#REPLY TO REVIEWERS MS bgd-12-2745-2015, 'Modelling the climatic drivers determining photosynthesis and carbon allocation in evergreen Mediterranean forests using multiproxy long time series' by Gea-Izquierdo and coauthors.

Dear editor, please see below a detailed response to reviewers' comments. We have focused to better explain the methods and the analysis as requested by the reviewers. The detailed responses are in bold between lines. When we refer to the "revised version" we mean the version with track changes that we will submit together with the response.
We would like to thank you and the reviewers for your suggestions.
Yours sincerely.

Guillermo Gea-Izquierdo & coauthors

Reviewer #1:
If I understood correctly, the authors attribute the decline in LAI since ~1990 to a decline in precip. Why did E (and gs) remain constant while LAI and Precip declined (and water stress presumably increased, as the authors say)?
Yes, we attribute the decline in LAI (Figure A3) in the Q. ilex woodland to the decline in precipitation observed at that site (Figure A1). However, please see that gs and E did not remain constant: E shows a decline similar to that in GPP (Figure A3) while gs decreases in the late 1970s and then remains constant. We show Figure A3 with another scale to depict clearer these effects and rewrite the text to be clearer in the discussion (see lines 30-34, 462-480 of the revised version). Similar acclimation processes at the canopy level (LAI) have been observed in different drought experiments (e.g. Limousin et al. Misson et al. in the text).

Since E is so much smaller than precip (~50% in Fontblanche), one could think that the site is not water limited. What's the potential ET? Where does the difference between P-ET go? (I presume that's a flat site, no run-off)
Yes it is a flat site, but both sites are on a calcareous substrate, which means much water will be percolated into the soil and not available for plants. Additionally in the studied site precipitation generally happens on stormy episodes. We set maximum water holding capacity to field measurements carried out within the studied sites (see references within the ms). E values shown in the ms are of similar magnitude to those in Gaucherel et al. 2008 for a similar ecosystem.

The authors claim to have addressed the source vs sink debate. I was wondering as to whether the effects of eCO2 could be discussed under this angle (sink, and not source, controls). The model really is one driven by assimilation and, as the authors point out, the results are driven by the equations used. However, we don't know, for instance, whether Leuning's model is or not an accurate representation of responses to eCO2 (potentially affecting the interpretation of iWUE) and, if growth is sink driven, then it could affect the statement of: "Thus, the absence of a long- term increase in GPP and growth would not mean that enhanced [CO2] was not beneficial for model outputs: growth and photosynthesis would have been lower had we used constant [CO2] with the same model parameters."
Yes, we agree. Please, see the discussion particularly in lines 602-607 where we add "…, particularly in the case of C-source limitation".

We have a few models that link assimilation with growth. Why another one? What's the justification for deriving such a new model? How does it compare with other models? Could the results obtained from this model not have been obtained by using the existing ones?
The model we used is not new. It was based on an existing one (MAIDEN; Misson 2004) in which we have made a number of developments in order to improve model performance in the light of the data used and hypotheses assessed. We have cited other models in the discussion to show how they perform in terms of goodness-of-fit (lines 570-574). To check how they perform more in detail compared to our results they should need to be analysed on "ad-hoc" modeling comparison. Likely, our results of GPP should be similar to those process-based forest models based on similar photosynthesis equations, but differ in the allocation pattern particularly with those models considering allocation constant.

I find Fig. 5 quite puzzling as it seems to indicate that an extreme drought is the most favorable environment for growth (at least, for allocation to growth), yet water scarcity is likely to limit growth under those conditions. I presume AN under those conditions will be close to zero anyway because of respiration, but what's the theoretical basis for assuming that growth (driven by turgor) is less sensitive than allocation to the hot and dry?
Please, note that in Fig 5 we show the opposite, namely that more humid conditions lead to more carbon allocated to stem growth and less to storage. Therefore, we agree with your comment.

