TIMING OF CELL PRODUCTION IN TREE RINGS: AN AUTOMATIC TWO-STEP PROCEDURE IN R

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ABSTRACT

The study of intra-annual dynamic of wood formation is one of the most progressive and fast-growing fields in plant sciences. The main anatomical characteristics of tree-ring structure, e.g. number of cells and radial cell size, are closely related to the kinetics of cell production. In this case, the timing of seasonal production is a fundamental aspect of plant development and functioning. To better assess the impact of specific climatic events to the timing and dynamic of growth, a process-based modeling can be a very useful tool. The Vaganov-Shashkin model was proved to provide reliable estimates of tree growth under strong limited conditions. Based on the assumption that climate conditions are determining cell differentiation mostly in the cambial zone, the model computes daily growth rate and converts it into the rate of cell production. In this work we present a two-steps approach combining the process-based VS-modeling and the timing procedure for cell production. An automatic method to identify the formation time of new cell transfer to the enlargement zone of tree ring was developed in R. The main advantage of a new approach was the ability to estimate daily values of growth rates and timing of cell formation in the forest-steppe zone in southern Siberia over a long period of direct climate observations without labour-intensive field measurements. The significant correlation between the original algorithm and its updated automatic version proves correctness and reliability of the new method.

Keywords: cambial activity, cell size, tracheidogram, Vaganov-Shashkin model, southern Siberia

INTRODUCTION

Xylem phenology dependent on weather conditions determines tree radial growth and wood productivity [1], [2]. Studying the anatomical structure of tree annual growth and analysis of its heterogeneity is one of the tools to develop new climate reconstruction methods with higher time resolution (up to day). A significant number of papers convincingly show that the anatomical tree-ring structure reflects the seasonal dynamics of external conditions, for instance, intra annual density fluctuations, frost rings, or multiple rings, reduction of cell number in the latewood as a reaction to the early growth cessation [2].The main anatomical characteristics of tree-ring structure, e.g. number of cells, radial cell size and cell walls thickness, are closely related to the kinetic characteristics of seasonal tree-ring formation, especially to the kinetics of cell production [3]. There are a number of publications disclosing an impact of cell differentiation rate on anatomical structure of tree rings [4], [5]. The internal factors of cell growth and maturation in combination with external conditions are reflected in the tree-ring anatomy of conifers [6]. For example, drought effects on Scots pine can affect the formation of a functional xylem structure by reducing cell lumen and wall thickness [7].

Due to specificity and complexity of labor-intensive experimental methods to trace tree-ring formation, mathematical modeling can be considered as a one of possible approaches to simulate cell production by cambium and differentiation of cambial derivatives [8], [9]. Such an approach requires developing adequate mathematical methods and corresponded software components. To describe development of tree-ring formation and predict structural characteristics of wood, a process-based modeling of wood formation can be very useful [10].

The results of the successful application of process-based VS-model are presented in significant number of papers describing climate variability based on radial tree growth in different geographic areas [11], [12], [13], [14], [15]. The calculated growth rate curve can be interpreted as an impact of climate on seasonal growth variability excluding other external and internal factors forcing tree-ring growth. The modeling is an extremely important step because the simulated daily tree-ring growth rate *Gr(t)* is a basis to evaluate intra-seasonal variation of new cells [3].

This paper presents an innovative two-steps approach combining the VS-model used for growth rate simulation and an automatic timing procedure of cell production. An automatic method to identify the formation time of new cell transfer to the enlargement zone of tree ring was developed in R due to the complexity and large number of iterations of the original timing algorithm.

STUDY AREA AND SAMPLE PREPARATION

This study is based on tree-ring data from Malaya Minusa (53°43′ N, 91°47′ E, 251 m a.s.l.), a forested site located within the Minusinsk depression in the forest-steppe zone in Siberia (Russia). The site is covered by a mixed forest of *Betula pendula* and *Pinus sylvestris*. The climate of this area is cold semi-arid. Long-term records from the 25 km close meteorological station “MIN” (53°41' N, 91°40' E, 254 m a.s.l.) indicate an average annual temperature of 1.0°C and annual precipitation of 330 mm, with 90% falling from the end of April to the beginning of October.

Tree-ring width and anatomical measurements were obtained from wood cores collected in 2013 from a selection of 20 damage-free, mature dominant *Pinus sylvestris* trees. One core per tree was prepared to identify tree rings, and their widths were measured with a resolution of 0.01 mm using a LINTAB measuring table connected to the TSAP software (Rinntech, Heidelberg, Germany). The obtained time-series were then visually cross-dated and verified by *COFECHA* software (Version 6.02P; http://www.ldeo.columbia.edu/tree-ring-laboratory/resources/software). For the cell anatomical measurements, we selected cores from five trees showing the highest correlation with the residual chronology ($R > 0.70$). Cell anatomy was assessed for each ring from 1964 to 2013 by measuring the lumen radial diameter (LD) and radial thickness of the double cell wall (2CWT) of all tracheids along the five radial files in each ring.

