

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 untuned 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.