A minor comment: I found the nomenclature a bit confusing. For instance, the authors refer to allocation to stem and allocation to storage as different things, yet a large part of storage happens in the stem. I presume the authors mean allocation to stem growth?
Yes, this is true. We modify this now for the sake of clarity, please, see e.g. new lines 23, 89, 329

Anonymous Referee #2
Comments General comment. It's unclear how climatic drivers can limit carbon allocation. I think climatic drivers will change patterns of carbon allocation, but not limit allocation itself. In addition, secondary growth is considered, but what about primary growth. I know is difficult to have a record of annual growth of the overall parts of the tree (branches, secondary shoots, roots, etc. . .). However, it's difficult to discard this important annual sink of carbon if a realistic model has to be elaborated.
We change now "limit carbon allocation" to "change patterns in carbon allocation", e.g. see line 44.
Primary growth is included either in what we called "allocation to the canopy" or in "allocation to roots". See e.g. line 313. We agree this is a critical point that merits further development when there is availability of such data.

Specific comments: Line 13 of abstract what kind of environmental changes are being considered by authors? Temperature increase in future? Concentration of CO2 in atmosphere? Drought? Evaporative demand? Recurrence of dry periods? All together? Authors must be more explicit.
We now state "to enhancement in water stress", which is driven by higher temperatures and also lower precipitation at one site (Puechabon). See new line 29.

Line 15 Details of how ecosystem WUE was estimated should be pointed out.
Please, see lines 418-419 (the last in the M-M) where we specify how we calculate WUE and iWUE following Beer et al. (2009)

Line 16 It seems GPP followed a decrease according to a progressive lowering of rainfall in one of the sites. However, it's a little misleading for reader to what are referring authors, whether total annual rainfall or increase of variability in annual or monthly rainfall.
We specify now "annual", line 34.

Problems in using average annual values for LAI and SLA.
We do not use an average value of LAI but let LAI vary during the year with leaf shedding and leaf flush (in Figure 1 we show an outline of leaf phenology). In figure A3 we show the maximum annual value used. Regarding SLA, we use an average value. It is known that there is certain variability in SLA in response to environmental forcing, we are aware of this (see references therein). However we did not have a way to estimate how this variability works at the stand level in space and time and preferred to simplify and use average values to avoid adding extra sources of complexity in the model that we could not accurately take into account.

Considering Rd as a direct function of An can include important bias in the model. Rd changes with temperature following an exponential function with a change in the sensitivity of parameters as Q10 with water stress. In Mediterranean systems carbon losses are as important as carbon uptake. Thus, modelling respiration should not be oversimplified by a mere linear dependence with An. Maybe, modifying exponential response to temperature of Rd, according to water stress, would improve the models in a more realistic way that a mere linear dependence of Rd with An. On other hand the linear dependence of Rd-An assumes implicitly a constancy in the An/Rd that is well known from ecophysiology not true. A similar shortcoming arises from the linear dependence of Jmax with Vcmax (line 22, page 2752). It's true both are highly coupled, but it's unclear how the Jcoef is inferred.
We agree with the statements presented here. But as we state in lines 196-202 we tried different formulations when developing the model including also explicitly SWC but decided to leave the direct function as the best option for our application. Regarding Jmax/Vcmax, we tried also several formulations as from De Pury and Farquhar 1997 and Masseyk et al. 2008, but decided to leave a simpler relationship because the model proofed better and more stable (when compared to the data used for calibration). Even if the processes themselves have been shown to be non-linear functions of climate, performance of our model was better through further simplifications of these relationships. This is because there is a less complex parameterization to be done and also because of the nature of our data-driven approach. We acknowledge that there are always simplifications in models and try to state them clearly in the text (M-M).

Minor comment authors change abbreviator from An to Ac without a clear rationale. In addition, I do not see necessary to include the sub-index (i) in the formulations. It's clear most parameters are variables which value depend of some constants or other functional variables.
It can be inferred from lines 196-199 that An=Ac-Rd, and that Rd=f(Ac).
We prefere to leave the subindices to show more clearly when different variables are a function of different time steps to avoid misinterpretation of equations.

In the last years it's beginning to be clear the need to consider Cc instead of Ci in the model of Farqhuar in order to take into account effect of some functional parameters as mesophyll conductance to CO2. This seems not to be relevant for authors, though a comment is included

in passing when coupling stomatal conductance with photosynthesis from a modified version of Leuning (1995) equation (line 4 page 2754). At least a brief comment on the matter should be included to justify the use of Ci instead of Cc in the Farqhuar model.
Yes, this is also true. Please, see new lines 208-213 and 245-248 where we further explain how this is address in the model and acknowledge the effect of possible simplifications applied.

