Relative branch size in branch clusters modelled through a Markovian process

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ABSTRACT

Information on tree canopy architecture is crucial in forestry practice because the quality and price of standing trees and final logs directly depend on it. Simultaneously, accurate empirical or functional–structural models require information based on field observations. *Pinus radiata* is a polycyclic species that follows an acrotony law when forming a new branch cluster, showing smaller branches in its base and larger ones at the top of a forming cluster. The objective of this study was to describe the acrotony of the branches in a branch cluster as a Markov chain. Markov chains represent stochastic processes in discrete time that undergo a transition from one state to another among a finite number of possible states. The probability of transition from state i to a state j depends only on the current state, i. For modelling acrotony, the relative vigour (expressed as relative branch diameter in relation to the largest one) of each branch was selected as the stochastic variable and the states corresponded to five possible relative size ranges.

The branches observed within a *P. radiata* cluster were ordered following their relative sizes (from largest to smallest), and Markovian transition matrixes were calculated for each branch cluster (whorls of 3–12 branches). The transition matrixes were defined as the probabilities of one branch being followed by an equal-sized or smaller branch when observing the cluster from the top down. The obtained Markov chain matrixes were used in a stochastic data simulation, which was validated with an independent dataset. The presented matrixes can be incorporated into traditional simulation models or functional–structural models. The validation results show that the proposed methodology accurately reflects the variability of the branch sizes in a cluster, and we suggest its application to other species that display a clustered organisation of branches.

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1. Introduction

The value of the wood as a raw material is affected by its quantity as well as it quality. While the quantity is a relatively easy parameter to measure, quality is more difficult (e.g., it changes depending on the industry). So it is important to study the tree raw material, on one hand by the stem diameter/volume and on the other hand by the potential quality of sawn timber (e.g., branch characteristics and knot locations, sizes and numbers). The quality and price of standing trees and final logs directly depend on tree structures. Thus, information on the architecture of the canopy, i.e., on branch numbers, sizes and positions, is crucial in forestry practice because

branches become knots, which are internal defects of the wood that directly decrease the mechanical properties of it, as well as aesthetic aspects of the final products. Therefore the capacity to predict the quality and value of forest products is necessary to improve the wood supply chain. For instance, there are several studies (e.g., Grace et al., 1998; Todoroki et al., 2001) that consider the diameter of the largest branch in a cluster to be an important parameter to take into account when referring to wood quality.

The architecture of a plant depends on the nature and relative placement of each of its parts, which at any given time arises from the balance between the expression of the endogenous growth process and exogenous constraints conferred by the environment. The concept of a balanced structural component for predicting growth allocation in the structures of trees has been widely studied (e.g., Mäkelä et al., 2002; Mäkelä, 2012). Thus, the objective of the architectural analysis of a tree is, in general, to identify these endogenous processes through observation (Barthélémy, 2003; Barthélémy and

Caraglio, 2007). Within this context, modelling of tree knots based on branch data is an important aspect.

Tree and wood modelling involves increasing quality parameters to support forestry decision-making systems related to the quantity and quality of products. For these purposes, functional-structural models, which require information based on observed allometric relationships are useful. Modelling of forest tree allometry has many applications, from understanding physiological relationships (e.g., the allometry between sapwood and leaf area, Monserud and Marshall, 1999) to building empirical equations to calculate one component of a tree by measuring another (e.g., determining above-ground biomass from crown length, Kantola and Mäkelä, 2006). As the canopy represents the centre of photosynthesis and biomass production in a tree, obtaining a deeper understanding of its organisation is of particular interest in highly productive forest species, such as *Pinus radiata* D. Don. In the last decades, wood quality modelling based on tree development processes and crown architecture has increased. For instance, Mäkelä and Mäkinen (2003) presented a process-based tree and stand growth model to predict the stem structure with a 3D geometry and its internal knots, in Scots pine (*Pinus sylvestris* L.). In this study, statistical models were used to create individual branch information from the vertical profile of branch basal area. Ikonen et al. (2003) also demonstrated how Scots pine tree stem properties were linked to the properties of sawn timber. Particularly they concentrated on branch growth and distribution in the crown (and the corresponding knottiness of the sawn wood) and the influence of local light conditions on their attained size. Kantola et al. (2007) adapted an existing process-based growth model, PipeQual, to Norway spruce (*Picea abies* [L.] Karst.); it describes stand development and timber properties (stem taper, heartwood formation and branchiness). The model includes a branch module that calculates the annual dynamics of individual branches and their properties in each whorl. All calculations in the branch module are based on empirical, stochastic models that use tree and whorl level variables as input. Following the same research line, Lyhykäinen et al. (2009) developed models for estimating yields of lumber grades and by-products of individual Scots pine trees using stem and crown dimensions as explanatory variables. The model uses a data set simulated by a process-based growth model, which provides information about stem form and branch properties. The simulated stems are sawn using the WoodCim sawing simulator that grades the individual sawn pieces, as well as by-products. For other conifers as Douglas fir (*Pseudotsuga menziesii*) Hein et al. (2008) modelled branch number, diameter of the thickest branch and the relative branch diameter in the cluster, using non-linear models. As independent variables they used site index, relative height of the cluster, height diameter ratio and tree diameter at breast height among others. Weiskittel et al. (2010) modelled the number of branches/m of crown, maximum branch diameter in the crown and relative distribution of branch size within the crown for five conifers. Particularly, this study highlighted the range of variability in key crown structural attributes.

