We are glad the reviewers found this paper interesting and in particular that they found the combination of the light-use efficiency model and the tree growth model in order to explicitly simulate tree ring widths a useful and novel approach. We are also very glad of the encouragement to continue with the development of this modeling approach! Here we respond to the reviewers' comments and requests for additional clarification. Our response is in italic and changes to the manuscript are given in bold italics.

Response to Anonymous Reviewer 1

a) Whereas the model descriptions conclude meaningful interpretation of single equations and parameters, the parameterization needs for more detailed description.
We agree that the derivation of values for key parameters is important, and that our description of how we did this (Section 2.2.2) was rather brief.
We have expanded the description of the field measurements that were used to derive some of the parameters, by adding the following sentences in Section 2.2.1
The 400 trees included all individual of this species in the 35 plots. Tree height and diameter were measured directly, and crown area measured as the area of projected ground coverage.
We realize that we did not explain where we got the sapwood density value. This was also based on measurements at the study site and we have added this into the text (Section 2.2.2) as follows:
We used a value of sapwood density derived from three measurements at the sampling site (Table 1).
We have clarified which of the parameters were derived from field measurements on Pinus koriensis taken in northeastern China (i.e. in the region of our study site and therefore likely to have similar values). We realize that we did not include the uncertainties for some of the values taken from the literature, so that our statement that the range was small was not well supported, so we have now added these to Table 1. We have also modified the text to make it explicit that we used data from reviews that summarized field measurements of the variable in question, as follows:
We therefore used published values for other species of evergreen needleleaf trees, taken from papers that summarise results from a range of field measurements.

b) The step from a stand growth model to a tree basis needs for a reflection on competition for nutrients, water, and space besides the already mentioned PAR. Mentioning only "foliage cover" in the first sentence of 2.1.2 is not sufficient here.
Our basic assumption in combining the P and T-models is that the first-order signal of tree growth is determined by climatic conditions and light availability (which subsumes competition for water and space), and thus that each individual tree's growth will reflect the potential GPP at stand level. We recognize that this is a simplification, and that competition for nutrients may affect growth rates of individual trees. However, it is a necessary first step to modeling this system and our analyses suggest that it is a reasonable way to simulate the average response even though it may not account for variation amongst individuals – as we discuss later this variation is likely due to factors that are not taken into account in the current model. We think it

might be useful to state our basic assumption at the beginning of this section, as follows:

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

c) The inter-correlation among variables (line 244) determining the growth of trees should be reflected more in detail when the co-acting of multiple factors is discussed; the situation should not be described as "confusing" but as "complex". Accordingly, a more detailed description of the ontogeny and underlying processes is necessary. The development of trees is based on a development of stands with competition effects being probably affected e.g. by forest management (only mentioned e.g. at end of 3.3 or in lines 338/339). Respective description of forests' and trees' history in terms of e.g. regeneration, stand density, or thinning regimes is missing in the actual version.

The confusing situation that we refer to (line 244) is not that there are multiple factors that control the growth of trees, but rather the confusion in the tree-ring literature that arises from the implicit assumption that there is a single dominant control of tree growth, and which therefore leads to multiple single-factor explanations of the divergence problem or different interpretations of the impact of CO2 on tree growth. We think we can make this clearer by changing the phrase from "confusing situation" to "apparent conflicts".

Our discussion at the end of Section 3.3 does not refer to management, but rather to the potential impact of small-scale environmental variability. In fact, the forests in the Changbai Mountains are natural and unmanaged forests. It is for this reason that we do not need to consider the history of forest management. We do believe that small-scale environmental variability, whether this is in terms of water availability, nutrient availability or light availability, will have an impact on the growth of individual trees (see also response above). Our model effectively captures the response of an "average" individual, and cannot capture the much greater variability of response seen between individuals because of small-scale environmental variability.

We have added a sentence in Section 2.2.1 to make it clear that we are dealing with a natural forest, as follows:

This region was chosen because there is no evidence of human influence on the vegetation, and the forests are maintained by natural regeneration.

d) Single tree growth may increase with individual tree size (line 346), but this does not necessarily mean that stands of (a low number of) large trees produce as much biomass as young stands do which are built of (a high number of) smaller trees. Tree and stand growth have to be clearly distinguished and, in general, there is no contradiction between decreasing stand growth rates and increasing tree growth rates with age or individual tree size () e.g. delete "Although" in line 42).

We agree that there is no necessary contradiction between increasing growth rates with age for individuals and decreasing rates of stand growth rates with age. The point for us is that the impact on carbon accumulation with age is different. However, carbon-cycle models either do not explicitly deal with individual trees or do not evaluate how realistic the growth of the simulated individual is – and this could be one of the causes of uncertainties in carbon-cycle model predictions. Our argument is

that it is necessary to take account of individual growth rates, and to ensure that stand growth rates reflect the number and behavior of individuals correctly. To make this clearer, we have modified the sentence to read:

It is generally assumed that stand-level productivity stabilizes or declines with age (Ryan et al., 1997; Caspersen et al., 2011). However, recent analyses have shown that mass growth rate (and hence carbon accumulation) by individual trees increases continuously with tree size (Stephenson et al., 2014), pointing to a need to understand the relationship between individual and stand growth rates.

e) The differences among the cohorts are not described and explained in terms of any variable but age before the size of trees is used in the discussion (line 335). What led to the fact that old trees are smaller than the observed mature trees? The growth conditions mentioned in line 336 have to be described; possible impacts of plant origin (genetic aspects) or site quality are not mentioned. Clearly state, if this is due to missing availability of respective information. In addition the variation within the cohorts concerning growth, diameter or any other variable is not described although potentially of interest; a negative correlation to age is visible e.g. in figure 5.

We did describe the differences in size between the age cohorts when these were first defined (i.e. in Section 2.4) and before the discussion of the cohort results at line 325. However, we realize that the implications of differences in size were not made clear at this point, so we have modified this text as follows:

For statistical analyses and comparison with observations, the individual trees were grouped into three cohorts, based on their age in 1958: young (0-49 years), mature (50-99 years), and old (>100 years). Individual trees within each cohort exhibit a range of diameters: young ca 20-37 cm, mature: 9-59 cm, and old: 25-40 cm. These differences in size will affect the expression of ontogeny within each cohort.