It's unclear how authors split total LAI in sun and shade components. If a co- efficient of extinction is used to model in continuous LAI though the crown by following the Beer–Lambert law, how it's established the threshold to consider leaves of sun or shade type.
Total LAI is divided on sunny and shaded leaves. The amount of sunny leaves follows the expression in line 253 and then shaded leaves are just the total LAI minus LAIsunny (line 254, it was not properly expressed before). Photosynthesis is calculated for both leaves (sunny, shaded) and then integrated to the amount (i.e. proportion of LAI) of sunny and shaded leaves considered. There is no threshold, just LAI is divided in sunny and shaded components and integrated to get canopy values.

The model considers different allocation of carbon canopy, stem, roots or storage of non-structural carbohydrates (NSC), but losses as respiration are consider at the overall tree without any consideration of the specific respiratory patterns of the different carbon sinks (equation 7 in page 2754).
Yes, this is rigth. It is one of the assumptions of the model, for the same reasons explained above when we discuss why calculations of some parameters are simplified

Again the ratio root/leaf is considered constant to 1.5 whether it's well-known it changes with site, time and species. This kind of limitations, and those previously mentioned, should be addressed by authors at least with a brief comment.
Please, see lines 314-315 where we explained this point and that we use 1.5 since this is the value estimated for the studied places as in the references mentioned (and unpublished data available from coauthors of this paper)

Results The increase in iWUE but not in WUE could be explained only from an increase in LAI if interdecadal GPP did not change significantly. However, this not seems to be the case. How authors explain this mismatch between the two proxies of water use efficiency.
We have rewritten this point because it was not clear: there is a close match in the high-frequency annual response in both sites but there is a long-term mistmatch particularly in last years at the site where there is a decline in GPP (e.g. see lines 32-35, 474-480). The combination of gs, E+soil evaporation (=ET) and GPP determine this relationship, and just the last three are influenced by changes in LAI simulated.

Discussion In line 20 page 2761 What are authors meaning when they refer to leaf activity? Photosynthetic activity? Respiration? Phenological phase? Please make a more precise use of physiological concepts. Stomatal conductance is coupled to other diffusional and biochemical processes that affect carbon uptake.
We add "photosynthetic capacity" to be more precise (please, see line 488)

In line 21 page 2761, the model does not simulate carbohydrate storage. At the most, it simulates carbon allocation.
Yes, the model calculates carbon allocated to storage dynamically as a function of environmental variability and in relation to carbon allocation to other plant components. Please, see M-M

In line page 2762, growth is considered as the only carbon sink for trees, however in many ecosystems and especially Mediterranean ones carbon losses from respiration and VOC emissions are important carbon sinks. Again, authors should consider this issue briefly.
We now consider this point on lines 508-509

In page 2763 line 12- 14. It's valuable the work of authors in improving previous models. In my opinion, the endeavour for modelling in the future should be focussed to evaluate effects of intense perturbations over impact of average climatic values. In fact, variability in climate could be as important as changes in total precipitation or average temperature.
Yes, we agree this is an interesting point to address in models

To finish this review, I would have liked to see any comment on the changes in potential competitiveness of the species. The model addresses performance of two very different species at one of the study sites: Q. ilex and P. halepensis. Maybe, it would be interesting for reader to include a brief comment about the expected differential performance of both species in terms of carbon allocation and GPP.
We add now a statement on this subject, lines 627-630

Anonymous Referee #3
General comments
I generally find the changes to the model well described, however, it would be very helpful if the authors could give the physical meanings of the numerous parameters where applicable (I am aware that this will likely not be possible for all), or at least give some indication why the particular form of this equation was chosen. Otherwise the form of e.g. Eqs 8-11 can seem rather arbitrary. Following from this, why is allocation to the stem set as a function of climatic forcing in [P4], but not in [P3]? Some explanation of why this change in equation is made would be appropriate.
When possible we now describe more in detail some of the parameters with a physical interpretation (see M-M, e.g. lines 317-318). We refer to Gea-Izquierdo et al. 2013 to justify selection of allocation functions (lines 293-294). Regarding P3, please note that this is also set explicitly as a function of climatic forcing, see [E10] in line 320.

