1 Simulation of tree ring-widths with a model for primary production, carbon allocation

2 and growth

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11 Abstract

12 We present a simple, generic model of annual tree growth, called 'T'. This model accepts input from a first-

13 principles light-use efficiency model (the P model). The P model provides values for Gross Primary

14 Production (GPP) per unit of absorbed photosynthetically active radiation (PAR). Absorbed PAR is estimated

15 from the current leaf area. GPP is allocated to foliage, transport-tissue, and fine root production and

16 respiration, in such a way as to satisfy well-understood dimensional and functional relationships. Our

17 approach thereby integrates two modelling approaches separately developed in the global carbon-cycle and

18 forest-science literature. The T model can represent both ontogenetic effects (impact of ageing) and the

19 effects of environmental variations and trends (climate and CO_2) on growth. Driven by local climate records,

20 the model was applied to simulate ring widths during 1958~2006 for multiple trees of *Pinus koraiensis* from

21 the Changbai Mountain, northeastern China. Each tree was initialised at its actual diameter at the time when

22 local climate records started. The model produces realistic simulations of the interannual variability in ring

23 width for different age cohorts (young, mature, old). Both the simulations and observations show a significant

24 positive response of tree-ring width to growing-season total photosynthetically active radiation (PAR_0) and

25 the ratio of actual to potential evapotranspiration (α), and a significant negative response to mean annual

26 temperature (MAT). The slopes of the simulated and observed relationships with PAR_0 and α are similar; the

27 negative response to MAT is underestimated by the model. Comparison of simulations with fixed and

28 changing atmospheric CO_2 concentration shows that CO_2 fertilization over the past 50 years is too small to be

29 distinguished in the ring-width data given ontogenetic trends and interannual variability in climate.

30 1 Introduction

31 Forests cover about 30% of the land surface (Bonan, 2008) and are estimated to contain 861±66 PgC (Pan et
32 al., 2011). Inventory-based estimates show that forests have been a persistent carbon sink in recent decades,
33 with a gross uptake of 4.0±0.5 PgCyear^{-1} and a net uptake of 1.1±0.8 PgCyear^{-1} between 1990 and 2007 (Pan
34 et al., 2011). This is a significant amount in comparison with the amounts of carbon released from fossil fuel
35 burning, cement production and deforestation (9.5±0.8 PgCyear^{-1} in 2011: Ciais et al., 2013) and thus, forest
36 growth has a substantial effect on atmospheric CO_2 concentration and climate (Shevliakova et al., 2013).
37 However, there is considerable geographic variability in the trends in the carbon sink as well as the factors
38 controlling regional trends, and uncertainty about how forest growth and carbon sequestration will be affected
39 by climate change, and climate-driven changes in wildfire (Ciais et al., 2013; Moritz et al., 2013). The
40 changing importance of disturbance, and its influence on forest age, is likely to have a significant impact on
41 the ability of forests to act as carbon sinks. It is generally assumed that stand-level productivity stabilizes or
42 declines with age (Ryan et al., 1997; Caspersen et al., 2011). However, recent analyses have shown that mass
43 growth rate (and hence carbon accumulation) by individual trees increases continuously with tree size
44 (Stephenson et al., 2014), pointing to a need to understand the relationship between individual and stand
45 growth rates. Predictions of future changes in the terrestrial carbon cycle (e.g. Friedlingstein and Prentice,
46 2010) rely on ecosystem models that explicitly represent leaf-level processes such as photosynthesis, but in
47 most cases do not incorporate the response of individual trees. In models that do consider individual tree
48 growth (e.g. ED: Moorcroft et al 2001, Medvigy et al. 2012; LPJ-GUESS: Smith et al., 2001; Claesson and
49 Nycander, 2013), little attention has been paid to evaluating the realism of simulated radial growth.
50 Incorporating the response of individual trees to climate and environmental change within such modelling
51 frameworks should help to provide more realistic estimates of the role of forests in the global carbon cycle.

52 Climate factors, such as temperature and moisture availability during the growing season, are important
53 drivers of tree growth (Harrison et al., 2010). This forms the basis for reconstructing historical climate
54 changes from tree-ring records of annual growth (Fritts, 2012). However, photosynthetically active radiation
55 (PAR) is the principal driver of photosynthesis. Models for primary production that use temperature, not PAR,
56 implicitly rely on the far-from-perfect correlation between temperature and PAR (Wang et al., 2014). PAR
57 can change independently from temperature (through changes in cloudiness affecting PAR or atmospheric
58 circulation changes affecting temperature) and this may help to explain why statistical relationships between
59 tree growth and temperature at some high latitude and high elevation sites appear to breakdown in recent
60 decades (D'Arrigo et al., 2008). CO_2 concentration also has an impact on tree growth, although its magnitude
61 is still controversial: trends in tree growth have been attributed to increasing atmospheric CO_2 concentration
62 in some studies (Wullschleger et al., 2002; Körner, 2006; Huang et al., 2007; Koutavas, 2013) and not others
63 (Miller, 1986; Luo et al., 2004; Reich et al., 2006). To resolve these apparent conflicts, and to understand tree
64 growth processes better, it is necessary to analyse the response of tree growth to multiple factors acting
65 simultaneously, including solar radiation, climate, CO_2, and ontogenetic stage.

66   Modelling is needed for this purpose. Empirical models of annual tree growth and climate variables

67   (temperature and precipitation) have been used to simulate tree radial growth (Fritts, 2012). Process-based

68   bioclimatic models might be preferable, however, because this allows other factors to be taken into account

69   (e.g. the direct impact of CO_2 concentration on photosynthesis) and for non-stationarity in the response to

70   specific climate variables. Vaganov et al. (2006) and Rathgeber et al. (2005) have used bioclimatic variables

71   (temperature, and soil moisture availability) chosen to reflect physiological processes to simulate radial tree

72   growth. The MAIDEN model (Misson, 2004; Misson et al., 2004; see also MAIDENiso: Danis et al., 2012)

73   models the phenological and meteorological controls on NPP and explicitly allocates carbon to different

74   carbon pools (including the stem) on a daily basis using phenological stage-dependent rules. Nevertheless,

75   MAIDEN still requires tuning of several parameters.

76   Simple equations representing functional and geometric relationships can describe carbon allocation by trees

77   and make it possible to model individual tree growth (Yokozawa and Hara, 1995; Givnish, 1988; Falster et al.,

78   2011; King, 2011). Such models are built on measurable relationships, such as that between stem diameter

79   and height (Thomas, 1996; Ishii et al., 2000; Falster and Westoby, 2005), and crown area and diameter or

80   height (Duursma et al., 2010) that arise because of functional constraints on growth. The pipe model

81   represents the relationship between sapwood area and leaf area (Shinozaki et al., 1964; Yokozawa and Hara,

82   1995; Mäkelä et al., 2000). The ratio of fine root mass to foliage area provides the linkage between above and

83   below ground tissues (Falster et al., 2011). These functional relationships are expected to be stable through

84   ontogeny, which implies that the fraction of new carbon allocated to different compartments is variable

85   (Lloyd, 1999). In this paper, we combine the two modelling approaches previously developed in the global

86   carbon-cycle (ecophysiology) and forest-science (geometric and carbon allocation) literature to simulate

87   individual tree growth.