P. radiata is the main species involved in forestry industry in Australia, Chile and New Zealand. The industrial and economic importance of this species in the last 30 years has stimulated intensive studies aimed at improving the productivity and the quality of its wood. Within a growing season, *P. radiata* species may produce one growth unit per year on the main stem or multiple units in a polycyclic sequence (Fernández, 1994; Grace et al., 1998), and they are therefore considered polycyclic species. The set of growth units produced during a single growing season makes up the annual shoot. The polycyclic behaviour of *P. radiata* has been demonstrated by many authors, such as Jacobs (1936), Fielding (1960), Bannister (1962), Bollmann and Sweet (1976) and Fernández et al. (2007), among others. However, some of these trees may occasionally produce only one growth unit along the main axis in some years. Nevertheless, in all cases, the growth units end with a cluster of branches or of branches and cones.

The branches of *P. radiata* and many other forest species whose branches develop within a cluster generally present varying degrees of vigour. Barthélémy et al. (1997) explained this phenomenon based on the principle of acrotony, whereby the greatest vigour of branches is observed in the distal part of a growth unit. According to Lauri (2007), acrotony is usually defined as an increase in vigour (e.g., in length, diameter, number of leaves) in the vegetative proleptic branches (from dormant buds) moving from the bottom to the top position of parental growth. In this case, the basal branches show less vigour than the last branches formed in the same cluster, showing a gradient of vigour from the bottom to the top of the cluster (Fig. 1). Pont (2001) demonstrated that this is the case in *P. radiata* branching. From the lower branch in a cluster to the largest one at the top, there is a short distance and a divergence angle. This angle has been observed in the phyllotaxis of many organs (e.g., leaves, branches, petals) and species, and in many cases, it is coincident with the golden angle, $\omega \approx 137.5$ (Prusinkiewicz and Lindenmayer, 1990). The ratio of this angle to its complement, $gr = \omega/(360 - \omega)$, corresponds to the golden ratio (gr), which is widely observed in nature. Pont (2001) demonstrated that the divergence angle of the branch primordia in *P. radiata* is coincident with ω. There have been some attempts to use empirical models to describe the characteristics of *P. radiata* branches, and in some cases, the diameter of the largest branch in a cluster has been taken as a reference unit (e.g., Grace et al., 1998). Similarly, Woollons et al. (2002) modelled the internode length and branch characteristics of *P. radiata* in New Zealand using traditional variables employed in common forestry inventories as inputs, such as tree height, diameter at breast height and the basal area per hectare of the top 100 stems. Fernández et al. (2007) studied the evolution of branch number, among other architectural characteristics, of the species along its life span. Further, Fernández et al. (2011) developed a functional–structural model for the species, modelling branchiness, growth unit frequency as well as internode length throughout different site and stand density scenario, using functional and also some stochastic models.

Empirical models are most commonly used to reflect the nature, but they do not completely reflect the real response of the studied tree/branch variables, that depend not only on site and tree structural considerations (site index, stand density, relative position of the branches in the crown, tree dominance) but also on natural stochastic events that might be affecting the tree and its components development. As stated by Barthélémy and Caraglio (2007) the architecture of a plant arises from the balance between the expression of the endogenous growth process and exogenous constraints conferred by the environment. Thus, the original architectural plan or model can take multiple expressions that a deterministic modelling approach do not represent, because by definition, it gives a unique response value under certain input. But the unpredictable events might be affecting directly or indirectly (for instance their neighbours) the modelled subject (for us a branch), generating variations in their expected relative vigour (given by acrotony). In the seek of modelling natural phenomena and its variability, we propose stochastic modelling which permits to capture the rich variability that is normally observed in nature, and particularly Markov chains, that have been used successfully to model tree architecture (branching, shoot structure, flowering, for instance) as can be seen in Guédon et al. (2001) and Guédon et al. (2007).

According to Gilks et al. (1996), Markov chains represent stochastic processes in discrete time and discrete events that undergo a transition from one state to another among a finite number of possible states. They are built from simple dependencies between successive random variables, and thus, the transition from