

# HOW ENVIRONMENTAL VARIABLES ARE RELATED TO SHOOT AND FOLIAGE DEVELOPMENT AND WOOD RING FORMATION: AN INTEGRATED ANALYSIS FOR FUNCTIONAL-STRUCTURAL MODELING PURPOSES

M. Paulina Fernández<sup>1,2</sup>, María Menéndez-Miguélez<sup>1,2,3</sup>

**ABSTRACT:** Growth and foliage development of *Pinus radiata* is modified by temperature and water balance, and possibly as well by the photoperiod, with significant changes around the solstice and equinox. Wood density also shows changes in annual growth rings, with increasing or decreasing trends in the same periods. We studied the relationship between environmental variables, stem and needle elongation, and the resulting wood cell production, as well as the relationship between these variables and intra-ring wood density variations. The most important environmental factor for the site conditions of the study (Mediterranean climate) was water balance, which was greater than the thermal effect. The coordination of all these processes by a functional-structural approach allows for interactively modelling stem and new foliage development and expansion, with wood formation and wood properties such as density.

**KEYWORDS:** wood density, wood ring formation, foliage development, shoot expansion, photoperiod, cambial cells.

## 1 INTRODUCTION

The commercial importance of fast-growing species like radiata pine (*Pinus radiata* D. Don) makes the exhaustive study of wood formation even more important. Most models of radiata pine, the main industrial forest species in Chile, New Zealand and Australia, are robust growth models, but few of them have a physiological base [1]. These models allow for estimating wood volume and different wood products per hectare, taking into account different silvicultural treatments [2]. Nevertheless, final wood quality and therefore final product quality and price depend on many factors that cannot be modelled by traditional simulators, such as branch diameters and the presence and size of knots, resin pockets and other defects, the length of internodes that represent more or less clear wood, wood ring width, wood anatomy (cell length and diameter and cell wall thickness), physical and mechanical properties of wood and properties relevant to paper production when appropriate [3,4,5].

Growth and development is a coordinated and complex process with many interactions among the growth

processes in various parts of the tree. These interactions often involve the distribution of nutrients, the movement of growth regulators and the changing rates of processes in different parts of the tree. The rate of cell division, as well as the structure and size of xylem cells, may be controlled by these growth regulators produced by the active stem apex or by the leaves [6]. Therefore, the structure and width of annual rings in trees are directly related to the level and duration of shoot growth [7].

Particularly, wood formation, or xylogenesis is a complex and fascinating physiological process, a more complete understanding of which can unlock strategies for the full exploitation of woody biomass [8]. It occurs as a series of inter-related processes that begin with the cellular division in narrow meristem tissue called cambium, and ends with the complete formation of empty conduits with lignified, thickened walls [9]. Once wood is completely formed, the physical properties of xylem tissues (e.g. wood density, lumen area, cell wall thickness, etc.) vary depending on the trees and sites studied as a consequence of many genetic and environmental factors [10-14].

The process of xylogenesis involves a) signalling that triggers the generation of a new cambial initial cell in the cambial zone, understood as the cambial cells and all the cambial initials close to them [6]. This is followed by b) the process of cells enlarging; c) cell walls thickening; d) and the emergence of fully mature cells [15, 16]. The duration and rate of enlargement define the final size of xylem cells, while the duration and rate of wall thickening define their final weight. The complex interaction between durations and rates of the sub-processes of xylogenesis determine the changes in cell features that create the

<sup>1</sup> UC School of Agronomy and Forest Engineering, Pontificia Universidad Católica de Chile

<sup>2</sup> UC Timber Innovation Centre, Pontificia Universidad Católica de Chile

<sup>3</sup> GIS-Forest Research Group, University of Oviedo, Spain  
[pfernan@uc.cl](mailto:pfernan@uc.cl); [mamenendez@uc.cl](mailto:mamenendez@uc.cl)

anatomical structure [17]. These changes directly affect wood density.

The variability of climatic conditions during the growing season can affect cambial activity [18, 19] and therefore tree ring properties by changing the number of cells produced and/or their anatomical properties [20]. Therefore, understanding the underlying processes related to climatic variables can shed light on long-term growth responses to climate warming and drought, the internal functioning and growth regulation of the tree and its resulting wood anatomy and properties.

