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Functional-structural modelling of tree and wood formation: new parameters and relations.

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Highlights: Foliage development and growth of *Pinus radiata* are modulated by temperature, water balance, and probably also by photoperiod, with marked tendency changes associated to solstices and equinoxes or at times close to them. Being a highly coordinated process, wood density of growing rings also vary, increasing or decreasing, according to current crown developmental trends. In addition, it appears that a constant thermal accumulation value triggers the formation of a new wood cell. A functional-structural model combines these phenomena and links new foliage development and expansion to wood formation and density.

Keywords: Photoperiod; crown development; thermal accumulation; foliage development; wood ring formation; wood density.

INTRODUCTION

The relationship between crown development and growth and wood ring formation is relevant to the understanding of the whole tree ontogeny, carbon allocation and structural design. Fernández et al. (2011) presented the first functional-structural model for *Pinus species*, and specifically calibrated for *Pinus radiata.* It models the development and growth of individual trees under different soil, climate and stand conditions. The model integrates physiological processes following morphological development rules based on thermal and photoperiod control signals. Allometric relationships between demanding foliage and the conductive structure of wood are satisfied. A biomass balance is established and photosynthates allocation hierarchies are assigned that lead to a stochastic production of new organs and structures turnover, to heartwood formation and self-pruning (Figure 1a). The model and sub-models were based on previous research work of several authors on *Pinus radiata* other *Pinus* species (Bollman and Sweet, 1976; Madwick, 1994; Ryan et al. 1996; Kozlowski and Pallardy, 1997; Mäkelä 2002; Rodríguez *et al.* 2003; Pilatti and Norero, 2004, among many others) as well as on personal research (Fernández and Norero 2006; Fernández *et al.* 2007; Fernández et al. 2011). The model has been written in the Lindenmayer Systems language (Prusinkiewicz and Lindenmayer 1990) that generates a 3D tree at monthly time steps. The results are expressed in terms of biometric variables (height, diameter, volume); biomass outputs and by wood characteristics, such as knots size and position in wood, width of growth ring and wood density (Figure 1b). The model yields satisfactory results except for wood density values and efforts to improve this subject were therefore undertaken. To this end, a better understanding of the close relationship between development and growth processes of the crown and of wood formation appears to be the key issue, as indicated by several authors (Richardson 1964; Larson 1969; Downes et al. 2002; Drew et al. 2012 among others). Thus, we began a new project to get answers concerning (a) the allometric relation between newly formed foliage and the new lumen area, the true or effective conductive area of the developing wood ring; (b) the relation between sexual maturation and external and internal

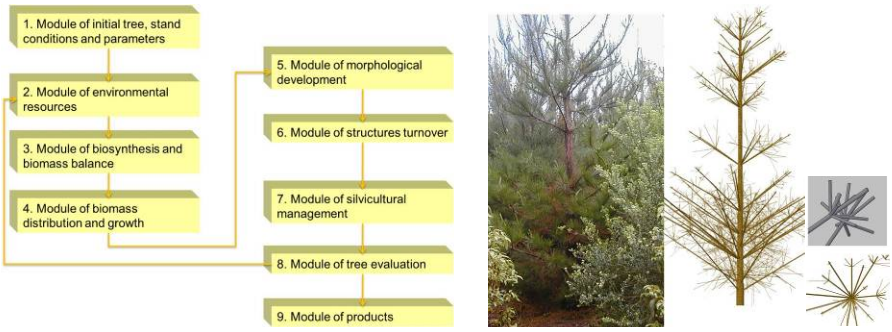

Figure 1: (a) General modular flowchart of the functional-structural model; (b) Some outputs of trees and structures.

characteristics of the tree; (c) the combined phenology of shoot, foliage and wood production, and (d) the relation between wood density and water conductivity.

The prospective presentation will show main results and how these results are to be incorporated into the structure of the above mentioned model.

MATERIALS AND METHODS

The development of foliage, main apex, and wood of 38 nine years old *Pinus radiata* trees of an unmanaged stand in the Mediterranean Central region of Chile were measured during the June 2009–August 2010 growing season. Every 15 days at the beginning of the season and every 30 days later on, microcores, 2 mm diameter x 12 mm length, were drilled out from each tree with a Trephor instrument, 40 cm above the ground surface. Simultaneously, the development of the main apex and of foliage was measured. In each occasion three trees were felled; their whole tree architecture measured and described, and discs from every growth unit cut and collected for further analysis. The entire biomass was weighed and classified according to position and age. Hourly temperature, rainfall, wind speed and solar radiation were recorded on a nearby weather station. These data were combined with pertinent soil conditions to compute changes in water balance and thermal accumulation according to the procedure of Fernández et al. (2011).