88

89   2 Methods

90   2.1 Model structure and derivation

91   We use a light-use efficiency model (the P model: Wang et al., 2014), driven by growing-season PAR, climate

92   and ambient CO_2 concentration inputs, to simulate gross primary production (GPP). The simulated GPP is

93   used as input to a species-based carbon allocation and functional geometric tree growth model (the T model)

94   to simulate individual tree growth (Fig. 1).

95   2.1.1 The P model

96   The P model is a simple but powerful light-use efficiency and photosynthesis model, which simulates GPP per

97   unit of absorbed PAR from latitude, elevation, temperature, precipitation and fractional cloud cover (Wang et

98   al., 2014). The climate observations used here are monthly temperature, precipitation and fractional cloud

99 cover, which are interpolated to a daily time step for subsequent calculations of the variables that determine

100 annual GPP.

101 Potential annual *GPP* is the product of the PAR incident on vegetation canopies (*PAR$_0$*), with the maximum

102 quantum efficiency of photosynthesis (*Φ_0*), the fraction of absorbed PAR (*fAPAR*), and the effect of

103 photorespiration and substrate limitation at subsaturating [CO_2] represented as a function of the leaf-internal

104 [CO_2] (*c_i*) and the photorespiratory compensation point (*Γ^**), as shown in Eq. (1).

105 $\quad GPP = \Phi_0 \, (PAR_0 \times fAPAR) \, (c_i - \Gamma^*)/(c_i + 2\Gamma^*)$ $\hspace{4cm}$ (1)

106 where *Φ_0* is set to 0.48 g C/ mol photon, based on a quantum efficiency of 0.05 mol C/ mol photon and a leaf

107 absorptance of 0.8. Daily PAR at the top of the atmosphere is calculated based on solar geometry and is

108 subsequently modified by transmission through the atmosphere, which is dependent on elevation and cloud

109 cover. Annual effective PAR (PAR0) is calculated as the annual sum of daily PAR but taking into account the

110 low-temperature inhibition of photosynthesis and growth, using a linear ramp function to downweight PAR on

111 days with temperatures below 10 °C. Days with temperatures below 0˚C do not contribute to PAR0. See

112 Wang et al. (2014) for details. In this application, we first calculated potential *GPP* with *fAPAR* set to 1.

113 *fAPAR* is not an input to the model but is calculated implicitly, from the foliage cover simulated by the T

114 model.

115 Leaf-internal [CO_2] is obtained from the ambient [CO_2] via the 'least-cost hypothesis' (Wright et al., 2003;

116 Prentice et al., 2014). Wang et al. (2014) provide a continuous prediction of the *c_i/c_a* ratio as a function of

117 environmental aridity, temperature and elevation based on this hypothesis:

118 $c_i/c_a = 1/(1 + C\sqrt{(\eta\sqrt{(D)}/K)})$ $\hspace{5cm}$ (2)

119 where *D* is the cumulative water deficit over a year (proportional to an annual "effective value" of the vapour

120 pressure deficit: VPD), *η* is the dynamic viscosity of water, *K* is the effective Michaelis-Menten coefficient for

121 Rubisco-limited photosynthesis, and *C* is a constant. The difference between the annual actual and equilibrium

122 evapotranspiration is used as a proxy for *D* (see Prentice et al., 2013). *D* is calculated using the daily

123 interpolated temperature, precipitation and cloudiness data. Annual actual evapotranspiration is derived from

124 equilibrium evapotranspiration and precipitation using a simple soil moisture accounting scheme with a daily

125 time step, as described in Gallego-Sala et al. (2010). The temperature dependences of *η* and *K* follow Prentice

126 et al. (2014). Both *K* and *η* change steeply with temperature: *K* changes from 196 ppm at 10 °C to 1094 ppm

127 at 30 °C ; *η* decreases from 1.31 mPa s at 10 °C to only 0.798 mPa s at 30 °C.

128 The temperature dependence of *Γ^** is described by an exponential closely approximating an Arrhenius

129 function (Bernacchi et al., 2003):

130 $\Gamma^* = \Gamma^*_{25} \exp(0.0512\Delta T)$ $\hspace{6cm}$ (3)

131 where *Γ^*_{25}* is the value of *Γ^** at 25 °C (4.331 Pa), and *ΔT* is the monthly temperature difference from 25 °C.

132   The P model has been shown to simulate well many of the global patterns of annual and maximum monthly

133   terrestrial GPP) by C_3 plants. The simulated seasonal cycle of GPP at different latitudes is supported by

134   analyses of CO_2 flux measurements (Wang et al., 2014).

135   2.1.2 The T model

136   We assume that potential GPP is the first-order driver of tree growth both at stand and individual level. The T

137   model translates potential GPP as simulated by the P model into individual tree growth, which depends on

138   foliage cover within the canopy and the respiration of non-green tissues, carbon allocation to different tissues,

139   and relationships between different dimensions of the tree. Although these relationships are often loosely

140   called "allometries", true allometries (power functions) have the undesirable mathematical property for

141   growth modelling that, if the power is greater than one, the derivative evaluated at the start of growth is zero;

142   if the power is between zero and one, the derivative is infinite. We have therefore avoided the use of power

143   functions, except for geometric relationships where they are unambiguously correct.

144
145   *Functional geometric relationship*

146   Carbon is allocated to different tissues within the constraint of the basic functional or geometric relationships

147   between different dimensions of the tree.

148   Asymptotic height-diameter trajectories (Thomas, 1996; Ishii et al., 2000; Falster and Westoby, 2005) are

149   modeled as:

150    $H = H_m \left[1 - \exp \left(-aD/H_m \right) \right]$ (4)

151   where H is the tree height, D is the basal diameter, H_m is the (asymptotic) maximum height, and a is the initial

152   slope of the relationship between height and diameter.