Auxin plays an essential role in the differentiation of procambial precursor cells [21, 22]. There is indirect evidence that auxin is the main limiting factor in normal primary xylem differentiation, as well as wound xylem formation [23]. Cytokinin and other plant growth regulators play a key role in cell division and regeneration [8] and in regulating tracheary element formation [24]. Cell proliferation is completely dependent on the presence of cytokinin in the medium. In the absence of cytokinin, no cell division and no cytodifferentiation occurs [24]. A growth hormone of the auxin family called Indole-3-acetic acid (IAA) plays an important role in xylem formation [25] and is generally accepted as the main growth factor in the tree. It is mainly produced by the young leaves of the principal apex [26] and its major sources in intact plants are buds and developing leaves [27]. Kramer has demonstrated the existence of a proportional correlation between the rate of xylem production and the mass of IAA per unit area on the cambial surface [28]. Changes in temperature have been correlated to changes in the level, transport and metabolism of auxin. Light conditions also appear to have significant effects on IAA turnover [29]. In *Pinus* spp., water stress has been found to increase IAA in roots [25] and it is generally assumed that under conditions where auxin regulates growth, the higher the IAA concentration, the higher the growth rate. [30] studied all these relationships between apex growth and yield, needle growth, hormones and cambial activity.

Wood formation of *Pinus radiata* is particularly interesting. [31, 32] determined that the cambium in *Pinus radiata* does not become completely dormant during winter as it does in many other species. In the same way using dendrometer measurements [31] showed that the diameter of *P. radiata* stem continues to increase slowly throughout the winter. The entire tree development process, carbon allocation and structural design can be better understood by considering the relationship between crown development and functioning, and corresponding wood ring formation. As a consequence, a clearer understanding of these relationships can lead to better interpretation of wood ring structure in relation to past environmental events for dendrochronology studies, as well as providing insights into the effect of future climatic events on wood production.

This article presents on-going research into the relationship between environmental variables, newly formed foliage and stem elongation, and wood ring formation and

characteristics. Our aim is to elucidate certain relations that will be useful for further functional and structural modelling of the species under changing environmental scenarios.

## 2 MATERIALS AND METHODS

We followed the development of foliage, main apex and wood of 38 9-year-old *Pinus radiata* in an unmanaged stand for a complete growing season (June of Year 1 to August of Year 2). The site has a Mediterranean climate in the central region of Chile (Libertador Bernardo O'Higgins Region, Cardenal Caro District, 34°40'12.52"S and 71°57'55.04"W). Detailed climate data is part of the research and given in the figures below.

Microcores were collected every 15 days at the beginning of the growing season and every 30 days subsequently. The microcores (2 mm in diameter and 12 cm long) were collected with a Trephor (Università degli Studi di Padova) at a height of 40 cm height from the base of standing trees. Measurements of the main apex and foliage were done simultaneously. On each occasion, 3 trees were felled, their architecture described and measured, and discs from each growth unit collected for further wood ring analysis. Total foliar biomass was classified after position and age were determined. Hourly environmental data (temperature, rainfall, wind speed, solar radiation) from a nearby weather station were recorded. In addition, soil information and a water balance sequence were gathered over the year, following [33], and expressed as the ratio between the evapotranspiration (ET) and maximum potential evapotranspiration ( $ET_{max}$ ) under particular radiation and temperature conditions if the soil were totally replenished with water.

We used a gamma function proposed by [34] as a thermal accumulation function to analyse the relationship between temperature and the development and growth of the stem, foliage and wood. As cardinal temperatures for the species we used the values proposed by [1], with  $T_{min} = 0^{\circ}C$  as the minimum cardinal temperature,  $T_{opt} = 23.3^{\circ}C$  as the optimum cardinal temperature,  $T_{max} = 35^{\circ}C$  as the maximum cardinal temperature;  $T$  is the environmental temperature at a certain moment,  $r$  is the speed of the process at environmental temperature  $T$  and  $R_{max}$  is the maximum speed the process can achieve at the optimum temperature.

$$\frac{r}{R_{max}} = \left( \frac{T_{max} - T}{T_{max} - T_{opt}} \right) \cdot \left( \frac{T - T_{min}}{T_{opt} - T_{min}} \right)^{\frac{(T_{opt} - T_{min})}{(T_{max} - T_{opt})}} \quad (1)$$

Using this equation with the daily temperatures allows for building a thermal accumulation model, expressed as the sum of the resulting values of Equation (1). Thermal accumulations were restricted when water stress was evident, as proposed by [1]. [35] proposed that there is a thermal requirement for the complete development of a crop or of certain phenological phases, and defined it as tautochrone or thermochronological integral. The

tautochrone of a certain phenological phase corresponds to the thermal accumulation necessary to fulfill a phase, and is expressed as the sum of the daily evaluation of Equation (1), until a certain level of thermal accumulation triggers the onset of a new organ, cell, or other process.

