

An interpreted language implementation of the Vaganov-Shashkin tree-ring proxy system model

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Abstract

We describe the implementation of the Vaganov-Shashkin tree-ring growth model (VSM) in MATLAB. VSM, originally written in Fortran, mimics subdaily and daily resolution processes of cambial growth as a function of soil moisture, air temperature, and insolation, with environmental forcing modeled as the principle of limiting factors. The re-implementation in a high level interpreted language, while sacrificing speed, provides opportunities to systematically evaluate model parameters, generate large ensembles of simulated tree-ring chronologies, and embed proxy system modeling within data assimilation approaches to climate reconstruction. We provide a versioned code repository and examples of model applications which permit process-level understanding of tree ring width variations in response to environmental variations and boundary conditions.

Keywords: dendroclimatology, xylogenesis, tree-ring, paleoclimate, cambium, proxy systems modeling, MATLAB

1. Introduction

2 Interpretations of climate influences on tree rings and the application of these relationships
3 to the reconstruction of past climate typically use empirical statistical models calibrated from the
4 overlapping periods of observed climate data and the tree-ring proxy measurements (Fritts et al.,
5 1971; Hughes, 2011). There are many strengths to this approach to dendroclimatology: these
6 methods are simple to use and interpret, they are usually and sufficiently linear (Hughes, 2002),
7 and they require no *a priori* knowledge of the biological response of any given species to cli-
8 mate in any particular region, and as discoverable models, can be applied regardless of species,
9 location, or climate regime. Many thousands of tree-ring chronologies have a biologically rea-
10 sonable association between local monthly or seasonal climate variability and tree growth (e.g.
11 Meko et al., 1993; Hughes, 2002; Breitenmoser et al., 2014; D'Arrigo et al., 2014; St. George,
12 2014; Zhao et al., 2019) that can be used to estimate past climate variability. Nevertheless, the
13 empirical statistical approach has its limitations. Most models of the association between ring
14 width and climate that are used for paleoclimate reconstructions assume a univariate, linear, and
15 stationary relationship (e.g. Cook, 1987; Hughes, 2002, 2011). However, any of these assump-
16 tions might be violated if there is a significant non-climatic or secondary environmental control

17 on tree-ring formation, if the relationship displays threshold or nonlinear behavior, or if the as-
18 sociation between tree growth and climate changes over time (Vaganov et al., 1999; Anchukaitis
19 et al., 2006; Evans et al., 2006) .

20 A complementary approach to empirical statistical methods is the use of forward models that
21 simulate the process of tree-ring formation as a function of multivariate and potentially nonlinear
22 responses to climate. Such a model can also permit better temporal resolution, as cellular-scale
23 processes that ultimately give a tree-ring proxy its characteristics can be simulated as they re-
24 spond to daily weather and other environmental influences and not constrained to monthly statisti-
25 cal associations. Formalized as a proxy systems model (Evans et al., 2013), they can be inverted
26 or used in a data assimilation framework to reconstruct multiple climate variables.

27 The Vaganov-Shashkin model of tree-ring formation simulates the characteristics of annual
28 conifer growth rings by linking temperature, precipitation, and sunlight to the kinetics of
29 secondary xylem development at a daily time step (Vaganov et al., 1990, 1999; Vaganov and
30 Shashkin, 2000; Vaganov et al., 2006; Evans et al., 2006; Anchukaitis et al., 2006; Vaganov
31 et al., 2011). The model’s foundations are based on observations that demonstrate that external
32 influences are associated with tree-ring proxy metrics through climatic controls on the cellular
33 processes in the cambial zone (Denne and Dodd, 1981; Vaganov et al., 1990; Deslauriers et al.,
34 2003; Deslauriers and Morin, 2005; Rossi et al., 2006; Vaganov et al., 2006; Gričar et al., 2006;
35 Rossi et al., 2007; Rossi and Deslauriers, 2007; Moser et al., 2009; Deslauriers et al., 2007,
36 2008; Vaganov et al., 2011; Lenz et al., 2013; Begum et al., 2013; Körner, 2015; Rathgeber
37 et al., 2016; De Micco et al., 2019; Fatichi et al., 2019). The model has been applied to simu-
38 lating a hemisphere-scale network of tree-ring chronologies (Evans et al., 2006), used to detect
39 and diagnose changes tree-ring climate growth relationships (Vaganov et al., 1999; Anchukaitis
40 et al., 2006), and employed in studying the origin of multivariate statistical climate associations
41 in a temperate mesic environment (Shi et al., 2008; Vaganov et al., 2011).

42 These prior applications of the model have used computer code written in the FORTRAN
43 language (Evans et al., 2006). Another version of the model has been coded in Pascal (Shishov
44 et al., 2016). Both of these are compiled languages, where the program source code is first
45 translated into machine-specific instructions in an executable file. The primary advantage of this
46 is speed – the computational overhead of preparing the executable file from the source code is
47 incurred only once and compiled programs tend to be faster than interpreted languages, where
48 the source code is parsed and executed during while the program runs. MATLAB, R, and Python
49 are all examples of interpreted languages in broad use in the earth and environmental sciences
50 that execute program code directly (or using a ‘Just In Time’ approach) and do not require prior
51 compilation. While the primary disadvantage of this is that execution is slower than compiled
52 code, among the benefits are that programs are platform-independent and readily modified and
53 integrated within other code bases, workflows, or environments. Unlike R or Python, MATLAB
54 requires an individual or institutional license. Nevertheless, MATLAB is widely used in scientific
55 and engineering fields, including paleoclimatology, and broadly available in universities and
56 industry.