153   The model also requires the derivative of this relationship:

154    $dH/dD = a \exp \left(-aD/H_m \right) = a \left(1 - H/H_m \right).$ (5)

155   The form of the stem is assumed to be paraboloid (Jonson, 1910; Larsen, 1963). It can be shown (assuming

156   the pipe model) that this form is uniquely consistent with a uniform vertical distribution of foliage area during

157   early growth, i.e. in the absence of heartwood. Here, the total stem mass (W_s) is expressed as a function of D

158   and H:

159    $W_s = (\pi/8) \, \rho_s D^2 H$ (6)

160   where ρ_s is the density of the wood, and $(\pi/8) \, D^2 H$ is the volume of a paraboloid stem.

161   The relationship of diameter increment to stem increment is then given by:

162    $dW_s/dt = (\pi/8)\, \rho_s \,[D^2 \,(dH/dD) + 2\, DH]\, dD/dt$ (7)

163   The projected crown area (A_c) is estimated from D and H using an empirical relationship:

164    $A_c = (\pi c/4a)\, DH$ (8)

165   where c is the initial ratio of crown area to stem cross-sectional area. This relationship was chosen as an
166   intermediate between previously published expressions that relate A_c either to D^2 or H. It is consistent with
167   reported allometric coefficients typically between 1 and 2 for the relationship between A_c and D.

168   Crown fraction (f_c) is also derived from H and D. As we assumed the stem to be paraboloid, the stem cross
169   sectional area at height z is :

170    $A_s(z) = A_s\, (1-z/H)$ (9)

171   where A_s is the basal area: $A_s = (\pi/4)D^2$. We find the height (z^*) at which the ratio of foliage area (A_f) to stem
172   area at height z^* ($A_s(z^*)$) is the same as the initial ratio of crown area to stem cross-sectional area (c). We
173   obtain crown area (A_c) from:

174    $A_c = c\, A_s(z^*) = c\, A_s\, (1-z^*/H)$.   (10)

175   Combining this with Eq. (8), we obtain $(\pi c/4a)\, DH = c\, A_s\, (1-z^*/H)$, which reduces to:

176    $f_c = (1-z^*/H) = H/aD$.   (11)

177   The initial slope (a) is in principle dependent both on species growth form and on ambient conditions,
178   including light availability. Here it is determined directly from observations.

179   *Carbon allocation*

180   Actual GPP (P) is obtained from potential GPP (P_0) using Beer's law (Jarvis and Leverenz, 1983):

181    $P = P_0\, A_c\, (1 - \exp(-kL))$ (12)

182   where k is the extinction coefficient for PAR, and L is the leaf area index within the crown.

183   Net primary production (NPP) is derived from annual GPP, corrected for foliage respiration (which is set at
184   10% of total GPP, an approximation based on the theory developed by Prentice et al., 2014 and Wang et al.,
185   2014), by further deducting growth respiration and the maintenance respiration of sapwood and fine roots.
186   Growth respiration is assumed to be proportional to NPP, following:

187    $P_{net} = y(P-R_m) = y\, (P - W \bullet_s\, r_s - \zeta\, \sigma\, W_f\, r_r)$ (13)

188   where P_{net} is NPP, R_m is the maintenance respiration of stem and fine roots, and y is the 'yield factor'
189   accounting for growth respiration. Total maintenance respiration of non-green parts comprises fine-root

190 respiration ($\zeta\, \sigma\, W_f r_r$, where ζ is the ratio of fine-root mass to foliage area, σ is the specific leaf area, W_f is the

191 mass of carbon in foliage $((1/\sigma)\, L\, A_c)$, and r_r is the specific respiration rate of fine roots), and stem (sapwood)

192 respiration ($W\bullet_s\, r_s$, where $W\bullet_s$ is the mass of carbon in sapwood, and r_s is the specific respiration rate of

193 sapwood). $W\bullet_s$ can be estimated from A_c through the pipe model:

194 $$W\bullet_s = L\, A_c\, v_H\, \rho_s\, H_f \qquad\qquad\qquad (14)$$

195 where v_H is the Huber value (ratio of sapwood to leaf area; Cruiziat et al., 2002), and H_f is the mean foliage

196 height $H\, (1 - f_c/2)$. The constraint that the initial sapwood area must be equal to the stem cross-sectional era

197 leads to the following identify: $L\, c\, v_H = 1$.

198 NPP is allocated to stem increment (dW_s/dt), foliage increment (dW_f/dt), fine-root increment ($\zeta\, \sigma\, dW_f/dt$),

199 foliage turnover (W_f/τ_f, where τ_f is the turnover time of foliage), and fine-root turnover ($\zeta\, \sigma\, W_f/\tau_r$, where τ_r is

200 the turnover time of fine roots). For simplicity, in common with many models, we do not consider allocation

201 to branches and coarse roots separately from allocation to stem:

202 $$P_{net} = dW_s/dt + (1 + \zeta\, \sigma)\, dW_f/dt + (1/\tau_f + \zeta\, \sigma/\tau_r)\, W_f. \qquad\qquad (15)$$

203 From Eq. (13) and Eq. (15), the stem increment (dW_s/dt) can now be expressed as:

204 $$dW_s/dt = y\, A_c\, [P_0\, (1 - \exp(-kL)) - \rho_s\, (1 - f_c/2)\, H\, r_s/c - L\, \zeta\, r_r]$$

205 $$- L\, (\pi c/4a)\, [aD\, (1 - H/H_m) + H]\, (1/\sigma + \zeta)\, dD/dt - L\, A_c(1/\sigma\tau_f + \zeta/\tau_r) \qquad (16)$$

206 The annual increment in (dD/dt) and all the other diameter-related indices are simulated by combining Eq. (7)

207 and Eq. (16).

208 2.1.3 Definition of the growing season

209 The season over which GPP is accumulated (i.e. the effective growing season) is defined as running from July

210 in the previous year through to the end of June in the current year. This definition is consistent with the fact

211 that photosynthesis peaks around the time of the summer solstice (Bauerle et al., 2012) and that maximum leaf

212 area occurs shortly after this (Rautiainen et al., 2012). Carbon fixed during the later half of the year (July to

213 December) is therefore either stored or allocated to purposes other then foliage expansion. Observations of

214 tree radial growth show that it can occur before leaf-out (in broadleaved trees) or leaf expansion (in

215 needleleaved trees), thus confirming that some part of this growth is based on starch reserves from the

216 previous year (Michelot et al., 2012). This definition of the effective growing season is also supported by

217 analyses of our data which showed that correlations between simulated and observed tree ring-widths are

218 poorer when the model is driven by GPP during the current calendar year rather than an effective growing

219 season from July through June.