Microcores were sliced in a microtome and photographed in a microscope. By means of image processing techniques, cells and lumen size, wall thickness and number of cells were computed. Wood density was estimated considering 1.410 kg m^{-3} the cell wall density. When trees were felled, an X-ray transversal profile of wood was obtained at the same level the microcores were sampled. As these measurements accumulated a correlation was apparent between both parameters. It was thus possible to define the consecutive limits of annual growth rings at a given date, and investigate relationships among ring characteristics, such as cell size, lumen size, wall thickness and X-ray wood density values. Each piece of the growth ring was dated. With this information it was possible to analyze, relate and model the connection between ring development, foliage and apex development and environmental variables.

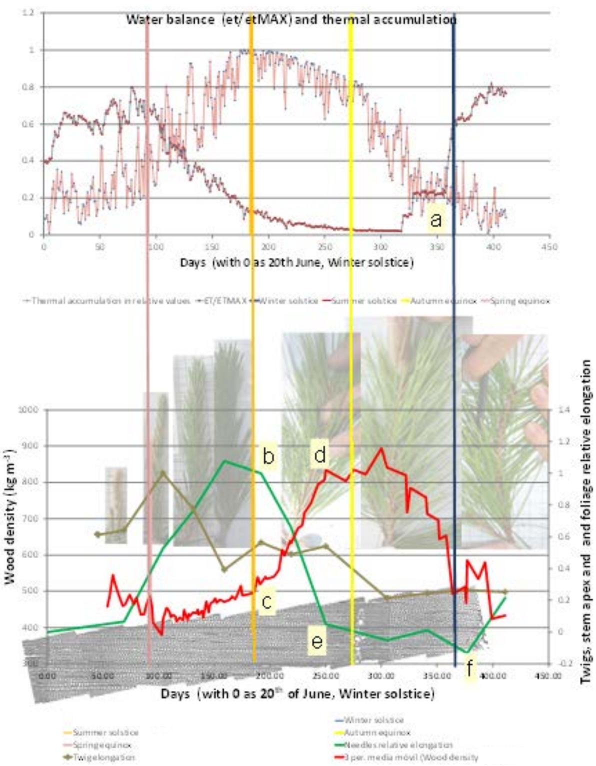

Figure 2: Upper image shows water balance (as et/etMAX) and thermal accumulation (in relative values). Lower image shows the simultaneous evolution of wood density, stem and twigs elongation, and foliage growth. Vertical lines connect both graphs at solstices and equinoxes.

RESULTS AND DISCUSSION

The upper part of Figure 2 shows the water balance of the sampling year, expressed as the ratio between Real Evapotranspiration (et) and Maximum Evapotranspiration (etMAX), and the thermal accumulation as a function of temperature (modified by water balance when too low). Solstices and equinoxes are indicated; time (x-axis) is given in days from June 21 as day = 1, the first day of the growing period (winter solstice in the southern hemisphere). Earlywood formation coincides with the period when needle elongation rate was steadily increasing. When this tendency changed (close to summer solstice) (Figure 2b) needles continued to enlarge but at lower rate the wood ring density changed sharply from a low to a high value (Figure 2c). Needles ceased to enlarge near the autumn equinox (Figure 2e) At this time (Figure 2d) wood density attained its highest values.

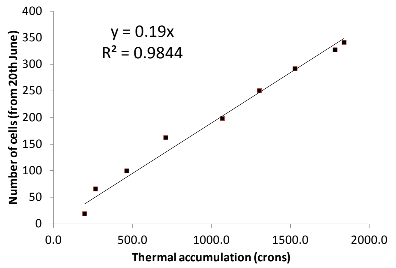

Figure 3: Relationship between thermal accumulation (in chron units, Fernández et al. 2011) and the accumulated number of new cells forming the wood ring.

Temperature has been recognized as a commanding factor on cambial activation and cambial rate of activity (Gricar et al, 2007; Begum et al., 2008). Figure 3 shows the relationship of thermal accumulation and number of cell produced during the sampling period. The linear relation indicates that it is necessary 5.26 thermal units or *chrons* (=1/0.19) for the production of one new cell. Wood density depends on wood cell size, cell wall thickness and lumen size. Cell wall thickness, in turn, depends on the rate of wood generation at the cambial zone, the permanence of the cell in the formation and enlarging area and the availability of material for cell wall build up (Taiz and Zeiger 2010). In increasingly warm periods (spring) with good water balance the thermal accumulation rises and the production of cells is accelerated. But as new foliage is at an early stage of development, the total amount of photosynthates is low compared to periods in full foliage display. As a result, there is a shorter time for enlargement and a lower availability of material leading to cell of large lumens and thin cell walls (= low wood density = earlywood type). During autumn, temperature and heat accumulation decrease, rate of new cell production slows down, but the period of enlargement increases. With all the new foliage fully displayed, *Pinus* photosynthesis continues to provide ample material to developing cells. As a result, larger amount of mass directed to fewer cells contribute to larger wall thickness. These findings will be incorporated into the above mentioned functional-structural model of *Pinus radiata* (Fernández et al. 2011) How this is to be achieved and what kind of results are to be expected of future simulations will be the subject and discuss during the presentation. We plan to extend the research to more sites conditions in order to confirm the generality of the relation of cells formation with thermal accumulations.

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