57 Here, we introduce an interpreted language version of the full Vaganov-Shashkin cambial
58 growth model (VSM) of tree-ring formation in MATLAB. Our core implementation of VSM
59 also works in the free Octave software. We briefly describe the model itself and its execution.
60 Three practical applications that demonstrate the utility of our interpreted language version of
61 the model program are demonstrated for *Pinus longaeva* in California (USA), *Tsuga canadensis*
62 in southern New York (USA), and *Larix cajanderi* in northern Yakutia (Russia). The model code
63 is freely available to use and can be adopted for additional development, platform-migration, and

64 integration in related applications.

65 2. Model Description

66 Complete details on development of the model and observations that support environmental
67 control on xylogenesis are available in Vaganov et al. (2006) and Vaganov et al. (2011). The orig-
68 inal FORTRAN code included three related modules: (1) a module that calculates environmental
69 conditions and determines a daily relative growth rate; (2) a module that simulates cambial activ-
70 ity based on the daily growth rate and ultimately determined the number cells in an annual ring,
71 (3) a cell size module that determines the characteristics of the individual cells in the ring and can
72 be compared directly to tracheidograms and measures of quantitative wood anatomy. Because
73 of the paucity of cellular-level measurements, nearly all applications of the Vaganov-Shashkin
74 model thus far have focused on the first two modules, primarily to investigate the climate controls
75 on the width of the annual rings.

76 Our implementation of the Vaganov-Shashkin model (VSM) therefore consists of the first
77 two modules, or blocks. The Growth (or Environmental) Block calculates daily climate and en-
78 vironmental conditions including temperature, solar irradiance, snow depth, soil moisture, and
79 evapotranspiration and determines a daily relative growth rate between 0 and 1 based on those
80 conditions. The Cambial Block then uses this growth rate to simulate the rate and timing of
81 growth and division of cells in the cambium. In this way, the kinetics of xylem formation are
82 explicitly modeled as a function of climate variability modified by environmental and cambial
83 processes. Our MATLAB version is identical to the original FORTRAN code, with two ex-
84 ceptions, also modified by Shishov et al. (2016): we impose a maximum depth of soil thaw in
85 permafrost environments no greater than the rooting depth itself. We also include additional
86 error catching to prevent unrealistic environmental parameters. In MATLAB the model is imple-
87 mented in double precision as opposed to single precision, which in some instances can create
88 non-trivial differences in model output between MATLAB and FORTRAN versions.

89 2.1. Growth (Environmental) Block

90 Daily growth rates are calculated by comparing daily (t) temperature (T) and soil moisture
91 (W) to piecewise linear growth functions (**Figure 1**, inset). Soil moisture (in units of v/v) is
92 updated daily by the model as a function of precipitation, snowmelt, evaporation (as a function
93 of temperature), and runoff (Thornthwaite and Mather, 1955). Solar irradiance is calculated from
94 the latitude corresponding to the tree-ring site or the origin of the temperature and precipitation
95 input data. Four parameters define the shape of the trapezoidal growth functions a minimum
96 (where $G(t) = 0$), lower and upper optimal bounds (where $G(t) = 1$), and a maximum (where
97 $G(t) = 0$). Between the minimum (or maximum) and the lower (or upper) bounds of the optimal
98 values for the climate parameter (temperature, sunlight, or soil moisture), growth rates will be
99 between 0 and 1. Relative growth rates are calculated for soil moisture ($g_W(t)$), temperature
100 ($g_T(t)$), and sunlight ($g_E(t)$). The determination of the overall daily growth rate $G(t)$ is calculated
101 as:

$$G(t) = g_E(t) \times \min [g_W(t), g_T(t)] \quad (1)$$

102 Because of the minimization term and the piecewise approximation of the nonlinear growth
103 function, the model behaves stoichiometrically and rates of cambial growth and division are
104 therefore controlled by the most limiting factor (Fritts, 1966, 1976) at a daily resolution.