2.2 Model application

221 2.2.1 Observations

222 We use site-specific information on climate and tree growth from a relatively low-elevation site (ca 128°02′E,

223 42°20′E, 800 m a.s.l.) in mixed conifer and broadleaf virgin forest in the Changbai Mountains, northeastern

224 China (Bai et al., 2008). This region was chosen because there is no evidence of human influence on the

225 vegetation, and the forests are maintained by natural regeneration. Data on tree height, diameter and crown

226 area were collected for 400 individual *Pinus koraiensis* trees from thirty-five 20m by 20m sample plots. The

227 400 trees included all individual of this species in the 35 plots, i.e. represent a complete sampling of the

228 variability in growth. Tree height and diameter were measured directly, and crown area measured as the area

229 of projected ground coverage. Tree-ring cores were obtained from 46 of these individuals in 2007. The

230 selected trees were either from the canopy layer or from natural gaps in the forest, and in both cases not

231 overshadowed by nearby individuals in order to minimize the possible effects of competition. An attempt was

232 made to select individuals of different diameters (diameter at breast height from 10 to 70 cm at time of

233 sampling), broadly corresponding to the range of diameters recorded in the original sampling. The 46 trees

234 were of different ages (ranging from < 50 to ca. 200 years at the time of sampling, 2006); subsequent analyses

235 show there is little relationship between age and diameter at breast height. Environmental conditions (e.g. soil

236 depth, light availability) were relatively uniform across the sampling plot. Monthly temperature, precipitation

237 and fractional cloud cover data, from 1958 onwards, were obtained from Songjiang meteorological station

238 (128°15′E, 42°32′E, 591.4 m a.s.l.), which is representative of the regional climate at low elevations in the

239 Changbai Mountains.

240 2.2.2 Derivation of T model parameter values

241 T model parameter values were derived from measurements made at the sampling site or from the literature

242 (Table 1). We estimated the initial slope of the height-diameter relationship (a: 116), the initial ratio of crown

243 area to stem cross-sectional area (c: 390.43), and maximum tree height (H_m: 25.33 m) using nonlinear

244 regression applied to diameter at breast height (D), tree height (H), and crown area (A_c) measurement on all

245 the 400 trees from the sample plots (Fig. 2). We used a value of sapwood density derived from three

246 measurements at the sampling site (Table 1). We used values of leaf area index within the crown (L), specific

247 leaf area (σ), foliage turnover time (τ_f), and fine-root turnover time (τ_r) for *Pinus koriensis* from field studies

248 conducted in northeastern China (Table 1). No species-specific information was available for the PAR

249 extinction coefficient (k), yield factor (y), ratio of fine-root mass to foliage area (ζ), fine-root specific

250 respiration rate (r_r), or sapwood specific respiration rate (r_s). We therefore used published values for other

251 species of evergreen needleleaf trees, taken from papers that summarise results from a range of field

252 measurements. Most of the published values for these parameters fall in a relatively narrow range (Table 1).

253 The uncertainty in fine-root specific respiration rate is not given in the original source paper (Yan and Zhao,

254 2007) but the average value is consistent with other studies (e.g. Zogg et al., 1996). The published values for

255   sapwood-specific respiration rate in pines show considerable variability, ranging from 0.5~10, or even 20

256   nmol/mol/s (Landsberg and Sands, 2010). Analyses (see Sect. 3.1) show that the model is sensitive to the

257   specification of sapwood respiration. We therefore selected the final value for this parameter based on

258   calibration of the simulated mean ring width against observations, constrained by the published range of

259   values for sapwood respiration rate.

260   2.3 Model application

261   We applied the model to simulate the growth of 46 individual *Pinus koraiensis* trees from the study site

262   between 1958-2006. The 46 trees were of different ages (ranging from <50 to ca 200 years at the time of

263   sampling, 2006) and different diameters (diameter at breast height from 10 to 70 cm at time of sampling).

264   Environmental conditions (e.g. soil depth, light availability) were relatively uniform across the sampling plot.

265   The start date for the simulations was determined by the availability of local climate data. Site latitude,

266   elevation, and observed monthly temperature, precipitation, fraction of cloud cover were used as input for the

267   P model. Each tree was initialised at its actual diameter at 1958, calculated from the measured diameter in

268   2007 and measured radial growth between 1958 and 2007. The model was initially run with a fixed CO_2

269   concentration of 360ppm. To examine the impact of changing atmospheric CO_2 levels on tree growth, we

270   made a second simulation using the observed monthly CO_2 concentration between 1958 and 2006 (310 - 390

271   ppm: NOAA ESRL).

272   2.4 Statistical methods

273   For statistical analyses and comparison with observations, the individual trees were grouped into three

274   cohorts, based on their age in 1958: young (0-49 years), mature (50-99 years), and old (>100 years).

275   Individual trees within each cohort exhibit a range of diameters: young ca 20-37 cm, mature: 9-59 cm, and

276   old: 25-40 cm. These differences in size will affect the expression of ontogeny within each cohort. The mean

277   and standard deviation (SD) of year-by-year diameter growth was calculated for each age cohort from the

278   observations and the simulations. The Pearson correlation coefficient and root mean squared error (RMSE)

279   were used to evaluate the degree of agreement between the observations and simulations. We used generalised

280   linear modelling (GLM: McCullagh, 1984) to analyse the response of tree growth to the major climate factors

281   and age. The GLM approach is helpful for separating the independent influence of individual factors on tree

282   growth, given the inevitable existence of correlations between these factors.

283

284   3 Results

285   3.1 Simulated ring width versus observation

286   There are only small differences between different age cohorts in the mean simulated ring width, with a mean

287   value of 1.43 mm for young trees, 1.31 mm for mature trees, and 1.37 for older trees. These values are

288 comparable to the mean value obtained from the observations (1.48mm, 1.29mm, 1.34mm respectively).
289 However, the general impact of ageing is evident in the decreasing trend in ring widths between 1958 and
290 2007 within any one cohort (Fig. 3). The slope is stronger in the observations than in the simulations,
291 indicating that the model somewhat underestimates the effects of ontogeny.

292 There is considerable year-to-year variability in tree growth. The simulated interannual variability (standard
293 deviation) in simulated ring width is similar in all the age cohorts (0.265 mm in the young, 0.265 mm in the
294 mature, and 0.264 mm in the old trees). This variability is somewhat less than shown by the observations,
295 where interannual variability is 0.274mm, 0.367mm, 0.245mm respectively in the young, mature and old
296 cohorts. The RMSE is 0.263mm, 0.332mm, and 0.284mm respectively for young, mature and old age cohorts.
297 The correlation between the observed and simulated sequence in each cohort is statistically significant (P =
298 0.000, 0.001, 0.009 respectively for young, mature and old age cohorts).

