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Interactive comment on "An inverse modeling approach for tree-ring-based climate reconstructions under changing atmospheric CO_2 concentrations" *by* É. Boucher et al.

É. Boucher et al.

boucher.etienne@uqam.ca

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Dear editor Brovkin

Enclosed is a revised version of the manuscript entitled "An inverse modeling approach for tree-ring-based climate reconstructions under changing atmospheric CO2 concentrations" following the comments by two reviewers. We find that the comments of the two reviewers were very constructive and useful, and will contribute to the production of a revised version that is much more solid, as it contains less opaque interpretations and analysis of our results and simulations. The main critic formulated by the two reviewers related to our interpretation of the CO2 fertilization effect in tree ring data, and

an important part of the present revision concerns that topic directly. In order to address the problem, we present detailed and perhaps more nuanced interpretation of our results and simulations.

Best wishes, and thanks to the two reviewers for their very helpful and constructive comments

E. Boucher

Legend—- [R1] = Reviewer 1 [R2] = Reviewer 2 [AC] = Author comment [...] = comments continued —-

COMMENTS BY REVIEWER 1

[R1] This is a well-written, scientifically sound, article that attempts to solve a fundamental problem recently identified by paleoclimatologists and ecophysiologists dealing with growth patterns and isotopic composition of tree-rings under changing atmospheric conditions. The authors argue correctly that the standard dendrochronological approach relies upon simple (linear) transfer functions to reconstruct historical climate, which could introduce an unanticipated bias due to a potential CO2-induced stimulation of tree growth. This confounding factor is expected to be particularly problematic in chronologies that extend through and beyond the beginning of the industrial era and has hindered accurate predictions of the effects of changes in climate and atmospheric composition on terrestrial ecosystems, as its reverberations on the ecophysiological performance of tree species are typically not accounted for. To solve the problem the authors propose a novel approach, tested using data from the Fontainebleau forest (France). They conclude that their inverse modeling method represents a better alternative to the traditional transfer function technique, with advantages such as the ability to distinguish between climatic and CO2 effects on tree growth. While I think this modeling exercise is valuable and agree with most of the proposed methodology, I have a number of concerns regarding the use and interpretation of growth and isotopic data, which in my opinion need to be (at least in part) reevaluated to reflect ongoing discussions in the specialized literature. Below I provide specific comments that when addressed will greatly improve the relevance and impact of the study, as well as its future contributions for the attribution of causality in the analysis of CO2-driven changes in tree growth patterns.

[...R1] General issues with growth patterns

[...R1] It is important to note that the present study does not represent the first attempt to address modern biases in dendrochronological analysis. Approaches other than simple transfer functions exist and these should be acknowledge and discussed to emphasize the relevance and unique value of the method proposed here. To mention one example, a likelihood perspective on tree-ring standardization aimed at eliminating sampling bias (which would also encompass CO2 effects) has been recently published Cecile et al. (Climate of the Past 9: 4499-4551, 2013). These authors describe a new standardization technique, using fixed effects that contain both classical regional curve standardization and flat detrending. Their assessment of the traditional approach revealed a significant negative bias in estimated tree growth over time, largely concentrated in the last 300 years of tree-ring growth data, which poses serious questions about the reliability of commonly used standardization techniques. These include the regional standardization used here (e.g., the adaptive regional growth curve technique used to produce the average chronology shown in Fig. 4) and therefore should be addressed.

[AC] →Cecile's paper (in review) deals with trends, biases and proposes a novel standardization similar to that of Melvin and Briffa (2008), but does not propose any solution for the CO2 effect, as there is no process model included in the method. Taking these comments into account, we thought it would be useful to examine if, in our own dataset, such a negative bias could have been introduced by the ARGC technique (not evaluated in Cecile's paper). A negative biais would lead to an underestimation of the tree's productivity, when, for example, the standardized growth is compared to the raw data. The comparison, represented in the graphic below (figure 1) , shows that, when we

compare raw latewood widths (corrected for mean =1, original trends preserved) to ARGC-standardized latewood widths, there is absolutely no visible negative bias produced by the ARGC method such as those described by Cecile et al for the last 300 yr. On the contrary, the ARGC produces a trendless series that seems to be in accordance with what we would expect from a "state or the art" standardization (figure 1) . If the method has any effect at all on our data, it is one that over-estimates the effect of CO2 on tree growth, as the standardized growth curve lies over the raw curve. However, since the raw curve is already decreasing, it is reasonable to assume that this correction does not imply an amplification of the CO2 effect, but simply reflects a more conventional correction for the age effect.