105 2.2. Cambial Block

106 The Cambial Block uses the output $G(t)$ from the Growth Block to determine the rate at
107 which cambial cells grow and divide (**Figure 1**). Each cell in the Cambial Block is characterized
108 by two variables at each daily step: its position (j) in the cellular file and its diameter. The growth
109 rate $G(t)$ calculated in the prior block is used to derive a specific growth rate, $V(j, t)$, for each cell
110 based on its position. For cambial cells, diameter increases until a maximum size when division
111 occurs, or until the cell loses the ability to divide as its growth rate falls below a minimum
112 threshold for the cell's position in the radial file. Cells that lose the ability to divide pass out of
113 the cambium and complete the cell cycle. Daily cellular growth rates below a critical minimum
114 threshold send the cambium into dormancy. The cells in the cambium at the end of one simulated
115 growing season will therefore be those which first grow and divide in the subsequent year, and
116 can influence the cambial dynamics and tree-ring structure of the following year. Activity in
117 the cambium is initiated each year when the sum of temperatures above a certain threshold over
118 a specified period of time (growing degree days) reaches a critical threshold. VSM therefore
119 integrates the essential features of cambial dynamics as described above: Annual xylem cell
120 production is related to the number of cells in the cambial zone, the size of which varies over
121 the course of the year in response to environmental variability. Specific cellular growth rates are
122 positional and depend on the distance of the simulated cell from the cambial initial. Ring width
123 is determined in VSM by the number of cells in each annual ring (**Figure 2**; Gregory and Wilson,
124 1968; Camarero et al., 1998; Vaganov et al., 2006, 2011; Martin-Benito et al., 2017; Zhang et al.,
125 2018) and reported as normalized (index) values by dividing the number of cells in each ring by
126 the average number of annual cells over the simulation.

127 2.3. Input Data, Parameters, and Model Output

128 The model uses daily precipitation and temperature from meteorological stations, gridded
129 data, or climate model output as required input data. The 28 primary model parameters are based
130 on empirical and experimental data, whose selection is discussed in detail by Vaganov et al.
131 (2006). Different parameter sets may be applied for different environments (Vaganov et al., 2006;
132 Evans et al., 2006; Anchukaitis et al., 2006; Shi et al., 2008; Vaganov et al., 2011), but in prac-
133 tice we have found that model output is sensitive to relatively few of the parameters (Anchukaitis
134 et al., 2006; Vaganov et al., 2011) and that the simulations are dominated by the climate vari-
135 ability and the parameters that specify the thresholds of the piecewise growth functions. Model
136 output includes the normalized tree-ring width chronology, the overall and component simulated
137 growth rates, and environmental variables. The model does not simulate additional biological or
138 ecological influences on patterns of tree-ring formation, including those caused by tree age and
139 geometry, carbon storage, canopy and root activity, or stand-level competition and disturbance.
140 The simulations can therefore be considered as perfectly detrended tree-ring chronologies.

141 3. Model Applications

142 3.1. *Pinus longaeva* in the White Mountains, California

143 Bristlecone pines (*Pinus longaeva*) in eastern California and Nevada are the longest living
144 non-clonal organisms on Earth, likely achieving ages in excess of 5000 years (Schulman, 1958;
145 Currey, 1965; Hallman et al., 2006). The climate signal embedded in the rings of these ancient
146 trees is complicated, however, empirically estimated as a mix of temperature and precipitation
147 sensitivity as a function of elevation and position on the landscape (LaMarche, 1974b,a; Hughes

148 and Funkhouser, 1998, 2003; Salzer et al., 2009; Bunn et al., 2011; Tran et al., 2017; Bunn et al.,
149 2018). Here we use the daily climate data from National Weather Service Cooperative Network
150 weather station 049632 (WHITE MTN 1, 1955 to 1977, 37.50°N, 118.18°W, 3094 m elevation)
151 to simulate bristlecone growth at the Methuselah Walk site (Hughes and Graumlich, 1996; Salzer
152 et al., 2009). We modify the temperature data for the difference between the elevation of the sta-
153 tion and chronology location using a simple lapse rate correction. Bunn et al. (2018) also recently
154 used VSM with a higher elevation composite meteorological record to investigate landscape-
155 scale topographic influences on the climate response of high elevation bristlecone pines in the
156 White Mountains.

157 We use VSM here to demonstrate how the model can be run iteratively to investigate the
158 sensitivity of the model to parameter choices, specifically the rate of soil water drainage from
159 the simulated soil column. Anchukaitis et al. (2006) found this parameter was important for
160 correctly capturing interannual growth variability at tree-ring sites in the southeastern United
161 States, but that soil type alone provided only a weak constraint on the parameter value itself. We
162 run the model iteratively using the White Mountains parameter set developed by Vaganov et al.
163 (2006) and a varying coefficient of drainage (dimensionless) from 0.001 to 0.02 by increments
164 of 0.0001. This generates 191 simulated chronologies which we then compare against the actual
165 Methuselah Walk chronology (**Figure 3a**). Correlations between the ensemble members and the
166 actual chronology range from $r = 0.37$ ($p = 0.09$) to $r = 0.79$ ($p < 0.001$), with a broad range
167 of drainage values yielding significant ($p < 0.05$) correlations between simulated and actual
168 chronologies (**Figure 3b,c**).