We also realize that our discussion of the age cohort results was too abbreviated, and thus that we did explain how, although the cohort results support the idea that the model correctly simulates the impact of ontogeny, the original differences between mature and old trees in terms of size explains the difference in their mean properties. Effectively, the ontogenetic effect is a property of individual trees, but mean properties reflect differences in life history (in this case indicated by differences in initial size). We have expanded this paragraph to make this clearer, as follows:

Our simulations suggest that after a brief but rapid increase for young plants, there is a general and continuous decrease in radial growth with age (Fig. 4). This pattern is apparent in individual tree-ring series, and is evident in the decreasing trend in ring widths shown when the series are grouped into age cohorts (Fig. 3). It is a necessary consequence of the geometric relationship between the stem diameter increment and cross-sectional area: more biomass is required to produce the same increase in diameter in thicker, taller trees than thinner, shorter ones. However, we find that ring widths in old trees in our study region are consistently wider than in mature trees, and this property is reproduced in the simulations (Fig. 5). This situation arises because the old trees are on average smaller than the mature trees at the start of the simulation (in 1958). Thus, while the difference between average ring-widths in the mature and old cohorts conforms to the geometric relationship between stem diameter increment and cross-sectional area, it is a response that also

reflects differences in the history of tree growth at this site which determined the initial size of the trees in 1958. Lack of climate data prior to 1958 or detailed information about stand dynamics precludes diagnosis of the cause of the growth history differences between mature and old trees.

f) The selection of the 46 trees for core analyses is not described. How do the selected trees represent the trees in the area and in the cohorts? Is any information available on their ontogeny (natural regeneration/planting, thinning regime, mortality . . .)?

We agree that our description was very brief, and we did not stress the reason for selecting either the plot sites or the individual for tree ring analysis. We have expanded the paragraph describing the original observations (Section 2.2.1) to explain that this is a natural forest and not managed in any way. We have also described the sampling strategy for the selection of individuals for tree ring analysis, and emphasized that this selection procedure was designed to minimize the possibility of competition between individuals having a major impact on tree growth. The text now reads:

This region was chosen because there is no evidence of human influence on the vegetation, and the forests are maintained by natural regeneration. Data on tree height, diameter and crown area were collected for 400 individual Pinus koraiensis trees from thirty-five 20m by 20m sample plots. Tree-ring cores were obtained from 46 of these individuals in 2007. The selected trees were either from the canopy layer or from natural gaps in the forest, and in both cases not overshadowed by nearby individuals in order to minimize the possible effects of competition. An attempt was made to select individuals of different diameters (diameter at breast height from 10 to 70 cm at time of sampling), broadly corresponding to the range of diameters recorded in the original sampling. The 46 trees were of different ages (ranging from < 50 to ca. 200 years at the time of sampling, 2006); subsequent analyses show there is little relationship between age and diameter at breast height.

The general impact of aging (line 250) is not the only driving force which could lead to a reduction of growth; decreasing ring widths are not necessarily an indication for reduced growth or biomass production (on tree as well as on stand level).

We are unclear what the additional issue is here. Reduced radial growth can result from aging (through the geometric constraint), from poor growth conditions which result in an overall reduction in production, or from a change in allocation so that more of the production goes e.g. into roots than into radial growth. As explained above, our sampling strategy was designed to minimize the impact of within-site variability and to allow us to explore the impacts of age and the geometric (size) constraint. We hope that the modification to the text given above makes this clearer.

g) Tuning of parameters based on the data which are also used for the model evaluation is always a tricky thing. The explorative character of the study, hence, should be pronounced.

We agree that tuning parameters using data that is subsequently used for model validation is tricky. One of the important things about our model is that we only tune one parameter, sapwood respiration. Other parameter values are taken from our own

observations or observations summarized in the literature. In tuning sapwood respiration, we tuned to obtain reasonable average values of tree ring width. The tuning did not involve tuning to match interannual variability or trends in the tree ring widths, and the tuned model would not necessarily be able to reproduce such features. In this sense, the demonstrated ability to capture trends (e.g. between cohorts) or to match the general patterns in interannual variability is an independent test.

To make this clearer, we have modified the text describing the tuning procedure (Section 2.2) to read:

We therefore selected the final value for this parameter based on calibration of the simulated mean ring width against observations, constrained by the published range of values for sapwood respiration rate.

We realize that the paragraph discussing the tuning in the final section could be clearer about what we have tuned and why this was necessary. We also feel that in discussing fine-root turnover rates we did not make it clear that this parameter was unturned but that better results could be obtained if there was more data available to derive values for this parameter. We have therefore modified the paragraph to read:

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

Technical corrections:
Line 100: "represnetd" > "represented"
Line 103: ".." > "."
Line 183: "rowots" > "roots"
Line 386: "goodrepresentation" > "good representation"

These corrections to the manuscript were already made during technical corrections, but we have checked again for typos in the current revised version.

Response to Anonymous Reviewer 3

Why is the maximum height (Hm) a fixed parameter? As growth responds to temperature, light and CO2 (in addition to other factors) also height growth and maximum height will change. It doesn't make sense that maximum height is fixed unless there is glass roof at the site. From fig 4 it seems the ring width is rather sensitive to Hm so it might be worth testing or at least discussing how large a realistic effect of the environmental factors on Hm might be. It may well be insignificant and then all is well and fine.