(see figure 1) [...AC] Figure 1. Comparison between raw (black) and ARGC-standardized (blue) latewood width curves.

[...AC] We will nevertheless underline that research on standardization such as those proposed by Cecile et al (in revision) or works by Melvin and Briffa (2008) will be very useful, in the future to help constrain the inversions with tree ring chronologies that contain as little bias and / or noise as possible.

[R1] More importantly, a central assumption of the present manuscript is the existence of a measurable "CO2 fertilization" effect, which supposedly has systematically increased the productivity of trees since the beginning of the industrial revolution, an assumption that has been proven incorrect in recent studies. For example, Gedalof & Berg (Global Biogeochemical Cycles, 24: 1-6, 2010) analyzed the global record of annual radial tree growth derived from the international tree ring data bank, 3 CO2 fertilization effect. They concluded that only 20 percent of sites globally exhibit increasing trends in growth that cannot be attributed to climatic causes, nitrogen deposition, elevation, or latitude, showing very limited direct evidence of CO2 fertilization of forests over the 20th century. More recently, Silva & Anand (Global Ecology and Biogeography 22:83-92, 2013) used dendrochronological and isotopic records to evaluate the impacts of atmospheric changes on tree growth across forest biomes. They concluded that over the past 50 years, tree growth decline has prevailed despite increasing atmospheric CO2. Furthermore, they found that the impact of atmospheric changes on forest productivity is latitude dependent, but empirical data suggest that globally CO2 fertilization of trees will not counteract emissions. It is therefore essential that the authors consider CO2 acclimation and warming- and drought-induced growth decline in their model. At least, they should discuss the implications of acclimation and growth decline evident in empirical datasets, addressing modeling scenarios other than CO2 stimulation of growth.

[...R1] General issues with isotopic patterns

[...R1] The inversion approach described here is largely based on the work of Danis et al (Can. J. Forest Res., 42, 1697–1713, 2012) and seeks at finding optimal combinations of input atmospheric data so that process-based simulations are as close as possible to observations of growth responses and isotopic composition (used to infer physiological responses to CO2) of tree rings. This approach ignores, however, ongoing discussion on limitations of the isotopic method. Particularly relevant here is the debate on whether the use of tree ring _13C data has overestimated responses to rising CO2. A recent study by Silva & Horwath (PLoS One 2013 8(1): e53089) reproduces global increases in water use efficiency using Monte Carlo simulations to show that autocorrelations in the derivation of physiological parameters from _13C largely overestimate responses to rising atmospheric CO2. These authors show that random _13C datasets lead to increasing water use efficiency, over time and across altitudinal gradients, of the same magnitude and direction as reported in recent field studies. This is explained by the fact that CO2 is used as an independent variable in the calculation, generating positive responses to rising CO2 levels regardless of actual physiological responses. The same calculation is used here (eq. 3), thus, a discussion on real versus artificial CO2 effects is necessary.

[...R1] This issue is connected with the pattern of growth decline and acclimation described above. For example, Silva & Horwath consider physiological responses as

those that cause changes in atmosphere to plant (source to product) 13C discrimination. Under this definition expected increases in photosynthesis or declines in stomatal conductance should lead to proportional changes in 13C discrimination, but they found that increases in water use efficiency occur independently of changes in discrimination or growth. They propose the use of a baseline (non-physiological) response curve, reflecting what would be observed if Ci increased proportionally with Ca, a conservative scenario compared with, for example, constant Ci which would represent strong increases in water use efficiency and growth. Stimulation of photosynthesis that characterize CO2 fertilization effects would tend to keep Ci constant and this has been empirically demonstrated by Linares & Camarero (Global Change Biology 2012 18:1000-1012), who tested temporal trends in water use efficiency under three theoretical scenarios for the regulation of plant-gas exchange at increasing CO2, using temperature and precipitation data to predict tree growth. In their study the theoretical scenario assuming the strongest positive response to CO2 (i.e. Ci constant) explained 66–81% of the water use efficiency variance and 28–56% of the observed tree growth variance, whereas climatic variables explained less than 11–21% of the growth variance. A theoretical assessment similar to that proposed by Linares & Camarero could be used here to distinguish physiological responses from artifacts of calculation. Alternatively, a simple response contrast analysis, based on the ratio between cumulative changes in growth and water use efficiency, could be used as proposed by Silva & Anand to integrate the effects of CO2 and climate variability on tree growth over time.