169 We can also use the model output to examine the environment controls on ring width forma-
170 tion (**Figure 4**). The best simulation (**Figure 4a**) shows that simulated mean annual snow depths
171 peak in April and decline through the middle of June and that this snowmelt recharges soil mois-
172 ture until a maximum in June (**Figure 4b**). Soil moisture then declines through the remainder
173 of the summer and autumn as rising temperatures lead to a maximum in evapotranspiration and
174 minimum soil moisture values are reached in September (**Figure 4b**). These environmental pat-
175 terns are reflected in the components of the daily growth rate as well. Starting in July, growth
176 rates due to soil moisture begin to decline and by early August are below the growth rate due
177 to the direct influence of temperature (**Figure 4c**). Growth limitation due to soil moisture con-
178 tinues until early September, when overall growth rates decline with the arrival of shorter days,
179 lower temperatures, and accumulating snowpack. The model output therefore confirms that the
180 moisture-sensitivity of bristlecone pines at the lower elevation Methuselah Walk site (LaMarche,
181 1974b,a; Hughes and Graumlich, 1996; Salzer et al., 2009; Bunn et al., 2018) is therefore due to
182 summer soil moisture deficits driven by progressive drying following the end of snowmelt, lim-
183 ited summer precipitation, and high rates of growing season evapotranspiration at these semi-arid
184 sites.

185 3.2. *Tsuga canadensis* at Shawangunk Ridge, New York

186 We previously investigated (Vaganov et al., 2011) the ability of the VSM to reproduce the
187 annual growth patterns and multivariate climate response of eastern hemlock (*Tsuga canadensis*)
188 trees growing on a talus slope in the Shawangunk Mountains near Mohonk Lake in the Hud-
189 son Valley of New York state (Cook and Jacoby, 1977; Cook and Jacoby Jr, 1979; Cook et al.,
190 2010; Cook and Pederson, 2011; Cook, 2014). We demonstrated that our simulation captured
191 the temporal variability in ring width at this steep and well-drained site, as well as mimicking
192 the multivariate climate response - a positive response to spring temperature and summer pre-
193 cipitation, and negative response to summer temperature for a broad range of the soil moisture

194 drainage rate parameter (Vaganov et al., 2011; Cook and Pederson, 2011). Here, we return to
195 this site to evaluate two additional parameters, the minimum temperature for growth ($T_{minimum}$)
196 and the lower end of range of optimal temperatures ($T_{lower\ optimal}$), which define the rising portion
197 of the piecewise growth function (**Figure 1**, inset). We use a Latin Hypercube sampling design
198 (Stein, 1987) to generate a set of 1000 coupled parameter values drawn from uniform distribu-
199 tions $U(0, 10)$ and $U(11, 20)$ for these temperature growth parameters, respectively. We use the
200 long continuous meteorological data from the nearby Mohonk Mountain House (Cooperative
201 Station 305426; Cook et al., 2010) to simulate growth. We then evaluated the correlation be-
202 tween the ensemble of simulations and the actual Mohonk hemlock tree-ring chronology (Cook
203 and Jacoby, 1977) during their period of overlap, 1925 to 1973. Use of an interpreted language
204 here permits us to easily use an iterative approach to sample from the parameter value space,
205 run VSM, generate a large ensemble of simulations, evaluate the resulting simulated tree-ring
206 chronologies, and plot and analyze the results and the detailed model output.

207 Consistent with our previous findings (Vaganov et al., 2011), we can successfully simulate
208 the Mohonk chronology ($r = 0.60$, $p < 0.01$) and capture the mixed temperature and sum-
209 mer precipitation signal in the actual tree-ring chronology (**Figure 5a**). Interestingly, significant
210 correlations between 1000 simulation ensemble members and Mohonk Lake tree-ring width are
211 observed for a wide range of minimum and optimal temperature parameters (**Figure 5b**). Min-
212 imum temperature even in the wide range between 0 and 10C still result in a positive response
213 to March or April temperatures that mirrors that of the actual chronology (**Figure 5c**). Param-
214 eters where the minimum and lower bound optimal temperature are both high have the lowest
215 correlations with actual tree-ring widths. This appears to be due to a reduction in sensitivity in
216 these runs to temperature in the spring, as growth both starts later in the year and the shallow
217 slope of the rising limb of the growth function reduces the magnitude of the model’s response to
218 temperature until soil moisture exerts control on growth in the summer. Both simulated and real
219 chronologies for Mohonk Lake have a negative response to May temperatures, which in model
220 simulations corresponds to a decline in soil moisture that makes it the most limiting growth fac-
221 tor (**Figure 5c**). The model simulations indicate that peak summer temperatures are sufficient to
222 drive growth rates due to temperature beyond the upper optimal bounds and onto the declining
223 limb of the piecewise growth function; however, decreased soil moisture remains even more lim-
224 iting for growth during the summer, and drives a positive response to May through July rainfall.