There are a few aspects of the results where it seems like the authors could be more definitive in their interpretations. For instance, on pg. 2761 it is stated that "the model simulated a decrease in GPP, which was likely driven by the prevailing decrease in precipitation". It should be possibly to definitively attribute this decrease in GPP to precipitation by also running the model with fixed precipitation data throughout (e.g. repeated 1960 precipitation cycles). Given that the model does not seem computationally heavy to run, I think this would be easily done.
We now state more clearly that it is a consequence of precipitation (see e.g. lines 462-463)

Likewise, on pg. 2761 it is suggested that differences in GPP between the two sites could also be explained by less limitation of carbon assimilation during the winter at due to higher winter temperatures at Fontblanche. Surely, using the model outputs, it is possible to be more definitive on this?
We state that temperature is likely the factor explaining this, however we think it is better to acknowledge that other factors (forest composition, for instance) can also be co-responsible

The model is intentionally formulated so that growth can be scaled down independently of photosynthesis, but as far as I can tell there is no scaling down of photosynthesis as a result of a reduced sink of carbon (this is a contentious point, I know). The result of this could be, however, that under certain conditions very high levels of NSC accumulate within the plants, perhaps even to levels that are physiologically unrealistic. Given the importance of NSC within this model, and the little we know about its allocation, it would be appropriate for the authors to display the evolution of NSC throughout the experiment (ideally both inter and intraannually), and also provide some discussion about what they observe, whether it is realistic, or whether it points to some deficiency and/or missing process in the model (e.g root exudates, down-regulation of photosynthesis in response to a reduced sink; Millard et al., 2007, New phytologist 175, 11-28; Körner, 2013, Nova Acta Leopoldina NF 114 , Nr. 391, 273 – 283).
We describe further how NSC are addressed in the model (M-M) and show their dynamics (intra and interannual) in new Figure A5. We lack detailed knowledge on their dynamics and how they are actually distributed in the studied forests, see lines 515-516. We add now the suggested references, which are helpful to address this point.
Photosynthesis is indeed downscaled as a function of sink carbon: if there is not sufficient carbon stored to build the canopy each year this results on a decrease in LAI (which is also downscaled in the case of protracted drought). See M-M (e.g. lines 303-305) where we explain how we do this and also the results and discussion (e.g. lines 504-…).
Further possible downscaling of photosynthesis is not addressed in the current model formulation.

The authors present the interesting result of differing trends of WUE between individual plants and the canopy-scale, however they do not discuss why this comes about in the model. I would guess that the reduced LAI at the Puechabon site leads to more radiation reaching the ground, and thus a strong increase in soil evaporation? Given that this difference in WUE is emphasised in the abstract, there should at very least be some discussion over why this difference occurs - better a definitive answer based on model outputs.
We add now several lines discussing this issue both in the results and discussion sections. Please, see lines 30-34 in the abstract or 475-480 where we further discuss these results and the rationale behind

The results regarding the decoupling of photosynthesis and growth are highly relevant for global environmental change studies, often carried out at large scale with models that only consider a carbon-source view of vegetation growth (e.g. Friend et al., 2013, PNAS 111(9), 3280-3285). The results herein might thus be highly relevant for such models (as described in Fatichi et al., 2014). It would be good for the authors to spend a few sentences in the discussion/conclusion highlighting the relevance of their results in this light.
We now address more thoroughly this point in the discussion; please see e.g. lines 503-518

Minor amendments
pg. 2747, l9: It would be good to be more specific in the abstract that you are acclimatising photosynthesis and allocation to water stress over the previous year, to immediately make clear to the reader that this study is not address the temperature acclimation of photosynthesis (a different problem).
Added, see line 22

pg. 2748, l7: [CO2] should be defined properly the first time it is used, presumably as atmospheric CO2 mixing ratio.
Done, line 61

pg. 2748, l16-19: It would help the uninitiated reader to make some short introduction of what is meant by the C-source and C-sink hypothesis. It would only require a couple of sentences to make this completely clear.
We provide now a brief explanation in the introduction, plus some extra references as kindly suggested by the reviewer. Please, see new lines 72-75 in the introduction and also further discussion later in the text

pg. 2748, l28 and throughout: "CO2" is often written with referring as to whether a flux or a mixing ratio is being considered. Presumably in this instance you mean flux, but this should be explicit every time you use it.
Added, see line 87

pg. 2749, l17: What is "at a greater scale" referring to? Spatial? Temporal? How big?
Spatial, at the regional scale (line 105)