299 Despite the fact that the model reproduces both the mean ring width and the interannual variability in tree
300 growth reasonably well, the range of ring widths simulated for individual trees within any one cohort is much
301 less than the range seen in the observations. This is to be expected, given that individual tree growth is
302 affected by local factors (e.g. spatial variability in soil moisture) and may also be influenced by ecosystem
303 dynamics (e.g. opening up of the canopy through the death of adjacent trees) – effects that are not taken into
304 account in the model.

305 3.2 Parameter sensitivity analysis

306 To evaluate the sensitivity of the model to specification of individual parameters, we ran a series of
307 simulations in which individual parameter values were increased or decreased by 50% of their reference
308 value. For each of these simulations, the T model was run for 500 years using constant potential GPP (the
309 mean GPP during the period 1958-2006).

310 The model simulates a rapid initial increase in ring width, with peak ring widths occurring after ca 10 years,
311 followed by a gradual and continuous decrease with age (Fig. 4). The model is comparatively insensitive to
312 uncertainties in the specification of fine-root specific respiration rate (r_r), fine-root turnover time (τ_f), and
313 specific leaf area (σ), while leaf area index within the crown (L), ratio of fine-root mass to foliage area (ζ) and
314 fine-root turnover time (τ_r) have only a moderate effect on the simulated amplitude of ring width. The largest
315 impacts on the amplitude of the simulated ring width are from initial slope of height-diameter relationship (a),
316 initial ratio of crown area to stem cross-sectional area (c), and sapwood density (ρ_s). Maximum tree height
317 (H_m) and sapwood-specific respiration rate (r_s) have the greatest influence on the shape of the simulated
318 ageing curve. These two parameters also have a large impact on the amplitude of the growth of old trees. The
319 parameters values for a, c, H_m and ρ_s are derived from observations, with uncertainties much less than 50%
320 (Fig. 2). Thus, the sensitivity of the model to these parameters is not important. However, model sensitivity to
321 sapwood respiration (r_s) both in terms of the shape of the ageing curve and the amplitude is of greater

322　concern, given the large range of values in the literature. Although some part of the uncertainty in the

323　specification of sapwood respiration may be due to differences between species, the difficulty of measuring

324　this trait accurately also contributes to the problem. For the final model, we tuned r_s against the ring-width

325　observations. The best match with the observations was obtained with a value 1.4 nmol/mol/s, which is within

326　the range of published values for pines (see summary in Landsberg and Sands, 2010). r_s is the only parameter

327　that was tuned.

328　3.3 Controls on tree growth

329　The GLM analysis revealed a strong positive relationship between PAR_0 and tree growth, while moisture

330　stress (as measured by α, an estimate of the ratio of actual to potential evapotranspiration) was shown to have

331　a less steep but still positive effect (Fig. 5 and Table 2). The observed partial relationship between mean

332　annual temperature and tree growth is negative. The Changbai Mountains are at the southern end of the

333　distribution of *Pinus koraiensis* in China, which makes it plausible that tree growth would be inhibited during

334　warmer years.

335　The model reproduces these observed relationships between climate factors and tree growth. The slope of the

336　observed positive relationship with α is statistically indistinguishable from the modelled slope, but the

337　observed positive relationship with PAR_0 is weaker, and the negative correlation with mean annual

338　temperature is stronger, in the observations than in the simulations. These differences between observations

339　and simulations could reflect the influence of an additional climate control, related to both PAR_0 and

340　temperature (e.g. cloud cover). The difference between observed and simulated effects of temperature may

341　also be because although simulated growth is inhibited by low temperatures (through the computation of

342　*PAR_0*), the current model does not include any mechanism for inhibition due to heat stress at high air and leaf

343　temperatures.

344　The GLM analysis also showed that age, as represented by the three age cohorts, has an impact on ring width:

345　young trees have greater ring widths than mature trees, while old trees have somewhat greater ring widths

346　than mature trees. This pattern is seen in both the observations and simulations, although the differences

347　between the young and mature cohorts are slightly greater in the observations.

348　The overall similarity in the observed and simulated relationships between growth rates and environmental

349　factors confirms that the T model performs realistically. The observed relationships are considerably noisier

350　than the simulated relationships (Fig. 5, Table 2), reflecting the fact that growth rates are affected by small-

351　scale variability in environmental conditions as well as time-varying competition for light.

352　3.4 Simulated CO_2 effect on tree growth

353　Elevated levels of CO_2 are expected to have a positive impact on tree growth (Hyvönen et al., 2007; Donohue

354　et al., 2013; Hickler et al., 2008; Boucher et al., 2014). This positive response to [CO_2] is seen in the

355   comparison of the fixed $[CO_2]$ and real $[CO_2]$ simulations (Fig. 5). In the first part of the simulation, prior to
356   1980, the actual $[CO_2]$ is lower than the level of 360 ppm used in the fixed $[CO_2]$ experiment: this results in
357   lower growth rates. The 50 ppm difference between the two experiments at the beginning of the simulation
358   results in a difference in ring width of 0.242 mm. After 1980, when the actual $[CO_2]$ was higher than 360
359   ppm, the tree growth in the simulation with realistic $[CO_2]$ is enhanced. The 30 ppm difference at the end of
360   the simulation results in a difference in ring width of 0.101 mm. Overall, the change in $[CO_2]$ between 1958
361   and 2006 results in a positive enhancement of tree growth of ca 0.343 mm/yr. However, this difference is very
362   small compared to the impact of ageing (> 1 mm from observations) or to the differences resulting from the
363   interannual variability of climate (1.212 mm) on tree growth.

364

365   4 Discussion

366   We have shown that radial growth (ring width) can be realistically simulated by coupling a simple generic
367   model of GPP with a model of carbon allocation and functional geometric tree growth with species-specific
368   values. The model is responsive to changes in climate variables, and can account for the impact of changing
369   CO_2 and ontogeny on tree growth. Although several models draw on basic physiological and/or geometric
370   constraints in order to simulate tree-ring indices (Fritts, 2012; Vaganov et al., 2006; Rathgeber et al., 2005;
371   Misson, 2004), and indeed the two approaches have been combined to simulate between-site differences in
372   ecosystem productivity and tree growth (Härkönen et al. 2010; Härkönen et al. 2013), this is the first time to
373   our knowledge that the two approaches have been combined to yield an explicit treatment of individual tree-
374   growth processes, tested against an extensive ring-width data set.