225 3.3. Larch in northern Yakutia, Russia

226 Large volcanic eruptions can cause anomalously cold summer temperatures for a year or
227 more following an event (Robock, 2000). Climate models and climate reconstructions, however,
228 disagree on the magnitude and duration of this cooling over the last millennium (Ammann et al.,
229 2007; D’Arrigo et al., 2013). Mann et al. (2012) adopted a simplified form of the Vaganov-
230 Shashkin model and used it to suggest that the cause of this discrepancy was the existence
231 of undetected missing rings in temperature-sensitive chronologies. Anchukaitis et al. (2012)
232 showed that the conclusions of Mann et al. (2012) were based on using unrealistic model param-
233 eter choices, in particular a choice for temperature below which growth cannot occur of $10^{\circ}C$,
234 which is much higher than observed in nature ($\sim 5^{\circ}C$; Anchukaitis et al. (2012) and references
235 therein). Here, we use VSM to simulate a high latitude temperature-sensitive tree-ring *Larix*
236 *cajanderi* chronology from the Indigirka region (northern Yakutia, Russia) (Hughes et al., 1999;
237 Kirilyanov et al., 2003; Sidorova et al., 2005; Guillet et al., 2017) as a demonstration of the influ-
238 ence of parameter selection on modeling tree-ring width in response to temperature changes. We
239 use daily meteorological data from the Global Historical Climatology Network weather station at

240 Chokurdakh, Russia (RSM00021946, 70.60°N, 147.86°E, 40m elevation; Vaganov et al. (2006);
241 Evans et al. (2006)). We run the model iteratively with a range of minimum growth temperatures
242 from 0°C to 10°C in 1°C increments and compare the simulated chronology against the actual
243 tree-ring width chronology from Indigirka (Guillet et al., 2017). We also record the number of
244 years with no simulated growth under these conditions.

245 The model overall produces statistically significant ($p < 0.05$) simulations for minimum
246 growth temperature values up to 8°C (**Figure 6a,b**). However, for a minimum growth tempera-
247 ture parameter of 5°C and higher, the model produces one or more years without growth in the
248 chronology (**Figure 6c**) - an entirely missing ring. Although there can be individual locally-
249 absent rings in the individual trees comprising the Indigirka chronology, there are no years for
250 which every ring in every tree is missing, evidence that these parameter values are inappropri-
251 ate for accurately simulating the actual chronology. Above a minimum temperature parameter
252 of 6°C, multiple non-growth years degrade the correlation between the simulated and actual
253 chronologies, and for a minimum growth temperature parameter above 8°C the frequency of
254 missing growth years causes the relationship between simulated chronology to become non-
255 significant ($p > 0.05$, **Figure 6b**). A similar result was found by Anchukaitis et al. (2012) and
256 here demonstrates the application of our MATLAB version of VSM for evaluating and identify-
257 ing realistic and appropriate model parameterization. More generally, sampling over reasonable
258 parameter space and observing the range of simulations as we have done here may be a way to
259 capture the range of stochastic growth variations – including locally absent rings – in a forest
260 stand. We note that the mismatch here in simulated vs. observed tree-ring width in 1991 could
261 also arise from heightened uncertainty in weather observations associated with the collapse of
262 the Soviet Union (Jones and Moberg, 2003; Dell et al., 2014).

263 4. Summary

264 We have described here an interpreted language version of the Vaganov-Shashkin model
265 (VSM) in MATLAB. In addition to the applications described above, the code can now be mod-
266 ified for additional functionality. For instance, the model might be modified to accept mea-
267 sured photosynthetically active radiation or soil moisture from observations or models in place
268 of the simple internal calculations of these metrics. VSM could also be deployed as a proxy sys-
269 tem model in support of data assimilation approaches to climate reconstruction (Evans et al.,
270 2013; Hakim et al., 2016). Integration of tree-ring modeling with forest growth simulation
271 could potentially improve tree growth, forest dynamics and carbon models (e.g. Mina et al.,
272 2016; Evans et al., 2016; Babst et al., 2018). Addition of a cell growth module could pro-
273 duce cell anatomical simulations that could be compared to emerging observations (c.f. Fonti
274 et al., 2010; Cuny et al., 2015; von Arx et al., 2016; Ziaco et al., 2016). Finally, the model
275 may also be ported to other open source languages, as has been done for the monthly resolu-
276 tion ‘lite’ version of the Vaganov-Shashkin model (VSL; Tolwinski-Ward et al., 2011, 2013).
277 Code for VSM, supporting utility functions, and the three examples shown here are all avail-
278 able at <https://github.com/kanchukaitis/vsm> under a Creative Commons Attribution-
279 NonCommercial-ShareAlike 4.0 license.