VS-MODELING

To assign timing for each cell production, we use the process-based VS-model, namely its visualization – VS-Oscilloscope – to estimate growth rates for every day over the study period from 1964 to 2013. It provides an opportunity to interactively adjust the parameter's coefficients and generate quickly comparisons between the observed and the simulated indexed tree-ring width chronologies. The model computes daily tree-ring growth by using daily temperature, precipitation and solar irradiance as inputs. and then calibrated for maximizing the Pearson's correlation and coefficient of synchronicity between the actual and simulated chronologies. To validate the model, the period of direct climate observations (1936-2013) was splitted in two parts: calibration (1960-2013) and verification (1936-1959) periods.

AUTOMATIC TIMING PROCEDURE

The model considers only the processes occurring in the cambium zone and excludes the stages of cell enlargement and cell wall-thickening. According to the hypothesis that final tracheid size is pre-determined by the rate of cell division in the cambial zone, we suppose a strong positive relation between radial tracheid diameter and the time of cell production [2].

In the timing procedure of cell production, we use an integral growth rate *Gr* which is estimated for each day of the growing season (Day of Year, DOY). To assign the time with each tracheid in the radial file, we first divided the total annual *Gr* (i.e. the sum of the daily *Gr* in a year) by the number of formed cells for each individual tree. It allows assessing the average *Gr* contribution of each cell to the simulated ring width. The timing of cell production has been obtained by defining the day when the *Gr* contribution of each cell in the radial files is achieved, assuming that the production of a successive cambium cell only occurs when the previous one is completed. Since the cumulative sum of daily *Gr* within a year is proportional to the indexed tree-ring width, we assigned the corresponding *Gr* with each tracheid considering its position in the radial file. The assignment of the time of cell production of the successive tracheid is calculated from the first day after the completion of the previous cell.

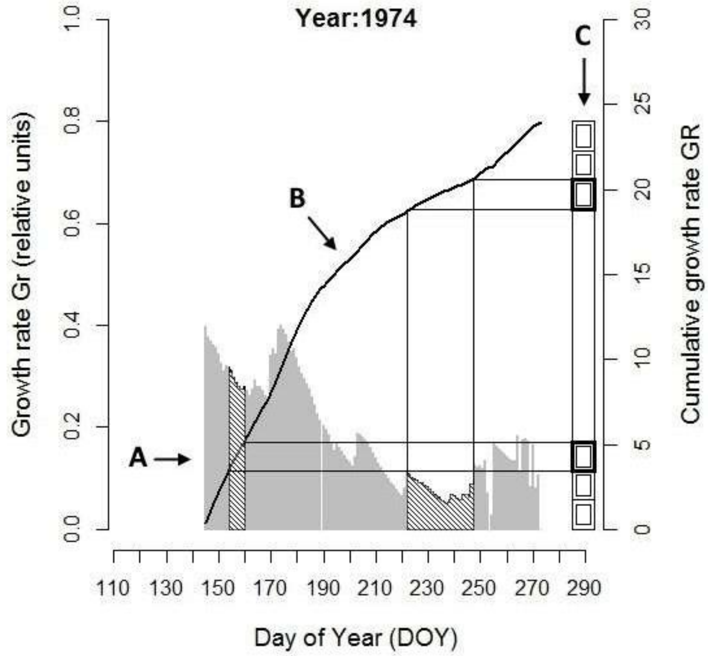

Fig.1 Daily integral growth rate Gr simulated for 1974 (A); cumulative growth rate GR (B); actual cell profile (C). At the start of growing season the formation of bigger cell needs less time than smaller cell at the end due to different rates of cell formation.

To calculate the cell production, the MeanProduction function was developed in R package. It is justified by the fact that the R language is widely spread among scientists in different fields because it allows creating as well as free distribution of simulating packages. The function uses the following algorithm (Fig. 2):

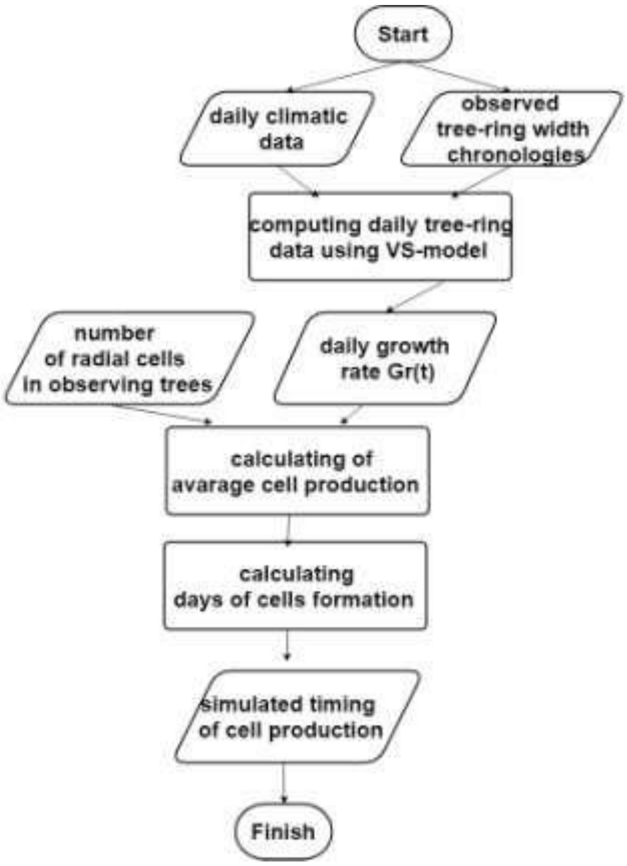

Fig.2. Flowchart of the automatic timing procedure.