375   Our simulations suggest that after a brief but rapid increase for young plants, there is a general and continuous
376   decrease in radial growth with age (Fig. 4). This pattern is apparent in individual tree-ring series, and is
377   evident in the decreasing trend in ring widths shown when the series are grouped into age cohorts (Fig. 3). It is
378   a necessary consequence of the geometric relationship between the stem diameter increment and cross-
379   sectional area: more biomass is required to produce the same increase in diameter in thicker, taller trees than
380   thinner, shorter ones. However, we find that ring widths in old trees in our study region are consistently wider
381   than in mature trees, and this property is reproduced in the simulations (Fig. 5). This situation arises because
382   the old trees are on average smaller than the mature trees at the start of the simulation (in 1958). Thus, while
383   the difference between average ring-widths in the mature and old cohorts conforms to the geometric
384   relationship between stem diameter increment and cross-sectional area, it is a response that also reflects
385   differences in the history of tree growth at this site which determined the initial size of the trees in 1958. Lack
386   of climate data prior to 1958 or detailed information about stand dynamics precludes diagnosis of the cause of
387   the growth history differences between mature and old trees.

388   Studies attempting to isolate the impact of climate variability on tree growth, including attempts to reconstruct
389   historical climate changes using tree-ring series, often describe the impact of ageing as a negative exponential
390   curve (Fritts, 2012). However, our analyses suggest that this is not a good representation of the actual effect of
391   ageing on tree growth, and would result in masking of the impact of climate-induced variability in mature and
392   old trees. The simulated NPP of individual trees always increases with size (or age). This is consistent with
393   the observation that carbon sequestration increases continuously with individual tree size (Stephenson et al.,
394   2014).

395   We have shown that total PAR during the growing season is positively correlated with tree growth at this site.
396   This is not surprising given that PAR is the primary driver of photosynthetic carbon fixation. However, none
397   of the empirical or semi-empirical models of tree growth uses PAR directly as a predictor variable; most use
398   some measure of seasonal or annual temperature as a surrogate. PAR is determined by latitude and cloudiness.
399   Although temperature varies with latitude and cloudiness, it is also influenced by other factors including heat
400   advection. Temperature changes can impact the length of the growing season, and hence have an impact on
401   total growing-season PAR, but this is a trivial effect over recent decades. In fact, we show that mean annual
402   temperature *per se* is negatively correlated with tree growth at this site. Given this decoupling, and the
403   potential that longer-term changes in cloudiness will not necessarily be correlated with changes in temperature
404   (Charman et al., 2013), we strongly advocate the use of growing-season PAR for empirical modelling as well
405   as in process-based modelling.

406   We found no age-related sensitivity to inter-annual variability in climate: the interannual variability in ring
407   width is virtually identical between age cohorts. The strength of the relationship with individual climate
408   variables is also similar between the three age cohorts. It is generally assumed that juvenile and old trees are at
409   greater risk of mortality from environmental stress than mature trees (e.g. Lines et al., 2010; McDowell et al.,
410   2008). This may be true in the case of extreme events, such as wildfires or windthrow, or pest attack. Our
411   results suggest that although climate variability has an important effect on tree growth it is not an important
412   influence on mortality.

413   We have assumed that the period contributing to growth (i.e. the effective growing season) in any year
414   includes carbon stores generated during the second half of the previous year. The total foliage area determines
415   the radial area of the stem, and once this is achieved NPP is allocated either to fine root production or stored
416   as carbohydrate for use in stem growth in the early part of the subsequent year. This is consistent with
417   observations that radial growth begins before leaf-out (Michelot et al., 2012) and that maximum leaf area is
418   generally achieved by mid-summer (Rautiainen et al., 2012), and the MAIDEN model also allows tree growth
419   to be influenced by a fixed contribution from the previous year's growth (Misson, 2004). Defining the
420   effective growing season as being only the current growth year had no impact on the influence of climate on
421   ring widths, or the shape of the aging curve. It did, however, produce a considerably lower correlation
422   between simulated and observed inter-annual variability in growth. Since tree ring-width reflects the

423 integrated climate over the "effective growing season", reconstructions of climate variables reflect conditions
424 during that season, not simply during the current calendar year.

425 The high degree of autocorrelation present in tree-ring series is often seen as a problem requiring pre-
426 treatment of the series in order to derive realistic reconstructions of climate variables (e.g. Cook et al., 2012;
427 Anchukaitis et al., 2013; Wiles et al., 2014). However, spatial or temporal autocorrelation is a reflection of the
428 causal mechanism underpinning the observed patterning. Here we postulate that the mechanism that gives rise
429 to the temporal autocorrelation in tree-ring series is the existence of carbon reserves that are created in one
430 year and fuel early growth in the next. If a large reserve of carbon is created in the second half of the growing
431 season, because of favourable conditions, this will offset poor conditions in the following year. However,
432 large reserves may not be necessary if conditions during the subsequent growing year are very favourable.
433 The fact that the relative influence of one year on the next can vary explains why the measured autocorrelation
434 strength in a given tree-ring series varies through time.

435 The T model is sensitive to the values adopted for some parameters, specifically the initial slope of height-
436 diameter relationship (a), the initial ratio of crown area to stem cross-sectional area (c), maximum tree height
437 (H_m), sapwood density (ρ_s), sapwood specific respiration rate (r_s), leaf area index within the crown (L), ratio of
438 fine-root mass to foliage area (ζ) and fine-root turnover time (τ_r). Several of these parameters are easily
439 derived from observations (e.g. a, c, H_m, ρ_s, L) and provided that sufficient site-based observations are
440 available should not pose a problem for applications of the model. However, the model is also sensitive to less
441 easily measured parameters, including sapwood respiration, root respiration and the ratio of fine roots to
442 leaves. Estimates of values for root respiration and root mass to foliage area in the literature do not show
443 substantial differences, and we therefore used an average value to parameterize our model. This approach
444 could be used for other applications. We parameterized fine-root turnover rates based on observations on
445 *Pinus koriensis* from Changbai. While this obviated the need for tuning in the current application, lack of data
446 on fine-root turnover rates in other regions (or for other species) could pose problems for future applications
447 of the model. The model is also highly sensitive to the parameter value used for sapwood respiration and the
448 range of reported values is large (Table 1). Because of this, we derived a value for sapwood respiration by
449 tuning the model to obtain a good representation of average ring width. This is the only parameter that
450 requires tuning in the current version of the T model. Although sapwood respiration is difficult to measure, it
451 would certainly be better if more measurements of sapwood respiration were available, as this would remove
452 the need for model tuning.