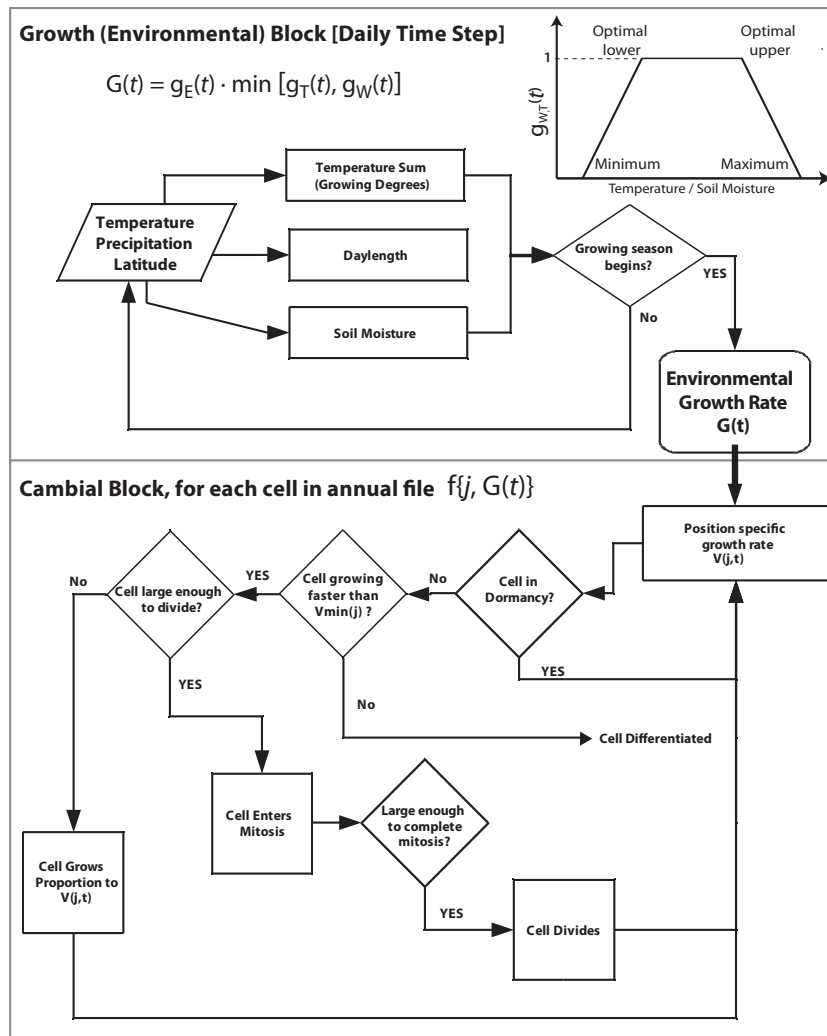


Figure 1: Vaganov-Shashkin growth and cambial model block processes from Vaganov et al. (2011). Daily growth rates due to the environment are determined by comparing daily temperature and soil moisture (calculated from precipitation, transpiration, and soil drainage) to piecewise linear approximations of parabolic growth functions (see inset) in the Growth (Environmental) Block. This growth rate is then used in the Cambial Block to calculate the cellular growth rate $V(j, G(t))$, which is a function of this environmental growth rate and the position of the cell in the radial file. Each cell is permitted to be dormant, differentiate, grow, or divide on an intraday time interval. When a non-differentiated cell reaches a critical size, it enters and completes the mitotic cycle, continuing its subsequent growth at a constant, environmentally independent growth rate until division occurs, resulting in two cells, each half the size of the original mother cell. Once differentiated, cells can no longer divide. Figure used with permission from Springer Nature.

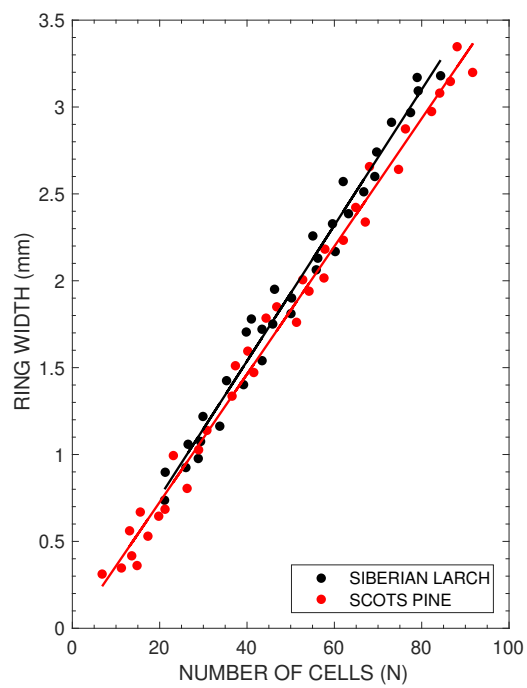


Figure 2: The association between the number of cells in the radial cellular tracheid file and the width of the annual ring. In conifers, the dominant control on ring width is the number of cells. Data from Vaganov et al. (2006)