[AC] → We acknowledge the fact that the existence of a fertilization effect in tree ring chronologies remains a highly controversial issue in the dendro community. On one hand, there are studies that argue against a possible fertilization effect, some of which were identified by reviewer 1 (eg. Gedalof and Berg, 2010; Silva and Anand, 2013). Most of these studies are based on empirical relationships, and conclude, after the removal of the portion of variance that is "explained" by climate only, that residual trends either do not exist or cannot be related to the CO2. On the other hand, there is a whole set of studies produced by researchers in plant physiology and that are based on direct measurements of gas exchanges between the vegetation and the atmosphere. Such studies, like the one recently published in Nature by Keenan et al (2013) conclude that WUE increase is significant (over the last two decades) and that the associated CO2 effect is even higher than that predicted by 13 physiological models. So this quick review just recalls that the issue is far from being resolved and that long-term adjustments of the vegetation to increasing CO2 concentrations are still largely debated in the community.

[AC] →In the context of this discussion, we find that reviewer 1's (and also reviewer 2) comments are useful in highlighting the fact that we might have pushed too far our argumentation concerning CO2 fertilization and its impact on the inversion. We concede that the inclusion of atmospheric CO2 (Ca), as an independent variable, leads to a proportional / direct increase in intercellular CO2 concentration (Ci), in order to keep the Ci / Ca ratio stable. Similarly, since WUE is directly proportional to that Ci / Ca ratio, a rise in WUE is inevitably expected. We will therefore revise our interpretations and downgrade the discussion of the fertilization effect by CO2 in the Fontainebleau forest, as well as the corresponding increase in WUE through time when the A1 scenario is used.

[...AC] We will nevertheless maintain that the A1 scenario is essential to adequately reconstruct climate through the inversion process, as this is clearly demonstrated in our paper, independently of the discussion on CO2 fertilization and gs-related adaptation to drought. An indirect proof for the important role of CO2 comes from the fact that, when the inversion is forced by constant, pre-industrial [CO2] (A2 scenario), the reconstruction fails to converge towards climate values that resemble those observed during the 1850-2000 period, which in turns produces a colder and wetter climate then what was actually observed at Fontainebleau during the same period. The divergence between real and reconstructed climate is apparent not only in the low frequency band (trends), but also in the high frequency band, yielding an anomalous amount of cold events after ca 1940. These results highlight the fact that MAIDENiso correctly bal-

ances the interplay between climate, CO2, tree growth and isotope fractionation, and that this interplay is not stationary through time. Without an increasing and thus realistic [CO2] scenario, the ecophysiological model needs to compensate by altering climate and bring both precipitation and temperature outside from the bounds of observed variability, so that simulated tree growth and isotope fractionation match with observations.

[...AC] Instead of focusing on fertilization effects and adaptation of Fontainebleau's oak trees to drought, which might be too much of a strong statement given the existing controversy, we nevertheless want to point out that our study brings some elements of answer on the ongoing debate on the mathematical formulation of stomatal conductance and the representation of acclimation. It is important to understand that there exist two main models for stomatal conductance that allow for the simulation of Ci and Ca ratio and thus, the simulation of gas exchanges between the plant and the atmosphere. The first model is from Jarvis (1976) and is based on a combination of empirical stomatal responses to environmental conditions that may be altered if plants grow in elevated [CO2]. This model was criticized for its inapplicability in iterative modeling procedures, as it does not integrate feedback loops among stomatal conductance, internal CO2, transpiration, humidity deficits and leaf water potential. The second one is the Ball-Berry (1987) model, which is based on the early works of Wong et al (1979), and was later modified by Leuning (1995). This model is used in MAIDENiso, and it is the most common way to represent stomatal conductance nowadays. Hence, we agree that the Ball-Berry-Leuning model implies a quasi-parallel response of Ci to increasing Ca. For that reason, it certainly engenders an exaggerated growth response at very high CO2 high concentrations (> 400 ppm. . .700-800 ppm) and it would not be reasonable to use it without taking into account important acclimation mechanisms to model growth under such conditions. But the debate remain open as to determine whether or not the model applies to the range of concentrations that we've experienced since the pre-industrial era (250-400ppm). We step in the debate and argue that the Ball-Berry-Leuning model enables the correct modeling of the interaction between climate, tree ring proxies and