453 Our modelling approach integrates the influence of climate, [CO_2] and ontogeny on individual tree growth.
454 Such a model is useful to explore the response of tree growth to potential future changes in climate, and the
455 impact of changes in tree growth on carbon sequestration. We also envisage that it could also be used to
456 investigate the impact of past climate changes on tree growth. Reconstructions of temperature changes beyond
457 the recent observational period, used as a baseline for the detection of anthropogenic influences on the climate

458 system, are largely derived from statistical reconstructions based on tree-ring series (Jones et al., 1998; Esper
459 et al., 2002; Hegerl et al., 2006; Mann et al., 2008; Ahmed et al., 2013). However, as we show here,
460 temperature is neither the only, nor the most important, influence on tree growth. This may help to explain
461 why correlations between ring-widths and climate at individual sites appear to have broken down in recent
462 decades (the so-called divergence problem: D'Arrigo et al., 2008). The availability of a robust model to
463 investigate tree growth could help to provide better reconstructions of past climate changes (see e.g. Boucher
464 et al., 2014) as well as more plausible projections of the response of tree growth to continuing climate change
465 in the future.

466

467 Acknowledgements.

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474   References

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666

667   Table and Figure Captions

668   Table 1. Parameter description and the derivation of parameter values.

669   Table 2. GLM analysis of tree growth response to the climatic factors and age, based on simulations and
670   observations. The dependent variable is mean ring width series (1958 to 2006) for each age cohort (young,
671   mature, old). The independent variables are the growing-season total annual photosynthetically active
672   radiation (PAR), mean annual temperature (MAT), the ratio of actual to potential evapotranspiration (α), with
673   age-cohort treated as a factor.

674   Figure 1. Model application flow. We combined the simple light-use efficiency and photosynthesis model (P
675   model) with a carbon allocation and functional geometric tree growth model to simulate tree growth (e.g. ring
676   width). The inputs to the P model are latitude, elevation, $[CO_2]$, and monthly temperature, precipitation, and
677   fractional cloud cover. Potential gross primary productivity (GPP), output by the P model, drives the T model,
678   together species-specific parameter values.

679   Figure 2. Estimation of parameter values for the application of the T model. Diameter at breast height (D),
680   tree height (H), and crown area (A_c) of the 400 trees from the sample plots were used for the estimation of the
681   initial slope of height-diameter relationship (a), and (asymptotic) maximum tree height (H_m). Relationships
682   among crown area (A_c) diameter at breast height (D) and height (H) (Eq. 7) are used to estimate the initial
683   ratio of crown area to stem cross-sectional area (c).

684   Figure 3. Comparison between simulations and observations for the three age-cohorts (young: 0-49 year,
685   mature: 50-99 year, and old >100 year). Each tree was initialised at its actual diameter at 1958, calculated
686   from the measured diameter in 2007 and measured radial growth between 1958 and 2007. The black line is
687   the mean of observations within each age-cohort, and grey bars are the standard deviation (SD) of individuals
688   within each age-cohort. The blue line and bars are the mean and standard deviation from the simulations.

689   Figure 4. Parameter sensitivity analyses for the T model. A constant input of gross primary productivity (GPP)
690   (mean during 1958-2006) was used to drive the T model to simulate tree growth for 500 years following
691   establishment. The black line was obtained with the reference value of each parameter. The effects of an
692   increase (150% of reference value, blue line) and a decrease (50% of reference value, red line) are also shown.

693   Figure 5. Tree growth response to climate and tree age: partial residual plots based on the GLM analysis
694   (Table 2), obtained using the visreg package in R, are shown.

695   Figure 6 CO_2 effect on tree growth. Two runs, one with a fixed 360ppm $[CO_2]$ (blue line), the other with
696   observed monthly $[CO_2]$ (red line), are compared to show the simulated effect of $[CO_2]$ on tree growth during
697   1958~2006.

Table 1

Parameter	Code	Value	Uncertainty or Range of value from literature	Value source: Observation or Published literature
initial slope of height-diameter relationship (–)	a	116	±4.35	Observation (fig. 2)
initial ratio of crown area to stem cross-sectional area (–)	c	390.43	±11.84	Observation (fig. 2)
maximum tree height (m)	H_m	25.33	±0.71	Observation (fig. 2)
sapwood density (kgC m^{-3})	ρ_s	200	±25	Observation
leaf area index within the crown (–)	L	1.8	1.5～1.96	Chen et al., 2004
specific leaf area (m^2 kg^{-1} C)	σ	14	13.22~16.82	Huo and Wang, 2007
foliage turnover time (year)	τ_f	4	-	Luo, 1996
fine-root turnover time (year)	τ_r	1.04	-	Shan et al., 1993
PAR extinction coefficient (–)	k	0.5	0.48-0.58	Pierce and Running, 1988
yield factor (–)	y	0.6	0.5~0.7	Zhang et al., 2009
ratio of fine-root mass to foliage area (kgC m^{-2})	ζ	0.17	±0.198	White et al., 2000
fine-root specific respiration rate (year^{-1})	r_r	0.913	-	Yan and Zhao, 2007
sapwood specific respiration rate (year^{-1})	r_s	0.044 (1.4 nmol/mol/s)	0.5~10 (20) nmol/mol/s	Landsberg and Sands, 2010

Table 2

		Intercept (mm)	PAR (mm/kmol photon m^{-2})	MAT (mm/°C)	α (mm)
Observation	Estimation	-3.123	0.625	-0.180	0.702
	Error	±0.784	±0.093	±0.042	±0.301
	p value	0.004	0.000	0.000	0.021
Simulation	Estimation	-7.139	1.056	-0.078	1.142
	Error	±0.169	±0.020	±0.009	±0.065
	p value	0.000	0.000	0.000	0.000