The relative allocation to height and to radial growth changes during the life of a tree. Observations indicate that in any one species and environment this relationship is asymptotic. The absolute maximum height that can be reached by a species is governed by hydraulic parameters and tree architecture, which determine the height to which water can be lifted against gravity. However, this absolute maximum height will only be reached in ideal growing conditions – this explains why the maximum realized height for a species varies geographically. But year-to-year variation in environmental conditions does not have a substantial impact on tree height. In order to be able to use the asymptotic relationship between height and radial growth, it is necessary to specify an achieved maximum height that is typical for the species at a given site. In deriving this for our site in the Changbai Mountains, we are assuming that the sampled trees have reached the maximum height possible for the present-day environmental conditions – a supposition that is supported by the evidence for a leveling off in observed heights for the oldest trees. Since the relationships are based on all the Pinus koriensis trees present at the site, as we stress in the manuscript, they represent a true sampling of the variability in growth parameters. Our sensitivity analyses show that an overestimation of maximum height would have a large impact on simulated tree-ring widths, but that the impact of underestimating maximum height is much smaller. (See Section 3.2 and Figure 2)

We think that it is important to point out more clearly than we have done that the asymptotic stem diameter and height relationship we model arises because of functional constraints on growth, and have modified the sentence in the introduction describing the tree growth models to read:

Such models are built on measurable relationships, such as that between stem diameter and height (Thomas, 1996; Ishii et al., 2000; Falster and Westoby, 2005), and crown area and diameter or height (Duursma et al., 2010) that arise because of functional constraints on growth.

Response to Joel Guiot

The model explained and tested in this paper is very interesting. Nevertheless it is presented as not needing tuning while MAIDEN or MAIDENiso (Misson, 2004,

Danis
et al, 2012) needs. It is written that "T model parameter values were derived from
measurements made at sampling site and from the literature (Table 1)". It is exactly
what we did with MAIDEN for which parameters are based on literature values, when
available, and calibration of the remaining ones is done eddy covariance stations fine
measurements and tree-ring series. Finally tuning is mentioned as necessary in the
discussion: "But, given the difficulty of measuring sapwood respiration and also the
comparative lack of data on fine-root turnover rates, it is likely that some form of
tuning
will be required in order to specify these parameters". It is what we did with
MAIDEN which is tuned on daily respiration, soil moisture and throughfall data
(Misson 2004).

*Calibration (or tuning, since the terms are synonymous) is a necessary evil in
modeling in a data-poor world, but as Reviewer 2 points out it can be dangerous to
tune parameters using the same data that is used for model validation. We do not
claim that the T model requires no tuning. We explicitly state that we have tuned
sapwood respiration. However, this is the only parameter (out of 13) that we tune in
any way; other parameter values are derived directly from measurements on site or
measurements summarized in the literature. In the description of MAIDEN in Misson
et al, 2004, there are 12 parameters that are explicitly tuned against observations
(Table 1). The tuning is conducted using several observed data sets, the goodness-of-
fit varies between different data sets (from 0.95 to 0.44) and the impact of the
uncertainties in the calibration on the subsequent simulation of the tree-ring index is
not discussed. It is highly likely that a tuned model will provide a good simulation of
the site for which it has been tuned, and indeed the MAIDEN model does simulate
bole increment well (r^2 of 0.44 for Quercus and 0.67 for Pinus). Our modeling
philosophy is somewhat different in that we have set out to develop a generic model
that can be applied to simulate tree-ring series anywhere with generic parameter
values and a minimum of site-specific tuning (as opposed to site specific
observations).*

Concerning the simulated CO2 effect on tree-growth, Fig. 6 shows interesting results
in
complete coherency with Boucher et al (published a few month ago in the same
journal
http://www.biogeosciences.net/11/3245/2014/bg-11-3245-2014.pdf).

*The Boucher et al. paper shows that it is necessary to include realistic values of
varying CO2 in order to reconstruct realistic (observed) climate parameters when
inverting the MAIDENiso tree-ring model to match an observed tree ring index from
Fontainebleau. The approach does not allow the impact of changing CO2 on tree-ring
width to be quantified, not does it allow the magnitude of the CO2 effect versus the
magnitude of interannual variability (or ontogeny) on tree-ring width to be quantified
– which is the main point we are trying to make in our analyses. So while it is
gratifying that Boucher et al confirm that CO2 has an impact on tree growth, and we
will add it to the list of references that indicate that such an impact is to be expected,
it does not provide a direct comparison with our results.*

I fully agree with "The availability of a robust model to investigate tree growth could help
to provide better reconstructions of past climate changes as well as more plausible projections of the response of tree growth to continuing climate change in the future." and I advise the authors to look at the Boucher et al paper above mentioned.
We agree that we could have cited the Boucher et al. paper here, as an example, of how a model could be used to make such reconstructions and will do so.

Another point to mention: it is true that this model integrates previous calendar year in the growing season. In MAIDEN, it is also the case with the possibility for the tree to make reserve from the end of the previous year to the beginning of winter. This permits also to increase correlation with tree-growth series, which are very often autocorrelated.
We are glad to have the opportunity to discuss the issue of autocorrelation further. The statistical term autocorrelation describes the tendency for the values at a point, in space or time, to be correlated with the values at adjacent points or time intervals. Examples of such autocorrelation include the tendency for the magnitude of a climate change registered at a given point to be similar to the magnitude of climate changes registered at adjacent points. In tree-ring analysis, autocorrelation is shown by the tendency for conditions in the previous year(s) to be correlated with the tree growth response in following years. Analyses show that the strength of such autocorrelations varies, both spatially and temporally. What is often forgotten in statistical analyses is that autocorrelation can be an expression of mechanism. Thus, spatial autocorrelation in reconstructions of climate change reflects the large-scale spatial patterns in the underlying climate field. Similarly, autocorrelation in climate time series can be brought about by feedbacks from e.g. climate-induced changes in land-surface conditions which affect water- and energy-exchanges and hence determine climate variables in subsequent intervals. In the case of the present analysis, the mechanism which gives rise to apparent autocorrelation in tree-ring series is the fact that tree growth during the early part of the season is crucially dependent on access to carbon stores formed in previous years. The amount of carbon stored, and thus available for early season growth, is obviously determined by climate conditions during the end of the previous growing season. However, when conditions in the current year are exceptionally good, the exploitation of stored carbon is likely to be less. Our focus here is on providing a mechanistic explanation for the influence of previous-year conditions, and a way of accounting for these influences which allows the relative importance of this influence vis-à-vis the influence of the current year conditions to be taken into account. We would note that statistical approaches to dealing with autocorrelation necessarily make assumptions about the time or space scales of this influence. Further, we would argue that our more mechanistic approach provides greater flexibility, and considerably more realism, than adopting standard statistical approaches to account for the apparent autocorrelation in tree-ring series. At the very least, it is explicitly based on an hypothesis which can be tested by experimental evidence.