Based on the environmental data and using the functional model proposed by [1], we simulated a daily relative value of Net Primary Production (NPP). The variables of the model are temperature, water balance, light conditions, solar radiation, and others.

The microcores (12 mm long and 2 mm in diameter) were fixed and sliced at 10 – 30  $\mu\text{m}$  with a sliding microtome. The sections were stained with safranin, mounted and fixed. The samples were examined with visible light under a light microscope (Motic BA130) and photographed at 10x magnification. Images were obtained with 2048 x 1536 pixels for areas of 0.85 x 0.64 mm. Every microcore is represented by a sequence of 21 photographs on average. The images in the sequence were correlated, generating a continuous single longitudinal image. A segmentation algorithm based on a two-band-pass filter in the Fourier domain was applied, splitting the color images into three areas: cell wall, lumen and the reminder. The latter represents defects in the wood such as holes, cracks and image background. ImageJ software was used to measure cell anatomy. The number of cells, lumen size and cell thickness were recorded. Wood density was estimated following [36]. The number of cells in the cambial and enlarging zone was counted following the definition of the two sections as given by [20].

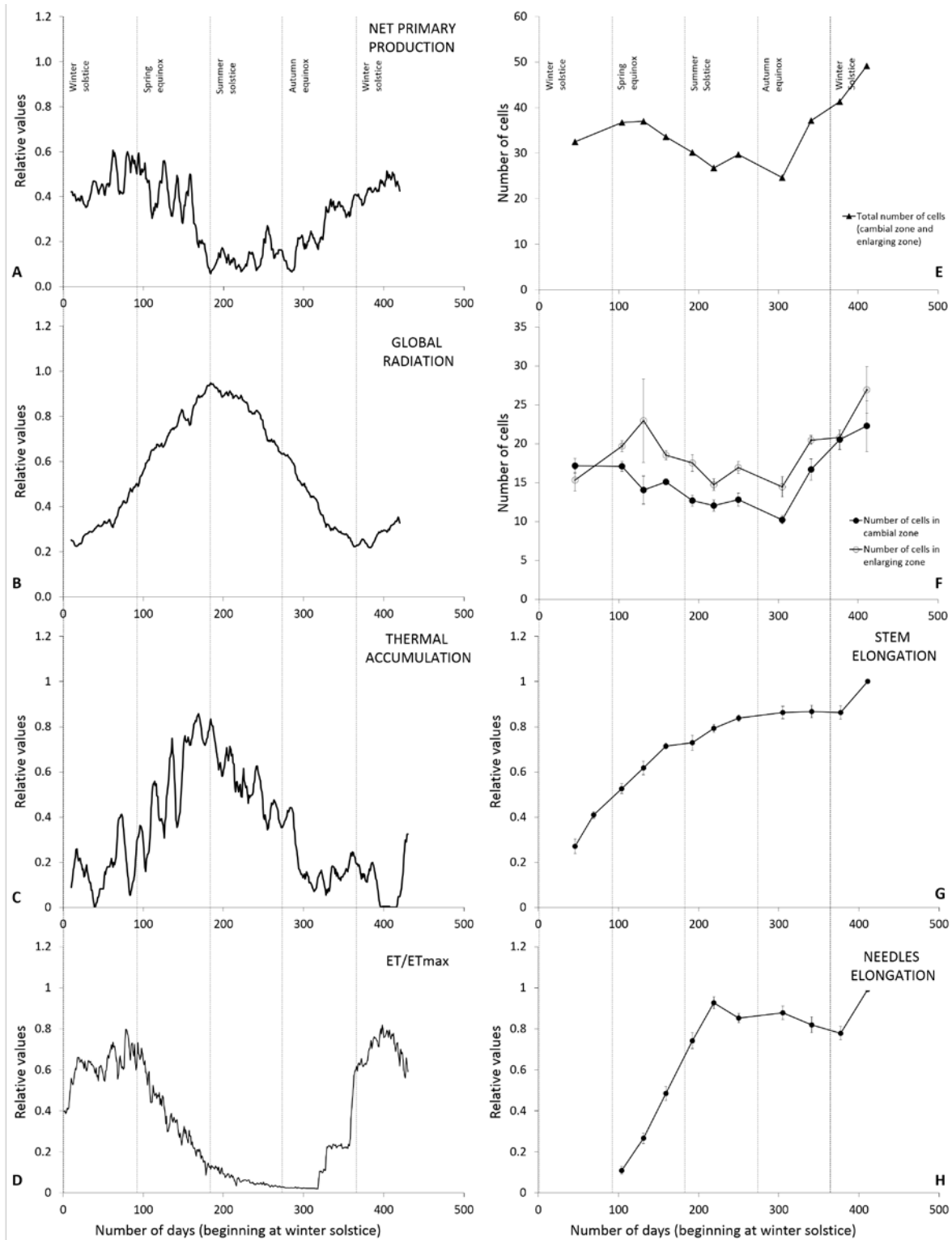
A transversal x-ray profile was obtained at the same level of microcore sampling. Time correlation techniques were used to match each microcore sample to the x-ray sequence to correlate the relations between ring characteristics (cell size, lumen size, wall thickness) and the x-ray wood density results. After dating each part of the growth ring, the relation between ring development, foliage and apex development and environmental variables were analyzed and modeled.