RESULTS AND CONCLUSION

The calibrated model provided a simulated chronology matching the actual tree-ring chronology with a correlation of 0.71 and coefficient of synchronicity S of 80% ($p < 0.001$; $n = 50$ years) over 1960-2013. The model verification shows significant similarity ($R=0.55$, $S=70\%$, $p<0.001$) between simulated and actual chronologies over 1936-1959. To provide the best fit of simulated tree-growth values with the actual tree-ring chronology, the adjustment parameters of the model were obtained (see more in [3], [15]).

We compared the simulated timing cell production with “snapshot” tracheidograms for the certain time moments (i.e. June, 09, 18, 29 and July 24) in growing seasons of 1979, 1980 and 1981. In 1980, at the 9th of June, the observed number of cells formed ranged between 10 and 14, and the simulated numbers of cells were 9-12. For the next date of observation (18.06.1980) the corresponded ranges were 18-23 cells for the observed sample and 16-21 for the simulated results.

For testing the new automatic procedure and comparison with the previous version of timing algorithm we used the verified anatomic data from Minusinsk forest steppe (Fig.3).

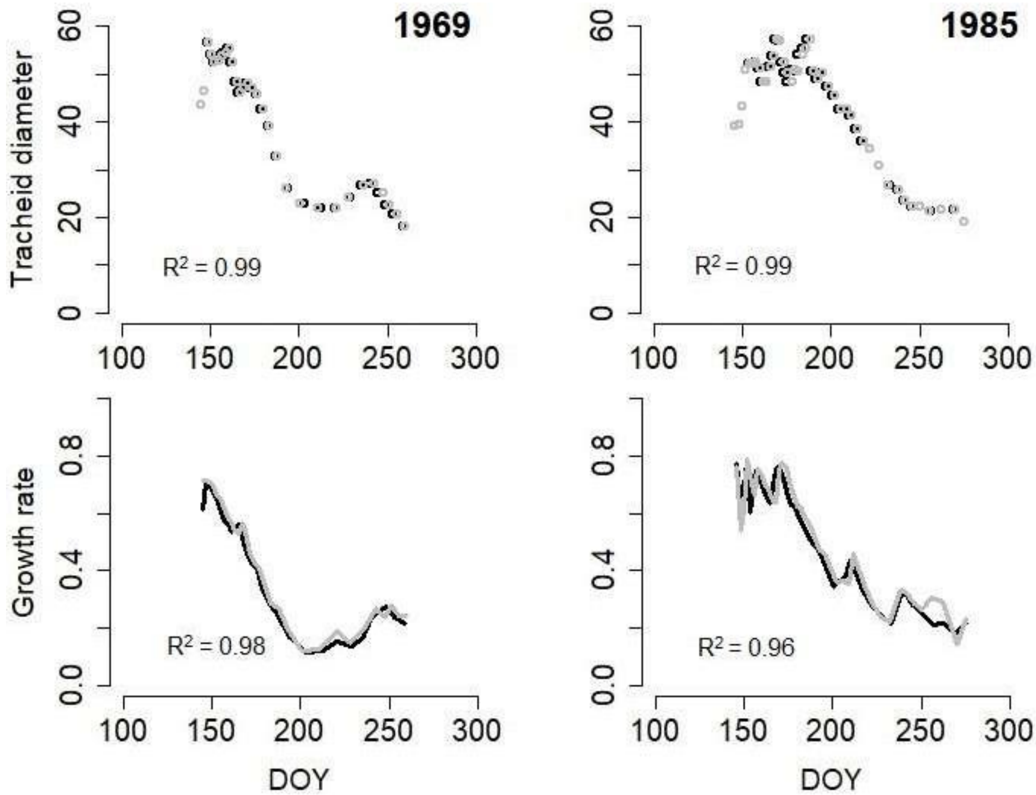

Fig.3. Assessment of cambial cell growth rates (on the bottom line) and its relationship to the tracheid diameter for two typical years (1969 and 1985). The grey color indicates the results of automatic approach; the black one shows the results obtained by the original algorithm.

The new automatic procedure was tested for all years of the available period and results of simulation were identical in 98% of cases with the previous version of the timing algorithm.

To conclude, an automatic method for identification of timing of new cell transfer to the enlargement zone in a tree ring was developed in R. The main advantage of a new approach was the ability to estimate daily values of growth rates and timing of cell formation in the forest-steppe zone in southern Siberia over a long period of direct climate observations without labour-intensive field measurements. The significant correlation between the original algorithm and its updated automatic version proves correctness and reliability of the new method.

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