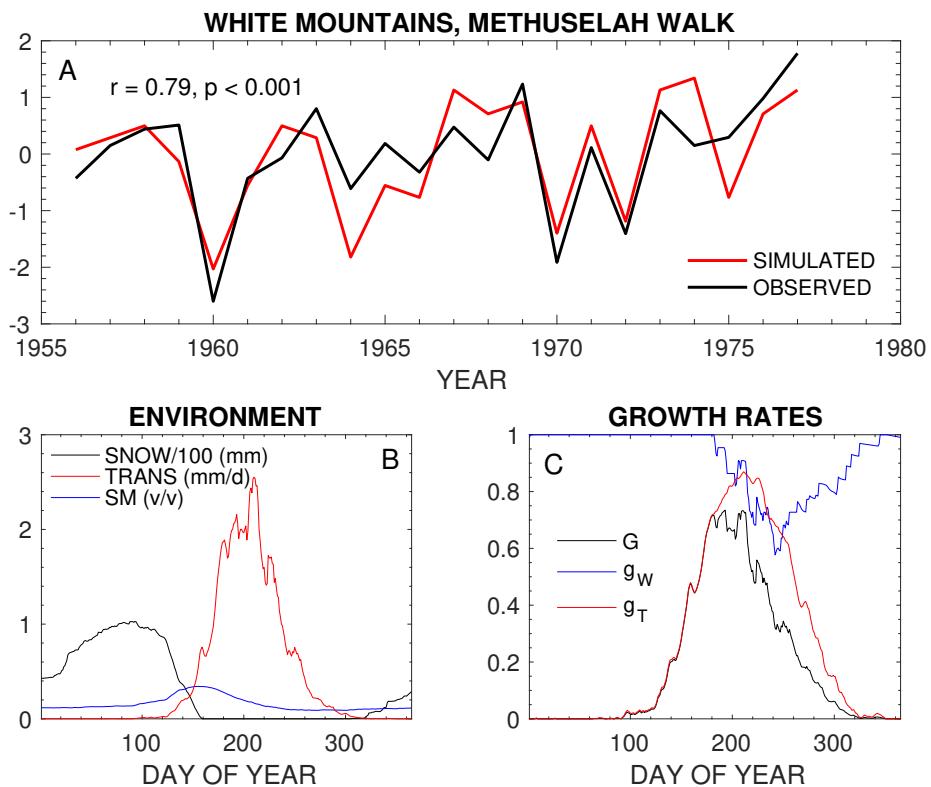


Figure 3: Ensemble reconstruction of the *Pinus longaeva* tree-ring width chronology from Methuselah Walk, Ancient Bristlecone Pine Forest, California. (A) Time series of ring width simulations and the actual Methuselah Walk chronology. Pink lines are all the ensemble members generated by modeling a range of soil moisture drainage parameters shown in panel (B). The red line is the ensemble member with the highest correlation with the actual chronology ($r = 0.79$, $p < 0.001$), which is shown in black. All values are normalized ring width indices. (B) The relationship between the soil drainage rate parameter and the correlation between the respective simulation and the actual chronology. Significance values are indicated by the color of each dot. (C) Histogram of correlation coefficients for the ensemble of simulated vs. actual chronology.

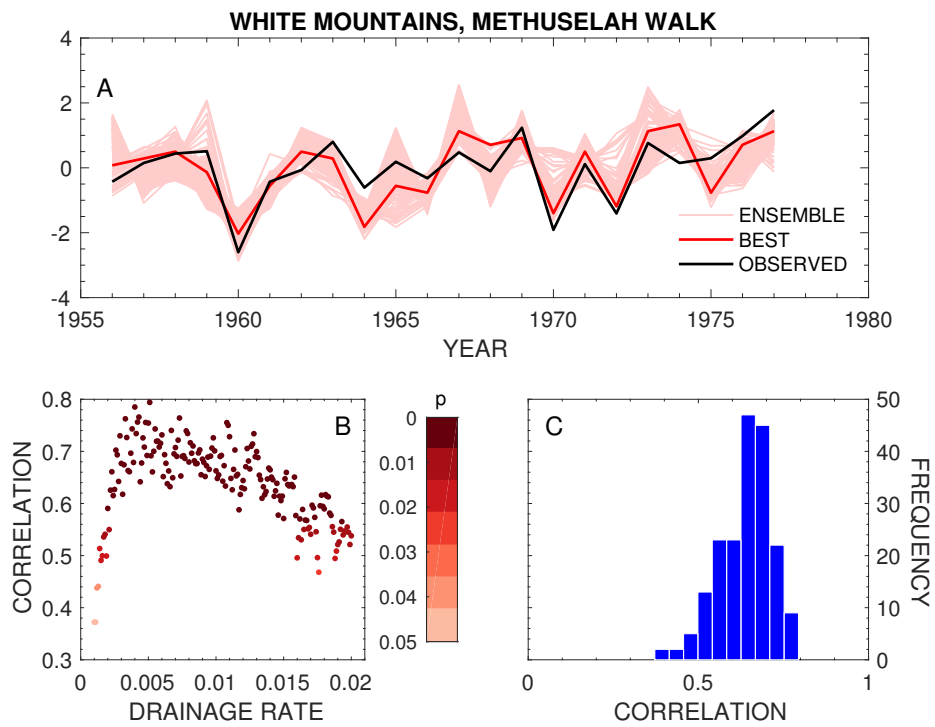


Figure 4: Model output details for the White Mountain *Pinus longaeva* simulations. (A) Simulated and actual ring width chronologies for the best simulation shown in Figure 3. (B) Mean daily environmental outputs for the best simulation. The snow depth values have been divided by 100 to allow all the metrics to appear on the same axis. (C) Mean daily overall growth rates ($G(t)$) and growth rates as limited by temperature ($g_T(t)$) and soil moisture ($g_W(t)$).