### 3 RESULTS

Figure 1 shows the results of a preliminary analysis of climatic variables, the cells in the cambial zone and enlarging cells (as an expression of cambial activity), and the evaluation of needle and stem elongation in the sampling year, beginning at winter solstice. Figure 1A

graphs typical net primary production, with highly variable values depending on particular daily conditions. The graph can be divided in three parts: from 0 to 200 days (close to summer solstice) net primary production presents the highest relative values, peaking around 0.6 and then decreasing. In the second part, from 200 to 300 days (summer), net primary production is almost always below 0.2, and a final part (over 300 days) in which net primary production begins to increase until reaching values relatively similar to those at the beginning of the year. This correlates highly with the water balance, expressed as  $ET/ET_{\text{max}}$ . Figures 1B (global radiation) and 1C (thermal accumulation as a function of temperature, but restricted by water balance when it is low) present similar patterns. With warm weather (spring) production values increase, and with a good water balance, thermal accumulation rises (approximately 0.8 at around 200 days). However, production values decrease after the summer solstice. A second period of change is around the winter solstice when global radiation begins to increase, while thermal accumulation begins to increase slightly earlier, at around 300 days. The water balance, expressed as the ratio between real evapotranspiration (ET) and maximum potential evapotranspiration ( $ET_{\text{max}}$ ) (Figure 1D) increases slightly until the spring equinox, when it abruptly begins to decrease until reaching its lowest relative value around 300 days, between the autumn equinox and the winter solstice. After that, the first rains produce a rapid increase in relative values in two phases, the first reaching a plateau around 0.2, and the second and more substantive reaches a peak of 0.8 in winter. These values are similar to those in the spring equinox.

The number of cells in the cambial zone, the number of enlarging cells or the number of the two together present the same pattern (Figure 1E): decreasing from the spring equinox to just after the autumn equinox (around 300 days), when the minimum value is reached, which is similar to changes in water availability. After the autumn equinox the number of cells increases abruptly and reaches a peak around 400 days. Stem elongation (Figure 1G) increased until the autumn solstice, when growth stopped until the winter equinox, following which growth began again. Figure 1H presents needle enlargement from onset at the beginning of spring until growth cessation during summer and autumn. Growth began again just after the winter solstice.



**Figure 1:** Net primary production (simulated) (A), global radiation (B), thermal accumulation (C), water balance (D), total number of cells (E), cambial and enlarging cells (F), stem elongation (G) and needle elongation (H) for the sampling year. Solstices and equinoxes are marked in the Figure. All the graphs have the same X-axis scale in days, with June 21<sup>st</sup> as the first day of the growing period (winter solstice in the southern hemisphere).