Section 2.2: Given the importance of WUE calculations to the overall conclusions, I think it would be appropriate to include a small summary of how plant transpiration and soil evaporation are calculated, so that the reader is not required to read a second paper. This need not be as detailed as for the processes which are newly presented here, but just give the salient aspects.
See M-M where we describe now more in detail this point, lines 181-185

pg. 2753, l1: Based on what criteria did it behave better?
Please see lines 219-220

pg. 2753, l17: Which surface does Cs refer to? Leaf surface? OR ground surface at some reference height?
Line 238, “leaf surface”

pg. 2754, l1: The daily soil water content is given in mm. Does this take into account the space taken up by soil structure, or is it a normalised value?
It is total SWC (in mm) taken into account the soil structure, not a relative or normalized value

pg. 2754, l9: Please give value of Kb used. C917
Line 254

pg. 2758, l20, l25 and Fig. 2: I think the units of stem biomass increment should be g m-2 year-1 ("-" missing)?
Yes, that was a mistake that now has been corrected along the manuscript

pg. 2759, l21: What is meant by "well-coupled"?
We delete now “well-coupled” for clarity

pg. 2760, l20: On page 2758 it was specified that carbon allocation was calibrated to stand-specific measurements. How then does the model assume species-specific carbon allocation responses?
The model analyses carbon allocation at the stand level together for both species (lines 389-392) at Fontblanche

pg. 2764, l8: I don't think it is possible using Fig. A4 to separate a pure CO2 effect on gs, from the effect of [CO2] on temperature? But it would be easy to make such a separation using factorial experiments (e.g. fixed [CO2] or fixed climate).
Yes, we agree, that is what we state in that sentence "that they apply simultaneously", line 592

Fig. 2: At which level of confidence are the confidence intervals displayed?
95 % (now specified)

Fig. 3: Grey dots are almost invisible. Perhaps used coloured dots instead?
Modified

Grammatical and typographical corrections
We appreciate these corrections, they have all been modified

There is a scattering of grammatical errors throughout, but I do not believe these sufficient to require copy-editing, instead I list them below.
pg. 2747, l15: "translated into a parallel increase"
Done

pg. 2747, l16-19: These sentences are confusingly phrased. Suggest, "In contrast, at the other site where long-term precipitation remained stable, GPP did not show a negative trend and the trees buffered the climatic variability."
Done

pg. 2748: "...such data are applied at..."
Done

pg. 2749, l17-20: The meaning of this sentence is unclear. Please rephrase.
Done

pg. 2750, l3: Are you trying to say that that these relationships differ between phenophases?
That they can be opposite, now rephrased
pg. 2750, l18: "...dense coppice in which..."
Done

pg. 2751, l25: Better to say "eddy co-variance fluxes", rather than data.
Done

pg. 2752, Eq. 1: I think the first instance of Ko in this equation should in fact be Kc?
Yes, that was a mistake, now corrected

pg. 2752, l15: "compensation point"
Corrected

pg. 2753, l8 and throughout: "leave" should be "leaf".
Corrected

pg. 2753, l9: Presumably this means "reduced lower leaf replacement rates in response to long-term water stress"?
Yes, "leave" should be "leaf" instead

pg. 2754, l21: "...phenological phases during the year..."
Modified

pg. 2757, l10: Presumably you mean "half-hourly net CO2 flux measurements"?
Yes, added “flux”

pg. 2757, l11: NEP is not yet defined.
Now defined just before

pg. 2757, l16: "In a second step..:"
Modified (line 347)

pg. 2764, l3: "...co-responsible for active acclimation of plant physiological pro- cesses..."
Modified (line 583)

pg. 2764, l11: I think you simulated increase WUE, rather than observed it?
We state that is simulated WUE “we observed an increase in simulated annual WUE”

pg. 2765, l6: Bouchard et al. (2014) is not in the reference list.
That should be “Boucher”, now corrected