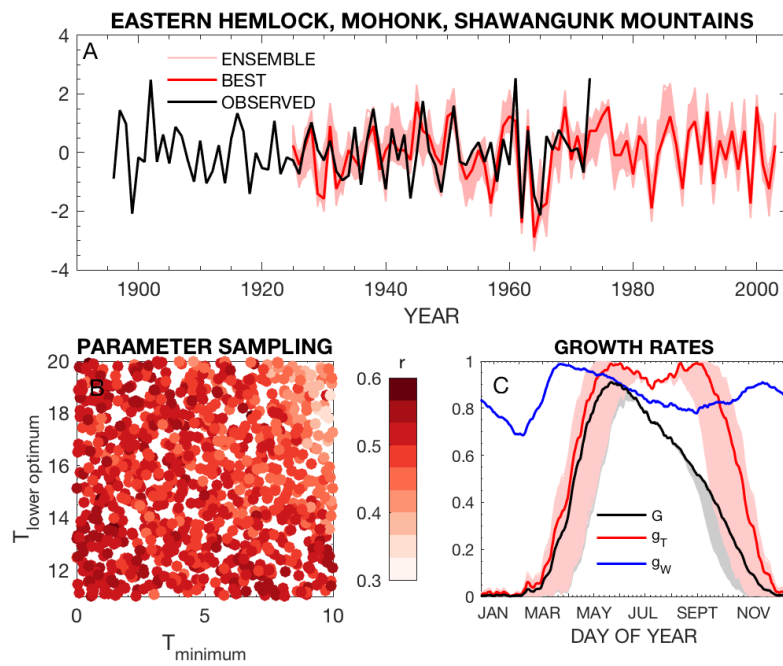


Figure 5: Simulations of the Mohonk Lake *Tsuga canadensis* tree-ring width chronology at Shawangunk Ridge, New York. (A) Ensemble simulations including the best match ($r = 0.60$, $p < 0.01$) with the observed Mohonk chronology (Cook and Jacoby, 1977). (B) Correlations (colored circles) between simulation ensemble members at the real chronology as a function of the minimum temperature and lower optimal temperature used for the piecewise growth function. (C) Mean daily growth rates due to temperature ($g_T(t)$), soil moisture ($g_W(t)$), and overall ($G(t)$). Light colored lines for temperature and overall growth rates are the individual ensemble members, while the dark heavy lines are for the simulation with the highest correlation to the actual chronology.

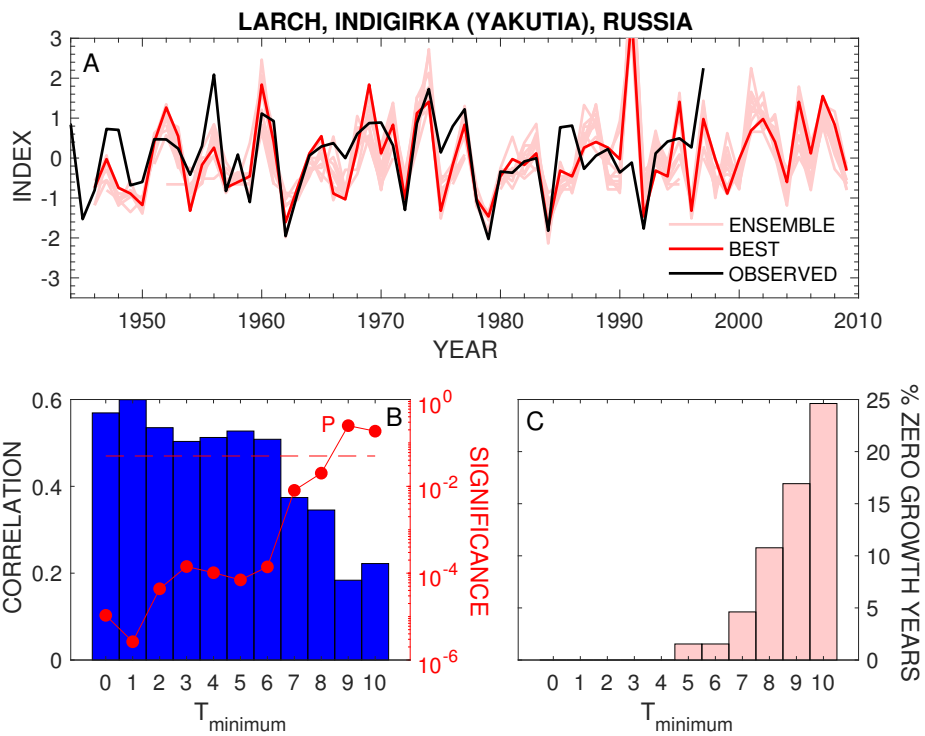


Figure 6: Simulations of the Larch tree-ring width chronology in Northern Yakutia, Russia. (A) Time series of ring width simulations and the actual Indigirka chronology. Pink lines are all the ensemble members generated by modeling a range of the minimum temperature parameter shown in panel (B). The red line is the ensemble member with the highest correlation with the actual chronology ($r = 0.79$, $p < 0.001$), which is shown in black. All values are normalized ring width indices. (B) Correlations (blue bars) and statistical significance (red line and circles) between simulations with different minimum growth temperature values and the actual chronology. The red dashed line marks the $p < 0.05$ significance level. (C) Percent of simulated years with no growth as a function of different minimum growth temperature values.

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