[CO2] at Fontainebleau. A corollary argument relating to that statement is that, if the MAIDENiso model is correct, acclimation mechanisms such as the ones proposed by Berninger et al. (2004) (nitrogen-temperature) limitation should not have had a large influence, at least in our context. Otherwise, the inversion would not be able to converge towards realistic climate scenarios when it is forced by the A1 scenario.

Specific comments (. . .) [AC]. → These comments will greatly improve the text. All authors / studies identified by reviewer 1 will be cited. Every unclear phrasing will be clarified, and all passages that relate to one of the two general comments described above (either standardization or fertilization) will be clarified in the light of the preceding discussion. A clear answer to the three questions presented in the introduction will be provided

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COMMENTS BY REVIEWER 2 [R2] The manuscript by Boucher et al. describes the application of an ecophysiological model to the problem of reconstructing past climate parameters. The authors test whether using an inverse approach can yield reliable reconstructions and how this methodology compares to simpler transfer function approaches based on multiple linear regressions. They further use the model to test possible effects of CO2 fertilization. I think the presented work is a notable contribution at the intersection of paleoclimatology and dendroecology.

[...R2] General comments

[...R2] The authors describe two topics: First, they show conclusively that the inverse approach is able to produce local reconstructions of past climate parameters and that the approach appears to have a number of advantages compared to simpler transfer functions. Second, they provide evidence from their modelling-study that indeed CO2 can have an effect on the reconstruction results and they present one hypothesis how the increased CO2 might have affected the plant. The first topic is handled convincingly and I have only minor comments on the presentation. However, their discussion of the

CO2 effect is vague on how the differences in water uptake efficiency (WUE) link to the plant growth or in terms of the model to the considered parameters (latewood widths, d18O and d13C).

[AC] → See discussion above, as this comment was common to both reviewers

[R2] Furthermore, this part is missing any discussion of how the quality of the reconstruction is affected. Overall I would appreciate if the authors presented more clearly the uncertainty of their results and the range of their probability densities. This would allow the reader to assess the differences between the different approaches. I detail this and my further minor concerns below. Further, I fully endorse the review comments of the anonymous referee #1.

[AC] → We agree that adding uncertainties would help to compare the different methods. When it is possible (eg figure 8-9), uncertainties and slopes will be added to the graphs. It is however important to note that it was not our intent to misguide the reader, as the results of the inversion are systematically presented with a 90% confidence band. The decision to not present the uncertainties over comparative graphs was an esthetic one: superposed uncertainties often results in blurry images.

Specific comments (...) [AC] → Reviewer 2 specific comments will be addressed. Unclear passages in the text (eg. complimentary signals and sources or noise) and in the captions (eg. fig 4) will be clarified. We will also add a paragraph in the introduction and also one in the discussion to present the advantages of the model (and its complexity) and clarify how the approach is distinct from regression-based transfer function approaches. For example, we will insist on the advantages that process-based models have to perform reconstructions in non-stationary climate-to-tree-growth relationships. This discussion will be written in light of the aforementioned discussion on CO2 effects. Citations to Tingley et al will be inserted. The answer to the three questions stated in the introduction will be clarified in the discussion (also requested by reviewer 1)

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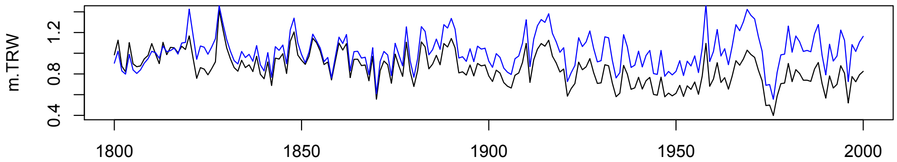

Figure 1. Comparison between raw (black) and ARGC-standardized (blue) latewood width curves.

Fig. 1.