface at the bark) was calculated and summed when branches originated from the same point at the stem's pith. We then applied a series of thresholds to select basal area peaks along the main stem. Secondly, we tested thresholds of minimum GU lengths, as some of the identified peaks occurred in close proximity, presumably as a result of reiteration (Bégin and Filion, 1999). Once each GU was located, we analyzed the circular branch distribution at the scale of both the tree and the growth unit. This was carried out using circular statistics and a Rayleigh test (Jammalamadaka and Sengupta 2001).

RESULTS AND DISCUSSION

The number of GUs along the stem was significantly underestimated when only external branch measurements were used. On average, the underestimation was 2.4 GUs per 2.5-m log (SD=3.7), or around 15% of the total. For a mature tree, this would represent approximately 16 GUs, which is unsatisfactory for the development of accurate models. One possible explanation is that black spruce contains a relatively large number of branches along each growth unit, but the diameter ranges of nodal (terminal) and internodal (median) branches overlap, so the delineation of GUs based on branch basal area might be problematic.

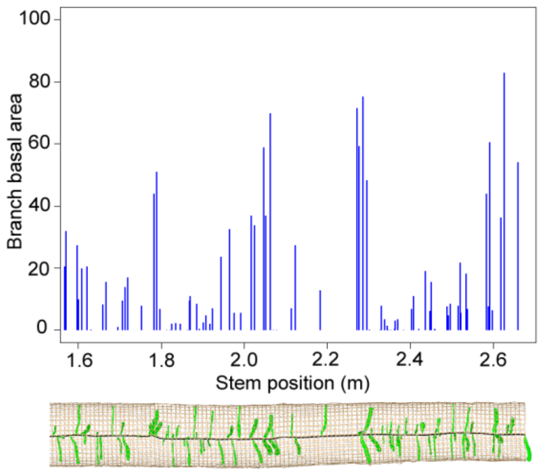

Fig. 1. Distribution of branch basal area along the stem from data extracted using the ImageJ Java plug-in 'Gourmand'.

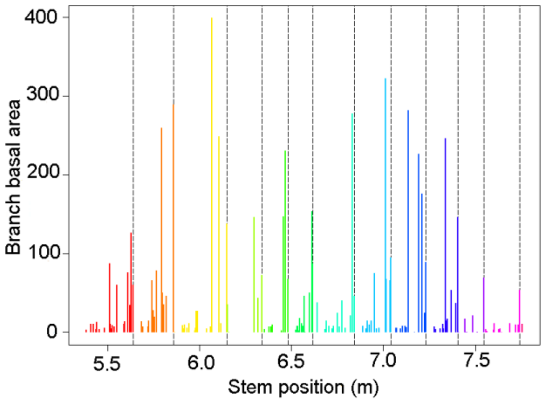

Fig. 2. Distribution of the branch basal areas along the stem and delineation of the separate growth units using our two-filter method.

For the identification of GUs using internal data, best results were obtained when 1) a GU limit was placed when the sum of branch basal areas initiating from the same point was above the 75th percentile for all branch initiation points within the log and 2) the next limit was located at a minimum distance of 7.5 cm along the main stem (Fig. 2). The utilization of the CT images coupled with this two-step method allowed us to significantly increase the accuracy of GU identification. The resulting mean bias in the number of GUs per log approached 0 (0.195). This represented a significant improvement compared to external assessment, although some variation remained (SD=2.8). The ability to identify branch initiation points at the pith of the main stem therefore allowed us to differentiate between nodal and internodal branches more accurately.

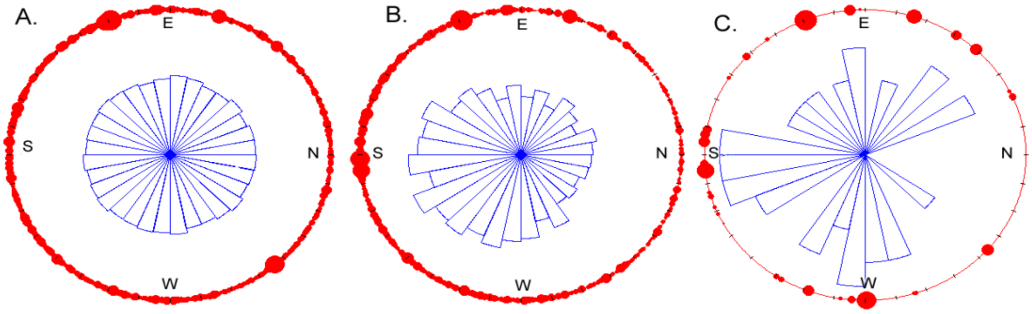

Fig.3. Distribution of branches around the stem by diameter (in red) and by number (in blue) for A) all branches, B) the largest diameter branch per GU and C) the largest diameter branch per tree.

Once we had obtained the best GU selection, we studied the circular distribution of the branches at the tree and the GU levels. For all branches on one tree, the distribution was uniform (Fig. 3A). However, the largest branch per GU had a preferential orientation of 194° (SD = 65°) and the distribution was non-uniform for 18 out of 33 sample trees (Fig 3B). The largest diameter branch in each tree had a similar mean orientation of 200° (Fig 3C). Future work will focus on 1) the influence of inter-tree competition on branch distribution around the stem, 2) testing the applicability of the two-filter method to other species and growing conditions, and 3) increasing data processing speed using automated knot detection and measurement algorithms (Longuetaud et al. 2012).

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