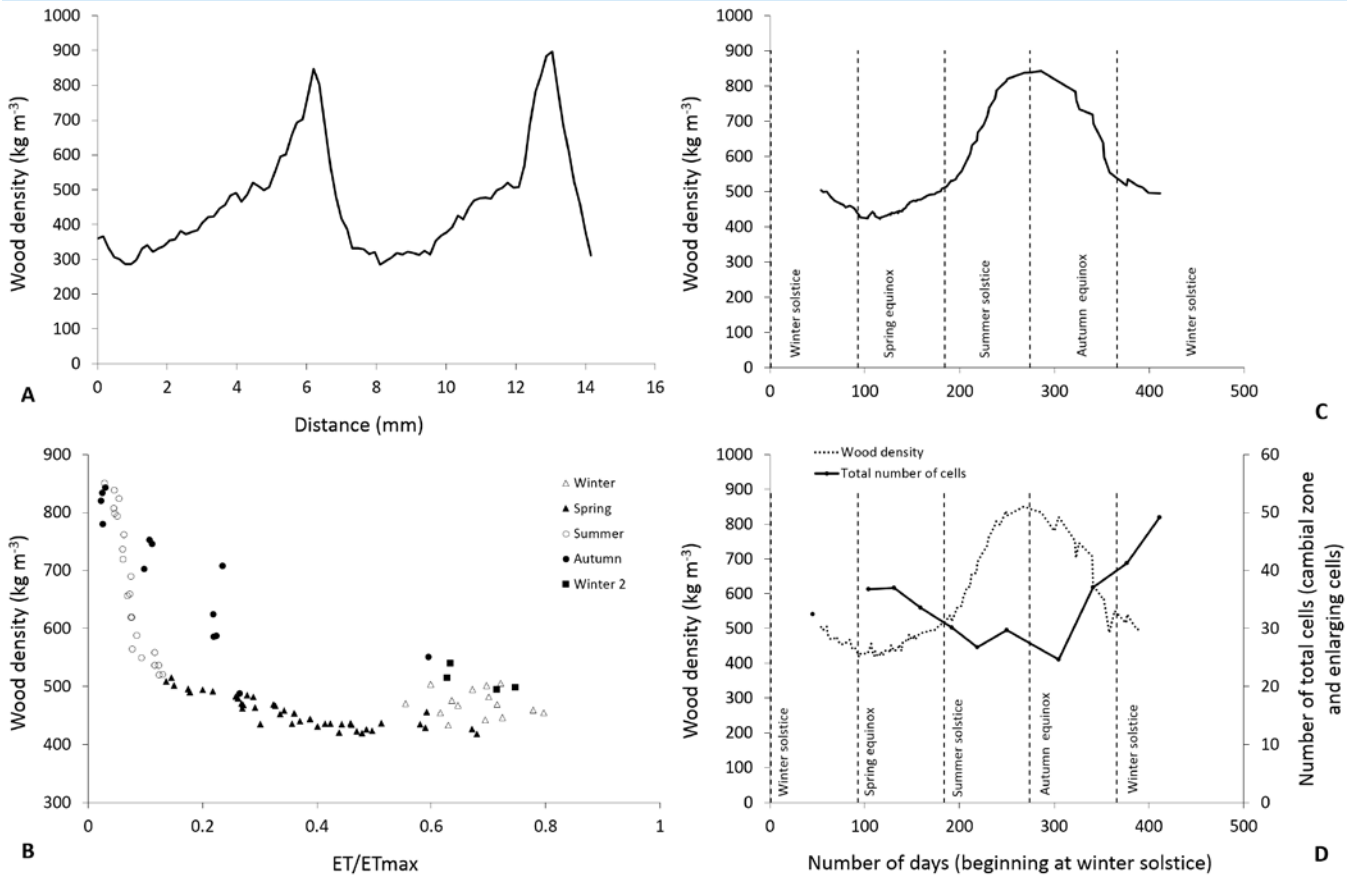
Figure 2A shows the wood density profiles obtained with X-ray densitometry of the last two rings of one of the studied trees. The image on the right is the entire ring of the studied year (two rings, the right one corresponds to the studied one), obtained from the last tree sampled at the end of the study. Thus, this ring is the result of a whole year of growth. Figure 2C shows an average ring of the studied period but rescaled to days instead of distance (X-axis). The lowest density production was in spring. After the summer equinox wood density rose abruptly and peaked at a density of over  $750 \text{ kg m}^{-3}$ , which in a normal wood density versus distance plot corresponds to a very narrow region, and in terms of days is around 90 (three months), from mid-summer to mid-autumn. Early wood formation coincides with the period when the needle elongation increased steadily. After the summer solstice and concurrent with the water shortage, needles

stop enlarging and even decrease in length, while stem elongation stops. This shrinkage of the needles may be due to dehydration. Coincident with this, wood density values reach their highest and the lowest level of cambial activity is observed.