		Intercept (mm)	PAR (mm/kmol photon m^{-2})	MAT (mm/°C)	α (mm)
		-3.123			
-7.139					

Figure 1

Figure 2

$$H = H_m\left(1 - e^{(-aD/H_m)}\right)$$
$p = 0$
$H_m = 25.33 \pm 0.71$
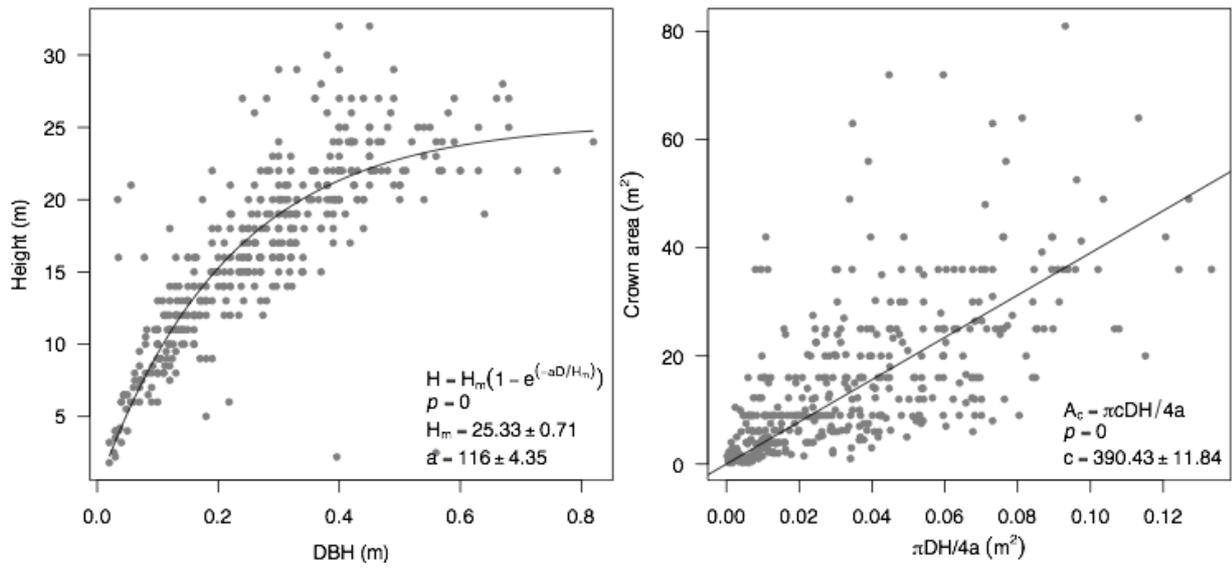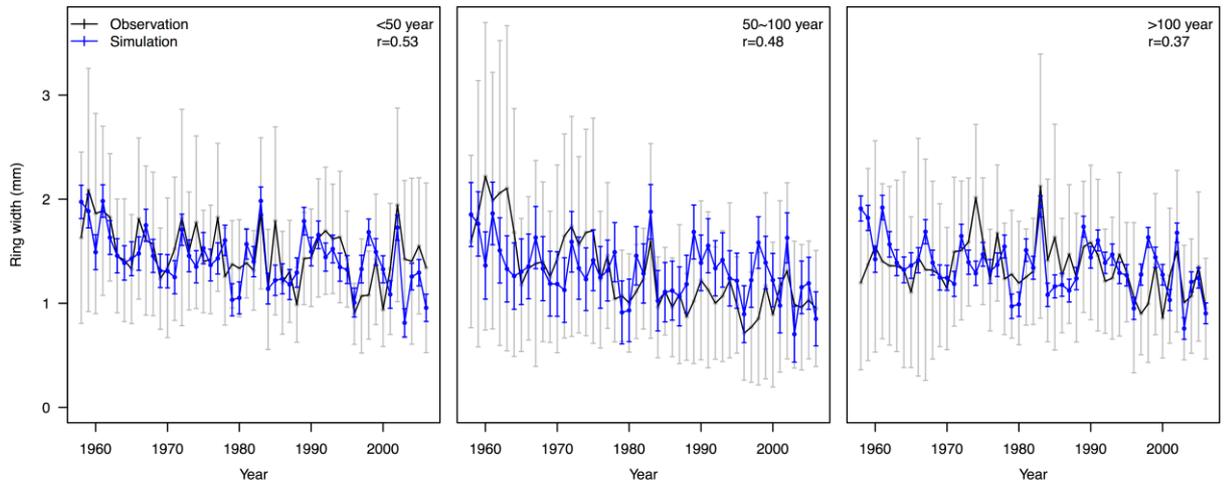$a = 116 \pm 4.35$

$$A_c = \pi cDH/4a$$
$p = 0$
$c = 390.43 \pm 11.84$
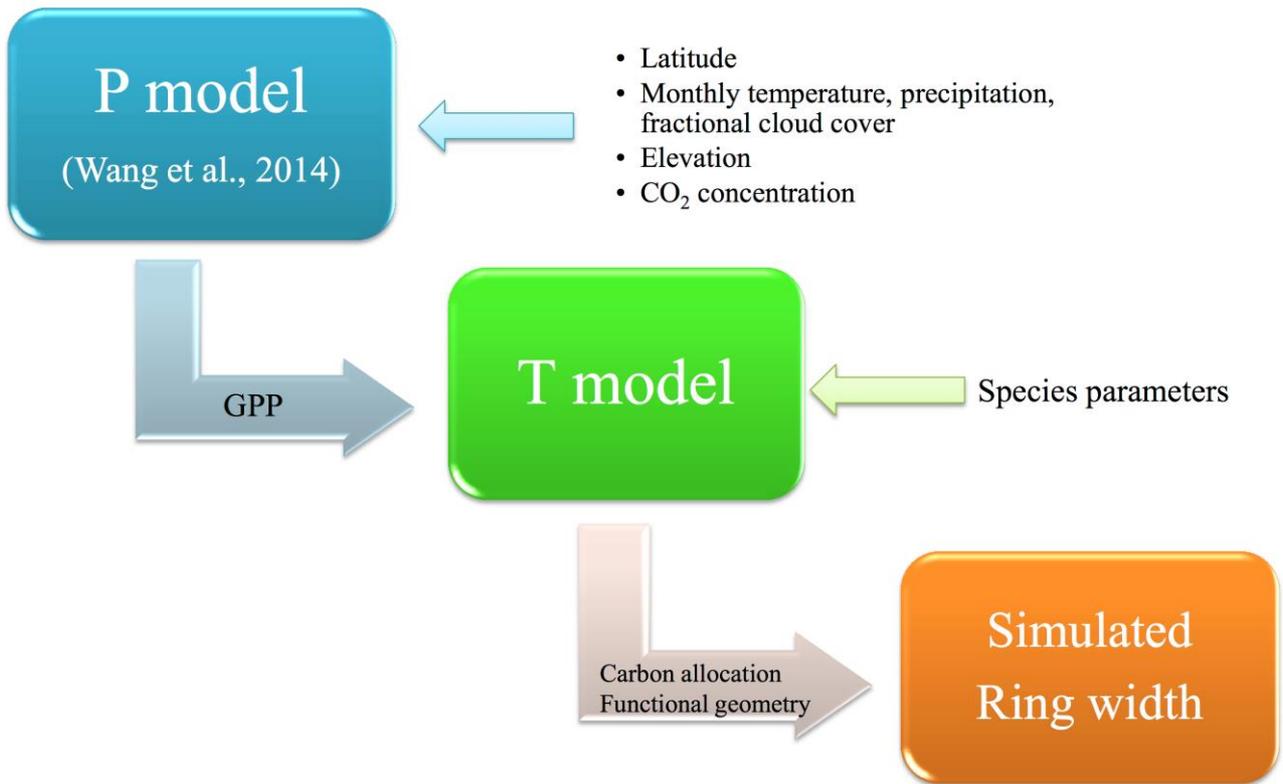
Figure 3

Figure 4

Figure 5

Figure 6