We will (a) indicate that the approach of allowing a carry-over from one year to the next is also in MAIDEN – though the degree of influence is fixed unlike the more flexible approach that we use – by modifying the sentence in the discussion as follows:

This is consistent with observations that radial growth begins before leaf-out (Michelot et al., 2012) and that maximum leaf area is generally achieved by mid-summer (Rautiainen et al., 2012), and the MAIDEN model also allows tree growth to be influenced by a fixed contribution from the previous year's growth (Misson, 2004).

We will add a paragraph on the implications of our approach for the understanding of autocorrelation in tree-ring time series as follows:

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

In conclusion, the paper is an important step towards the use of mechanistic models in dendrochronology, but it suffers to insufficiently acknowledge the progresses made during the last 10 years.

We are aware of the work that Joel's group have been doing and we cited the primary reference to both the MAIDEN and MAIDENiso models (Misson, 2004; Danis et al., 2012) in our introduction, and we also cite the Rathgeber et al (2005) paper, although we missed the chance to cite the recently published work of Boucher et al.. We will add the other references to the development of the MAIDEN model (i.e. Misson et al., 2004) in the Introduction, and we will cite the Boucher et al. paper as an example of how a model of tree ring growth could be used.

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

G. Li[1], S. P. Harrison[1, 2], I. C. Prentice[1, 3], D. Falster[1]

[1] Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia.

[2] School of Archaeology, Geography and Environmental Sciences (SAGES), Reading University, Reading, United Kingdom.

[3] AXA Chair of Biosphere and Climate Impacts, Grand Challenges in Ecosytem and the Environment, Department of Life Sciences and Grantham Institute for Climate Change, Imperial College London, Ascot, United Kingdom.

Correspondence to: G. Li (guangqi.li@students.mq.edu.au)

Abstract

We present a simple, generic model of annual tree growth, called 'T'. This model accepts input from a first-principles light-use efficiency model (the P model). The P model provides values for Gross Primary Production (GPP) per unit of absorbed photosynthetically active radiation (PAR). Absorbed PAR is estimated from the current leaf area. GPP is allocated to foliage, transport-tissue, and fine root production and respiration, in such a way as to satisfy well-understood dimensional and functional relationships. Our approach thereby integrates two modelling approaches separately developed in the global carbon-cycle and forest-science literature. The T model can represent both ontogenetic effects (impact of ageing) and the effects of environmental variations and trends (climate and CO_2) on growth. Driven by local climate records, the model was applied to simulate ring widths during 1958~2006 for multiple trees of *Pinus koraiensis* from the Changbai Mountain, northeastern China. Each tree was initialised at its actual diameter at the time when local climate records started. The model produces realistic simulations of the interannual variability in ring width for different age cohorts (young, mature, old). Both the simulations and observations show a significant positive response of tree-ring width to growing-season total photosynthetically active radiation (PAR_0) and the ratio of actual to potential evapotranspiration (α), and a significant negative response to mean annual temperature (MAT). The slopes of the simulated and observed relationships with PAR_0 and α are similar; the negative response to MAT is underestimated by the model. Comparison of simulations with fixed and changing atmospheric CO_2 concentration shows that CO_2 fertilization over the past 50 years is too small to be distinguished in the ring-width data given ontogenetic trends and interannual variability in climate.

1 Introduction

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

Climate factors, such as temperature and moisture availability during the growing season, are important drivers of tree growth (Harrison et al., 2010). This forms the basis for reconstructing historical climate changes from tree-ring records of annual growth (Fritts, 2012). However, photosynthetically active radiation (PAR) is the principal driver of photosynthesis. Models for primary production that use temperature, not PAR, implicitly rely on the far-from-perfect correlation between temperature and PAR (Wang et al., 2014). PAR can change independently from temperature (through changes in cloudiness affecting PAR or atmospheric circulation changes affecting temperature) and this may help to explain why statistical relationships between tree growth and temperature at some high latitude and high elevation sites appear to breakdown in recent decades (D'Arrigo et al., 2008). CO_2 concentration also has an impact on tree growth, although its magnitude is still controversial: trends in tree growth have been attributed to increasing atmospheric CO_2 concentration in some studies (Wullschleger et al., 2002; Körner, 2006; Huang et al., 2007; Koutavas, 2013) and not others

(Miller, 1986; Luo et al., 2004; Reich et al., 2006). To resolve these apparent conflictsthis confusing situation, and to understand tree growth processes better, it is necessary to analyse the response of tree growth to multiple factors acting simultaneously, including solar radiation, climate, CO_2, and ontogenetic stage.

Modelling is needed for this purpose. Empirical models of annual tree growth and climate variables (temperature and precipitation) have been used to simulate tree radial growth (Fritts, 2012). Process-based bioclimatic models might be preferable, however, because this allows other factors to be taken into account (e.g. the direct impact of CO_2 concentration on photosynthesis) and for non-stationarity in the response to specific climate variables. Vaganov et al. (2006) and Rathgeber et al. (2005) have used bioclimatic variables (temperature, and soil moisture availability) chosen to reflect physiological processes to simulate radial tree growth. The MAIDEN model (Misson, 2004; Misson et al., 2004; see also MAIDENiso: Danis et al., 2012) models the phenological and meteorological controls on NPP and explicitly allocates carbon to different carbon pools (including the stem) on a daily basis using phenological stage-dependent rules. Nevertheless, MAIDEN still requires tuning of several parameters.

Simple equations representing functional and geometric relationships can describe carbon allocation by trees and make it possible to model individual tree growth (Yokozawa and Hara, 1995; Givnish, 1988; Falster et al., 2011; King, 2011). Such models are built on measurable relationships, such as that between stem diameter and height (Thomas, 1996; Ishii et al., 2000; Falster and Westoby, 2005), and crown area and diameter or height (Duursma et al., 2010) that arise because of functional constraints on growth.). The pipe model represents the relationship between sapwood area and leaf area (Shinozaki et al., 1964; Yokozawa and Hara, 1995; Mäkelä et al., 2000). The ratio of fine root mass to foliage area provides the linkage between above and below ground tissues (Falster et al., 2011). These functional relationships are expected to be stable through ontogeny, which implies that the fraction of new carbon allocated to different compartments is variable (Lloyd, 1999). In this paper, we combine the two modelling approaches previously developed in the global carbon-cycle (ecophysiology) and forest-science (geometric and carbon allocation) literature to simulate individual tree growth.