Figure 1H shows that needles cease to enlarge before the autumn equinox. At the same time (Figure 2C) wood density reaches maximum values.

When the water supply begins to recover in mid-autumn (Figure 1D), cambial activity (Figure 1E and F) increases and wood density decreases (Figure 2D). Stem elongation and foliage expansion resume shortly after the winter solstice, but not when water availability rises, indicating a greater response to change in day duration.

The strongest relation between an environmental variable and wood density was with water availability ( $ET/ET_{max}$ ), as can be observed in Figure 2B.



**Figure 2:** (A) Wood density of a typical ring (right ring is from the studied year), scaled by distance in mm, measured by X-ray densitometry; (B) relationship between water balance and wood density; (C) average ring of the studied year but rescaled in relation to the days of the year; (D) comparison between wood density and cambial activity.

## 4 DISCUSSION

Intra-annual secondary growth has mainly been studied in high-altitude and boreal conifer species [37, 38, 39, 40, 41]. However, little is known about secondary growth of Mediterranean conifers, such as radiata pine, which are

subjected to very unpredictable water and climatic stress conditions, in addition to low temperatures [42, 43, 44].

The stem elongation period continues until just after the summer solstice when global radiation and thermal accumulation are at their maximum. The lack of water in summer drought period caused stomatal closure in order to

take advantage of stored water. According to [25], water stress in *Pinus* spp. increases the concentration of ABA hormone (abscisic acid), which causes stomatal closure and inhibits shoot growth [45], as Figure 1G shows for the summer period.

Nevertheless, although water stress was alleviated by the early rains in mid-autumn (Figure 1D), shoot and needle elongation did not reactivate until the winter solstice. This concurs with photoperiodic signalling, and corroborates the results of [46] for radiata pine and of [29] for *Lemna gibba*. As well, [45] states that gibberelins cause stem elongation in response to longer days.

[47] and [45] indicated that high concentrations of IAA and low concentrations of GA (Gibberelic acid) stimulate xylem production. That could have been the case in mid-autumn when cambial activity rose abruptly at the same time as water balance. [48] stated bud formation for the following season's growth in *Pinus* begins at about the time shoot extension ends for the current season. During the remainder of the growing season, formation of primordial organs within the developing bud occurs in an ontogenetic sequence. In our case, when shoots stopped enlarging close to the autumn equinox, we can infer that the process of bud formation had begun. [27] stated that buds and developing leaves are major sources of IAA in intact plants, thus in our study bud formation coinciding with the cessation of shoot elongation could have generated IAA and stimulated cambial activity. In parallel, [25] indicated that water stress in *Pinus* spp. increase IAA production. In our study, the lowest level of water availability occurred in mid-autumn (Figure 1D), and close to that period cambial activity (in terms of the number of cells in the cambial zone and enlarging cells, Figure 1F) increased again. A combination of the two processes (bud formation and water stress) could have acted on cambial activity. Our data shows that

cambial activity in radiata pine never stops, which is similar to what was found by [31].

According to [49] cell wall thickening is controlled by photosynthetic processes in foliated organs in the crown. In the first part of the season the photosynthates produced by the older needles are mainly used in growth of the newly elongating needles and expanding shoots, leaving only a small quantity of photosynthates available for wood formation of the enlarging spring wood cells. Therefore, only when shoot elongation stops and the newly formed needles mature close to the summer solstice, as can be seen in Figure 1G and 1H, the photosynthates produced by both newly formed and old needles become available for wall thickening, developing the typical summerwood or latewood.

## 5 CONCLUSIONS

Our results show the complex and coordinated process of development and growth of shoots, needles and wood. The findings of the key relationships of these processes with the environmental variables allows us to model the development and growth of the crown (as has already been done with models like that in [1], and concomitant to this, the characteristics of the development of woody cells.

Further research is necessary to more fully understand the complex pathway of hormones as intermediaries between environmental stimuli and plant reactions. But the current knowledge about hormones allows us to explain the phenomena of development and growth we have observed in our samples.

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