2 Methods

2.1 Model structure and derivation

We use a light-use efficiency model (the P model: Wang et al., 2014), driven by growing-season PAR, climate and ambient CO_2 concentration inputs, to simulate gross primary production (GPP). The simulated GPP is used as input to a species-based carbon allocation and functional geometric tree growth model (the T model) to simulate individual tree growth (Fig. 1).

2.1.1 The P model

The P model is a simple but powerful light-use efficiency and photosynthesis model, which simulates GPP per unit of absorbed PAR from latitude, elevation, temperature, precipitation and fractional cloud cover (Wang et al., 2014). The climate observations used here are monthly temperature, precipitation and fractional cloud cover, which are interpolated to a daily time step for subsequent calculations of the variables that determine annual GPP.

Potential annual *GPP* is the product of the PAR incident on vegetation canopies (PAR_0), with the maximum quantum efficiency of photosynthesis (Φ_0), the fraction of absorbed PAR (*fAPAR*), and the effect of photorespiration and substrate limitation at subsaturating [CO_2] represented as a function of the leaf-internal [CO_2] (c_i) and the photorespiratory compensation point (Γ^*), as shown in Eq. (1).

$$GPP = \Phi_0 \, (PAR_0 \times fAPAR) \, (c_i - \Gamma^*)/(c_i + 2\Gamma^*) \qquad (1)$$

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 absorptance of 0.8. Daily PAR at the top of the atmosphere is calculated based on solar geometry and is subsequently modified by transmission through the atmosphere, which is dependent on elevation and cloud cover. Annual effective PAR (PAR0) is calculated as the annual sum of daily PAR but taking into account the low-temperature inhibition of photosynthesis and growth, using a linear ramp function to downweight PAR on days with temperatures below 10 °C. Days with temperatures below 0°C do not contribute to PAR0. See Wang et al. (2014) for details. In this application, we first calculated potential *GPP* with *fAPAR* set to 1. *fAPAR* is not an input to the model but is calculated implicitly, from the foliage cover simulated by the T model.

Leaf-internal [CO_2] is obtained from the ambient [CO_2] via the 'least-cost hypothesis' (Wright et al., 2003; Prentice et al., 2014). Wang et al. (2014) provide a continuous prediction of the c_i/c_a ratio as a function of environmental aridity, temperature and elevation based on this hypothesis:

$$c_i/c_a = 1/(1 + C\sqrt{(\eta\sqrt{(D)}/K)}) \qquad (2)$$

where D is the cumulative water deficit over a year (proportional to an annual "effective value" of the vapour pressure deficit: VPD), η is the dynamic viscosity of water, K is the effective Michaelis-Menten coefficient for Rubisco-limited photosynthesis, and C is a constant. The difference between the annual actual and equilibrium evapotranspiration is used as a proxy for D (see Prentice et al., 2013). D is calculated using the daily interpolated temperature, precipitation and cloudiness data. Annual actual evapotranspiration is derived from equilibrium evapotranspiration and precipitation using a simple soil moisture accounting scheme with a daily time step, as described in Gallego-Sala et al. (2010). The temperature dependences of η and K follow Prentice et al. (2014). Both K and η change steeply with temperature: K changes from 196 ppm at 10 °C to 1094 ppm at 30 °C ; η decreases from 1.31 mPa s at 10 °C to only 0.798 mPa s at 30 °C.

The temperature dependence of Γ^* is described by an exponential closely approximating an Arrhenius function (Bernacchi et al., 2003):

$$\Gamma^* = \Gamma^*_{25} \exp(0.0512 \Delta T) \tag{3}$$

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

The P model has been shown to simulate well many of the global patterns of annual and maximum monthly terrestrial GPP) by C_3 plants. The simulated seasonal cycle of GPP at different latitudes is supported by analyses of CO_2 flux measurements (Wang et al., 2014).

2.1.2 The T model

We assume that potential GPP is the first-order driver of tree growth both at stand and individual level. The T model translates potential GPP as simulated by the P model into individual tree growth, which depends on foliage cover within the canopy and the respiration of non-green tissues, carbon allocation to different tissues, and relationships between different dimensions of the tree. Although these relationships are often loosely called "allometries", true allometries (power functions) have the undesirable mathematical property for growth modelling that, if the power is greater than one, the derivative evaluated at the start of growth is zero; if the power is between zero and one, the derivative is infinite. We have therefore avoided the use of power functions, except for geometric relationships where they are unambiguously correct.

Functional geometric relationship

Carbon is allocated to different tissues within the constraint of the basic functional or geometric relationships between different dimensions of the tree.

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

$$H = H_m [1 - \exp(-aD/H_m)] \tag{4}$$

where H is the tree height, D is the basal diameter, H_m is the (asymptotic) maximum height, and a is the initial slope of the relationship between height and diameter.

The model also requires the derivative of this relationship:

$$dH/dD = a \exp(-aD/H_m) = a (1 - H/H_m). \tag{5}$$

The form of the stem is assumed to be paraboloid (Jonson, 1910; Larsen, 1963). It can be shown (assuming the pipe model) that this form is uniquely consistent with a uniform vertical distribution of foliage area during early growth, i.e. in the absence of heartwood. Here, the total stem mass (W_s) is expressed as a function of D and H:

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

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

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

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

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

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

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

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

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

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 area at height z^* ($A_s(z^*)$) is the same as the initial ratio of crown area to stem cross-sectional area (c). We obtain crown area (A_c) from:

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

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

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

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

Carbon allocation

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

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

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

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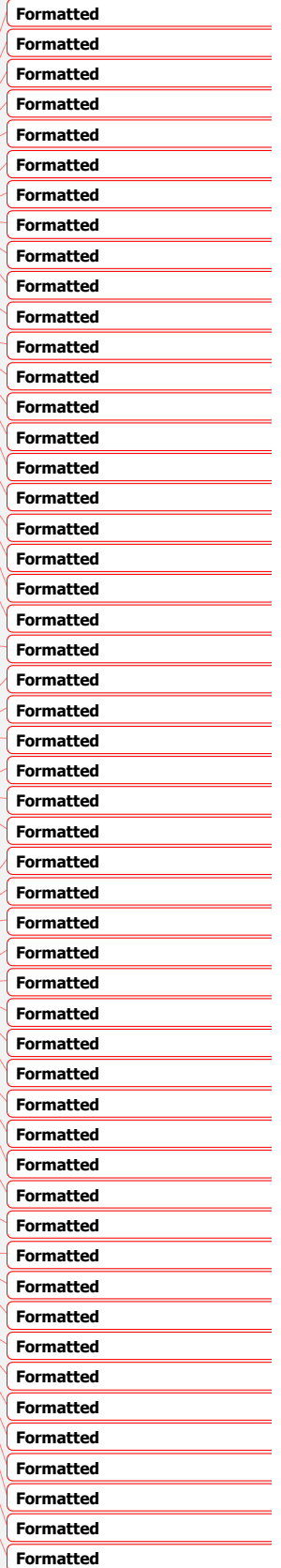
2014), by further deducting growth respiration and the maintenance respiration of sapwood and fine roots. Growth respiration is assumed to be proportional to NPP, following:

$$P_{net} = y(P - R_m) = y(P - W_{\bullet s} r_s - \zeta \sigma_a W_f r_r) \tag{13}$$

where P_{net} is NPP, R_m is the maintenance respiration of stem and fine roots, and y is the 'yield factor' accounting for growth respiration. Total maintenance respiration of non-green parts comprises fine-root respiration ($\zeta \sigma_a W_f r_r$, where ζ is the ratio of fine-root mass to foliage area, σ_a is the specific leaf area, W_f is the mass of carbon in foliage ($(1/\sigma_a) L A_c$), and r_r is the specific respiration rate of fine roots), and stem (sapwood) 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 sapwood). $W_{\bullet s}$ can be estimated from A_c through the pipe model:

$$W_{\bullet s} = L A_c v_H \rho_s H_f \tag{14}$$

where v_H is the Huber value (ratio of sapwood to leaf area; Cruiziat et al., 2002), and H_f is the mean foliage height $H (1 - f_c/2)$. The constraint that the initial sapwood area must be equal to the stem cross-sectional era leads to the following identify: $L c v_H = 1$.

NPP is allocated to stem increment (dW_s/dt), foliage increment (dW_f/dt), fine-root increment ($\zeta \sigma_a dW_f/dt$), foliage turnover (W_f/τ_f, where τ_f is the turnover time of foliage), and fine-root turnover ($\zeta \sigma_a W_f/\tau_r$, where τ_r is the turnover time of fine roots). For simplicity, in common with many models, we do not consider allocation to branches and coarse roots separately from allocation to stem:

$$P_{net} = dW_s/dt + (1 + \zeta \sigma_a) dW_f/dt + (1/\tau_f + \zeta \sigma_a/\tau_r) W_f \tag{15}$$

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

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

$$- L (\pi c/4a) [aD (1 - H/H_m) + H] (1/\sigma_a + \zeta) dD/dt - L A_c (1/\sigma \tau_f + \zeta/\tau_r) \tag{16}$$

The annual increment in (dD/dt) and all the other diameter-related indices are simulated by combining Eq. (7) and Eq. (16).

2.1.3 Definition of the growing season

The season over which GPP is accumulated (i.e. the effective growing season) is defined as running from July in the previous year through to the end of June in the current year. This definition is consistent with the fact that photosynthesis peaks around the time of the summer solstice (Bauerle et al., 2012) and that maximum leaf area occurs shortly after this (Rautiainen et al., 2012). Carbon fixed during the later half of the year (July to December) is therefore either stored or allocated to purposes other then foliage expansion. Observations of tree radial growth show that it can occur before leaf-out (in broadleaved trees) or leaf expansion (in needleleaved trees), thus confirming that some part of this growth is based on starch reserves from the

previous year (Michelot et al., 2012). This definition of the effective growing season is also supported by analyses of our data which showed that correlations between simulated and observed tree ring-widths are poorer when the model is driven by GPP during the current calendar year rather than an effective growing season from July through June.

2.2 Model application

2.2.1 Observations

We use site-specific information on climate and tree growth from a relatively low-elevation site (ca 128°02′E, 42°20′E, 800 m a.s.l.) in mixed conifer and broadleaf virgin forest in the Changbai Mountains, northeastern China (Bai et al., 2008). This region was chosen because there is no evidence of human influence on the vegetation, and the forests are maintained by natural regeneration. Data on tree height, diameter and crown area were collected for 400 individual *Pinus koraiensis* trees from thirty-five 20m by 20m sample plots. The 400 trees included all individual of this species in the 35 plots, i.e. represent a complete sampling of the variability in growth. Tree height and diameter were measured directly, and crown area measured as the area of projected ground coverage. Tree-ring cores were obtained from 46 of these individuals in 2007. The selected trees were either from the canopy layer or from natural gaps in the forest, and in both cases not overshadowed by nearby individuals in order to minimize the possible effects of competition. An attempt was made to select individuals of different diameters (diameter at breast height from 10 to 70 cm at time of sampling), broadly corresponding to the range of diameters recorded in the original sampling. The 46 trees were of different ages (ranging from < 50 to ca. 200 years at the time of sampling, 2006); subsequent analyses show there is little relationship between age) and different diameters (diameter at breast height, from 10 to 70 cm at time of sampling). Environmental conditions (e.g. soil depth, light availability) were relatively uniform across the sampling plot. Monthly temperature, precipitation and fractional cloud cover data, from 1958 onwards, were obtained from Songjiang meteorological station (128°15′E, 42°32′E, 591.4 m a.s.l.), which is representative of the regional climate at low elevations in the Changbai Mountains.

2.2.2 Derivation of T model parameter values

T model parameter values were derived from measurements made at the sampling site or from the literature (Table 1). We estimated the initial slope of the height-diameter relationship (a: 116), the initial ratio of crown area to stem cross-sectional area (c: 390.43), and maximum tree height (H_m: 25.33 m) using nonlinear regression applied to diameter at breast height (D), tree height (H), and crown area (A_c) measurement on all the 400 trees from the sample plots (Fig. 2). We used a value of sapwood density derived from three measurements at the sampling site (Table 1). We used values of fine-root specific respiration rate (r_r), leaf area index within the crown (L), specific leaf area (σ), foliage turnover time (τ_f), and fine-root turnover time (τ_r) for *Pinus koriensis* from field studies conducted in northeastern China (Table 1). literature. No species-specific information was available for the PAR extinction coefficient (k), yield factor (y), ratio of fine-root

mass to foliage area (ζ), fine-root specific respiration rate (r_r), or sapwood specific respiration rate (r_s). We therefore used published values for other species of evergreen needleleaf trees, taken from papers that summarise results from a range of field measurements.pines. Most of the published values for these parameters fall in a relatively narrow range (Table 1). The uncertainty in fine-root specific respiration rate is not given in the original source paper (Yan and Zhao, 2007) but the average value is consistent with other studies (e.g. Zogg et al., 1996). TheHowever, published values for sapwood-specific respiration rate in pines show considerableconsiderably greater variability, ranging from 0.5~10, or even 20 nmol/mol/s (Landsberg and Sands, 2010). Analyses (see Sect. 3.1) show that the model is sensitive to the specification of sapwood respiration. We therefore selected the final value for this parameter based on calibration of the simulated mean ring width againstwith observations, constrained by the published range of values for sapwood respiration rate.

2.3 Model application

We applied the model to simulate the growth of 46 individual *Pinus koraiensis* trees from the study site between 1958-2006. The 46 trees were of different ages (ranging from <50 to ca 200 years at the time of sampling, 2006) and different diameters (diameter at breast height from 10 to 70 cm at time of sampling). Environmental conditions (e.g. soil depth, light availability) were relatively uniform across the sampling plot. The start date for the simulations was determined by the availability of local climate data. Site latitude, elevation, and observed monthly temperature, precipitation, fraction of cloud cover were used as input for the P model. Each tree was initialised at its actual diameter at 1958, calculated from the measured diameter in 2007 and measured radial growth between 1958 and 2007. The model was initially run with a fixed CO_2 concentration of 360ppm. To examine the impact of changing atmospheric CO_2 levels on tree growth, we made a second simulation using the observed monthly CO_2 concentration between 1958 and 2006 (310 - 390 ppm: NOAA ESRL).

2.4 Statistical methods

For statistical analyses and comparison with observations, the individual trees were grouped into three age cohorts, based on their age in 1958: young (0-49 years), mature (50-99 years), and old (>100 years). Individual trees within each age cohort exhibit a range of diameters: young ca 20-37 cm, mature: 9-59 cm, and old: 25-40 cm. These differences in size will affect the expression of ontogeny within each cohort. The mean and standard deviation (SD) of year-by-year diameter growth was calculated for each age cohort from the observations and the simulations. The Pearson correlation coefficient and root mean squared error (RMSE) were used to evaluate the degree of agreement between the observations and simulations. We used generalised linear modelling (GLM: (McCullagh, 1984) to analyse the response of tree growth to the major climate factors and age. The GLM approach is helpful for separating the independent influence of individual factors on tree growth, given the inevitable existence of correlations between these factors.

3 Results

3.1 Simulated ring width versus observation

There are only small differences between different age cohorts in the mean simulated ring width, with a mean value of 1.43 mm for young trees, 1.31 mm for mature trees, and 1.37 for older trees. These values are comparable to the mean value obtained from the observations (1.48mm, 1.29mm, 1.34mm respectively). However, the general impact of ageing is evident in the decreasing trend in ring widths between 1958 and 2007 within any one cohort (Fig. 3). The slope is stronger in the observations than in the simulations, indicating that the model somewhat underestimates the effects of ontogeny.

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

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

3.2 Parameter sensitivity analysis

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

The model simulates a rapid initial increase in ring width, with peak ring widths occurring after ca 10 years, followed by a gradual and continuous decrease with age (Fig. 4). The model is comparatively insensitive to uncertainties in the specification of fine-root specific respiration rate (r_r), fine-root turnover time (τ_t), and specific leaf area (σ), while leaf area index within the crown (L), ratio of fine-root mass to foliage area (ζ) and fine-root turnover time (τ_r) have only a moderate effect on the simulated amplitude of ring width. The largest impacts on the amplitude of the simulated ring width are from initial slope of height-diameter relationship (a),

initial ratio of crown area to stem cross-sectional area (c), and sapwood density (ρ_s). Maximum tree height (H_m) and sapwood-specific respiration rate (r_s) have the greatest influence on the shape of the simulated ageing curve. These two parameters also have a large impact on the amplitude of the growth of old trees. The parameters values for a, c, H_m and ρ_s are derived from observations, with uncertainties much less than 50% (Fig. 2). Thus, the sensitivity of the model to these parameters is not important. However, model sensitivity to sapwood respiration (r_s) both in terms of the shape of the ageing curve and the amplitude is of greater concern, given the large range of values in the literature. Although some part of the uncertainty in the specification of sapwood respiration may be due to differences between species, the difficulty of measuring this trait accurately also contributes to the problem. For the final model, we tuned r_s against the ring-width observations. The best match with the observations was obtained with a value 1.4 nmol/mol/s, which is within the range of published values for pines (see summary in Landsberg and Sands, 2010). r_s is the only parameter that was tuned.

3.3 Controls on tree growth

The GLM analysis revealed a strong positive relationship between PAR_0 and tree growth, while moisture stress (as measured by α, an estimate of the ratio of actual to potential evapotranspiration) was shown to have a less steep but still positive effect (Fig. 5 and Table 2). The observed partial relationship between mean annual temperature and tree growth is negative. The Changbai Mountains are at the southern end of the distribution of *Pinus koraiensis* in China, which makes it plausible that tree growth would be inhibited during warmer years.

The model reproduces these observed relationships between climate factors and tree growth. The slope of the observed positive relationship with α is statistically indistinguishable from the modelled slope, but the observed positive relationship with PAR_0 is weaker, and the negative correlation with mean annual temperature is stronger, in the observations than in the simulations. These differences between observations and simulations could reflect the influence of an additional climate control, related to both PAR_0 and temperature (e.g. cloud cover). The difference between observed and simulated effects of temperature may also be because although simulated growth is inhibited by low temperatures (through the computation of PAR_0), the current model does not include any mechanism for inhibition due to heat stress at high air and leaf temperatures.

The GLM analysis also showed that age, as represented by the three age cohorts, has an impact on ring width: young trees have greater ring widths than mature trees, while old trees have somewhat greater ring widths than mature trees. This pattern is seen in both the observations and simulations, although the differences between the young and mature cohorts are slightly greater in the observations.

The overall similarity in the observed and simulated relationships between growth rates and environmental factors confirms that the T model performs realistically. The observed relationships are considerably noisier

than the simulated relationships (Fig. 5, Table 2), reflecting the fact that growth rates are affected by small-scale variability in environmental conditions as well as time-varying competition for light.

3.4 Simulated CO_2 effect on tree growth

Elevated levels of CO_2 are expected to have a positive impact on tree growth (Hyvönen et al., 2007; Donohue et al., 2013; Hickler et al., 2008; Boucher et al., 2014).). This positive response to [CO_2] is seen in the comparison of the fixed [CO_2] and real [CO_2] simulations (Fig. 5). In the first part of the simulation, prior to 1980, the actual [CO_2] is lower than the level of 360 ppm used in the fixed [CO_2] experiment: this results in lower growth rates. The 50 ppm difference between the two experiments at the beginning of the simulation results in a difference in ring width of 0.242 mm. After 1980, when the actual [CO_2] was higher than 360 ppm, the tree growth in the simulation with realistic [CO_2] is enhanced. The 30 ppm difference at the end of the simulation results in a difference in ring width of 0.101 mm. Overall, the change in [CO_2] between 1958 and 2006 results in a positive enhancement of tree growth of ca 0.343 mm/yr. However, this difference is very small compared to the impact of ageing (> 1 mm from observations) or to the differences resulting from the interannual variability of climate (1.212 mm) on tree growth.

4 Discussion

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

Our simulations suggest that after a brief but rapid increase for young plants, there is a general and continuous decrease in radial growth with age (Fig. 4). This pattern is apparent in individual tree-ring series, and is evident in the decreasing trend in ring widths shown when the series are grouped into age cohorts (Fig. 3). It This is a necessary consequence of the geometric relationship between the stem diameter increment and cross-sectional area: more biomass is required to produce the same increase in diameter in thicker, taller trees than thinner, shorter ones. However, we find that ring widths in old trees in our study region are consistently wider than in mature trees, and this property is reproduced in the simulations (Fig. 3, 5). This situation arises because the old trees are on average smaller than the mature trees at the start of the simulation (in 1958). , presumably reflecting relatively poor growth conditions pre-1900. Thus, while the difference between average

ring-widths in the mature and old cohorts conforms to the geometric relationship between stem diameter increment and cross-sectional area, it is a response that also reflects differences in the history of tree growth at this site which determined the initial size of the trees in 1958. Lack of climate data prior to 1958 or detailed information about stand dynamics precludes diagnosis of the cause of the growth history differences between mature and old trees.

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

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

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

We have assumed that the period contributing to growth (i.e. the effective growing season) in any year includes carbon stores generated during the second half of the previous year. The total foliage area determines the radial area of the stem, and once this is achieved NPP is allocated either to fine root production or stored as carbohydrate for use in stem growth in the early part of the subsequent year. This is consistent with observations that radial growth begins before leaf-out (Michelot et al., 2012) and that maximum leaf area is

generally achieved by mid-summer (Rautiainen et al., 2012), and the MAIDEN model also allows tree growth to be influenced by a fixed contribution from the previous year's growth (Misson, 2004).). Defining the effective growing season as being only the current growth year had no impact on the influence of climate on ring widths, or the shape of the aging curve. It did, however, produce a considerably lower correlation between simulated and observed inter-annual variability in growth. Since tree ring-width reflects the integrated climate over the "effective growing season", reconstructions of climate variables reflect conditions during that season, not simply during the current calendar year.

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

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

~~But, given the difficulty of measuring sapwood respiration and also the comparative lack of data on fine root turnover rates, it is likely that some form of tuning will be required in order to specify these parameters.~~

Our modelling approach integrates the influence of climate, $[CO_2]$ and ontogeny on individual tree growth. Such a model is useful to explore the response of tree growth to potential future changes in climate, and the impact of changes in tree growth on carbon sequestration. We also envisage that it could also be used to investigate the impact of past climate changes on tree growth. Reconstructions of temperature changes beyond the recent observational period, used as a baseline for the detection of anthropogenic influences on the climate system, are largely derived from statistical reconstructions based on tree-ring series (Jones et al., 1998; Esper et al., 2002; Hegerl et al., 2006; Mann et al., 2008; Ahmed et al., 2013). However, as we show here, temperature is neither the only, nor the most important, influence on tree growth. This may help to explain why correlations between ring-widths and climate at individual sites appear to have broken down in recent decades (the so-called divergence problem: D'Arrigo et al., 2008). The availability of a robust model to investigate tree growth could help to provide better reconstructions of past climate changes (see e.g. Boucher et al., 2014) as well as more plausible projections of the response of tree growth to continuing climate change in the future.

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Table and Figure Captions

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

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

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

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

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

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

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

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

Figure 1

- Latitude
- Monthly temperature, precipitation, fractional cloud cover
- Elevation
- CO_2 concentration

P model
(Wang et al., 2014)

GPP

T model

Species parameters

Carbon allocation
Functional geometry
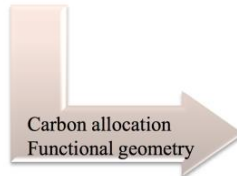
Simulated
Ring width

Figure 2

$$H = 25.33(1 - e^{(-116D/25.33)})$$
$p = 0$
$H_m = 25.33$
$a = 116$

$$A_c = \pi 390.43 DH / 4a$$
$p = 0$
$c = 390.43$

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

$$A_c = \pi 390.43 DH/4a$$
$p = 0$
$c = 390.43$

Figure 3

Figure 4

Figure 5

Figure 6